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Original
Effect of river flow fluctuations on riparian vegetation dynamics: Processes and models / Vesipa, Riccardo; Camporeale, CARLO VINCENZO; Ridolfi, Luca. - In: ADVANCES IN WATER RESOURCES. - ISSN 0309-1708. - STAMPA. - 110:(2017), pp. 29-50. [10.1016/j.advwatres.2017.09.028]

Availability:
This version is available at: 11583/2686652 since: 2017-10-18T12:27:14Z

Publisher:
Elsevier

Published
DOI:10.1016/j.advwatres.2017.09.028

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12 October 2024

Effect of river flow fluctuations on riparian vegetation dynamics: processes and models

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Abstract

Several decades of field observations, laboratory experiments and mathematical modelings have demonstrated that the riparian environment is a disturbance-driven ecosystem, and that the main source of disturbance is river flow fluctuations. The focus of the present work has been on the key role that flow fluctuations play in determining the abundance, zonation and species composition of patches of riparian vegetation. To this aim, the scientific literature on the subject, over the last 20 years, has been reviewed. First, the most relevant ecological, morphological and chemical mechanisms induced by river flow fluctuations are described from a process-based perspective. The role of flow variability is discussed for the processes that affect the recruitment of vegetation, the vegetation during its adult life, and the morphological and nutrient dynamics occurring in the riparian habitat. Particular emphasis has been given to studies that were aimed at quantifying the effect of these processes on vegetation, and at linking them to the statistical characteristics of the river hydrology. Second, the advances made, from a modeling point of view, have been considered and discussed. The main models that have been developed to describe the dynamics of riparian vegetation have been presented. Different modeling approaches have been compared, and the corresponding advantages and drawbacks have been pointed out. Finally, attention has been paid to identifying the processes considered by the models, and these processes have been compared with those that have actually been observed or measured in field/laboratory studies.

Keywords: rivers; riparian environment; disturbance-induced phenomena; climate changes.

1. Introduction

This work is based on two key conceptual changes that are taking place in the hydrological community. The first one concerns the growing interest in riparian vegetation as an active element of river dynamics (e.g., Corenblit et al., 2009; Camporeale et al., 2013; Bertoldi et al., 2014; Kui et al., 2014). For many years river engineers and hydrologists have been generally looking at riparian vegetation as a passive fluvial element, which is capable of altering flow resistances or substrate cohesion, but which has not been considered a determinant to describe river dynamics. Basically, the fluvial environment has been described as a result of the interaction of only two components: the stream and the sediments, which could be eroded, transported and deposited.

However, a new perspective is currently emerging. The hydrological scientific community is becoming aware of the fact that riparian vegetation plays a key role in river dynamics, (e.g., Van Dijk et al., 2013; Surian et al., 2015; Vesipa et al., 2015; Wang et al., 2016) and that there are actually three components of equal importance that shape the river environment: the water stream, sediments and riparian vegetation. These three components interplay over a wide range of spatial and temporal scales, exhibit complex (nonlinear) spatio-temporal dynamics, and constitute a *unicum* which should be studied and modeled as a whole. This emerging picture has been attracting a great deal of interest among scientists, as witnessed by the growing number of modeling, experimental and field works devoted to this theme (e.g., Robertson and Augspurger, 1999; Dykaar and Wigington Jr., 2000; Merritt and Cooper, 2000; Rood et al., 2005; Corenblit et al., 2007).

The second root of the present work stems from the recent awareness of the key role that stochasticity plays in environmental processes. In the last few years, the research has been moving from a view in which only deterministic features determine the behavior of dynamic systems - and random fluctuations only have the effect of disturbing and hiding the deterministic dynamics - to a view where random components have a fundamental constructive role and are able to create particular dynamic behaviors that would not exist in purely deterministic dynamics (e.g., Puckridge et al., 1998; Johnson, 2000; Naumburg et al., 2005; Greet et al., 2011b; Marshall et al., 2013; Formann et al., 2014; Pasquale et al., 2014). The coexistence of multiple equilibrium points, structural changes in the probability distribution of time-series, the occurrence of

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spatial patterns, stochastic equilibrium states, and so on, are some examples of the disturbance-induced phenomena that occur extensively in many environmental processes and which are changing the standard way of looking at the role of random components (Ridolfi et al., 2011).

The growing interest in the stream-sediment-vegetation triadic interaction and the new way of considering random components in dynamic systems explain the efforts that scientific community has been making to investigate the role of stochasticity in the river environment (e.g., Camporeale and Ridolfi, 2006; Muneepeerakul et al., 2007; Doulatyari et al., 2014). Rivers exhibit various random forcings, the main of which is the flow variability. As many (biotic and abiotic) fluvial processes depend on the stream stage and velocity, it is easy to imagine that the river environment is one of the most extensive and important environments in which disturbance-induced processes occur. These processes play a crucial role in shaping rivers as we know them.

The present work concerns this novel and challenging topic in river hydrology, and it reviews the most recent advances. In particular, we focus on the stream-vegetation side of the triad (although a number of sediment-based and geomorphological processes are described when they mediate between randomness and vegetation). This choice is due to sake of space and the existence of other reviews dedicated mainly to the interaction between stream stochasticity and geomorphology (e.g., see Camporeale et al., 2013; Solari et al., 2016).

The work is organized in four sections. Section two describes all the major vegetation processes that depend on river flow fluctuations. The third section is devoted to recalling the key statistical features that characterize fluctuations. The fourth section describes the main modeling approaches that have included stream stochasticity and the quantitative results that have been obtained. Finally, the key results that have emerged so far and possible future developments are presented in the Conclusions section.

2. Biological, physical and chemical effects of river flow fluctuations

River flow fluctuations (RFFs hereafter) in watercourses are the key drivers of riparian vegetation dynamics. These fluctuations have a profound effect on vegetation at any stage of plant life, from the seed dispersal and germination stages to the seedling development and adult phase. The river flow determines a large number of bio-morphological vegetation characteristics (e.g., root architecture, shoot biomass, trunk diameter), and is the main determinant of the ultimate survival of vegetation. Moreover, RFFs influence many abiotic processes that play fundamental roles in shaping the riparian habitat.

The effects of river flow fluctuations on riparian vegetation are discussed in this section. The current literature is reviewed from a processes-based perspective, and the most relevant mechanisms are identified and discussed. We will identify the processes that affect: (i) the recruitment of vegetation, from seed dispersal to the settling of the young plants (section 2.1); (ii) vegetation during its adult life (section 2.2); and (iii) the morphological and nutrient dynamics of the riparian habitat (section 2.3).

River flow variability induces fluctuations in the water stage and in the stream velocity. In the following, we will consider: (i) mechanisms induced by river flow fluctuations (RFF), i.e., those processes in which the simultaneous changes of water stage and velocity is crucial; (ii) mechanisms mainly influenced by water stage fluctuations (WSF); and (iii) processes mainly driven by water velocity fluctuations.

2.1. Effects on vegetation recruitment

Over a vast range of environments, the recruitment of new vegetation usually occurs after a site has been cleared by a major disturbance (Shafroth et al., 2002). The recruitment of vegetation in the riparian zone is a crucial and fragile process that takes place after major floods (Van Dijk et al., 2013; Fraaije et al., 2015). River flow fluctuations affect the recruitment of riparian vegetation through a number of processes (see Table 1 for a synthesis): (i) the formation of sites that are suitable for seedling recruitment; (ii) the dispersal of reproductive material; (iii) the recruitment of seedlings; and (iv) the survival of recruited seedlings.

Formation of suitable sites for recruitment. Environmental drivers and physical disturbances play central roles in clearing river margins forested by old vegetation. The recruitment of pioneer vegetation is rarely successful in already vegetated patches (Johnson, 2000; Miller et al., 2013). As a result, the creation of suitable (barren) sites is necessary for the recruitment of young flora that can undergo the succession toward the adult stage (Stella et al., 2013). In the riparian zone, the main disturbance that contributes to the formation of nursery sites is related to river flow fluctuations. RFFs of sufficient magnitude remove former vegetation and deposit a layer of fresh alluvial substrate on isolated sand bars, on the tails of established sand bars and on point bars. These fresh sediments are perfect location for the recruitment of new plants (Cooper et al., 1999). Several studies have demonstrated that barren nursery sites are only created after major floods (Bovee and Scott, 2002), and that the recruitment of young vegetation is closely related to these large inundations (Bradley and Smith, 1986). In contrast, in watercourses where high spring flows are suppressed by river regulation, no new vegetation has been observed to have established from the beginning of the dam operations (Polzin and Rood, 2000).

Dispersal of reproductive material. The dispersal of seeds is the most effective (and sometimes the only, Menges and Hawkes, 1998) way by which local riparian flora colonize river margins (Nilsson et al., 1994). Hence, the dispersal of seeds is the main limiting factor of colonization in many river bank sites (Merritt and Wohl, 2002). The dispersal of seeds is either driven by wind, or

Formation of sites for recruitment	
• Creation of barren sites	Bovee and Scott (2002), Stella et al. (2013)
• Removal of former vegetation	Bradley and Smith (1986), Johnson (2000), Polzin and Rood (2000), Miller et al. (2013)
• Deposition of fresh alluvial substrate	Cooper et al. (1999)
Dispersal of reproductive material	
• Dispersion of seeds and other reproductive material (by hydrochory)	Johansson and Nilsson (1993), Nilsson et al. (1994), Menges and Hawkes (1998), Merritt and Wohl (2002), Steiger et al. (2005)
• Scouring and transport of seeds (high river flows)	Nilsson and Svedmark (2002), Braatne et al. (2007), Carthey et al. (2016)
• Deposition of seeds (low river flows)	Merritt and Wohl (2002), Goodson et al. (2003), Carthey et al. (2016)
• Zonation of seed deposition	Karrenberg et al. (2002), Goodson et al. (2003), Greet et al. (2011a), Greet et al. (2011a), Stella et al. (2013)
Seedling recruitment	
• Prevention of seed germination in submerged zones	Johnson (2000)
• Determination of moisture conditions in substrate (crucial for germinability and growth rate of different species)	Bakker and Berendse (1999), Trowbridge (2007), Fraaije et al. (2015)
Seedling survival	
• Killing of seedlings by drought (receding rate too fast)	Mahoney and Rood (1992), Johnson (2000), Rood and Mahoney (2000), Amlin and Rood (2002), Braatne et al. (2007), Miao et al. (2009), González et al. (2010), Stella et al. (2010), Garssen et al. (2014)
• Killing of seedlings by burial and scouring (high river flow)	Johnson (2000), Polzin and Rood (2006), Braatne et al. (2007), Perona et al. (2012)
• Selection of the most resistant and adapted riparian species	Steiger et al. (2005), Polzin and Rood (2006), Stella et al. (2010), Garssen et al. (2014), Fraaije et al. (2015), Garssen et al. (2015)

Table 1: Synthesis of the RFF-induced processes involved in the recruitment of vegetation

occurs through hydrochory (dispersal by water). Often, seed dispersal is the outcome of both processes, as wind transports seeds closer to the watercourse (Chambert and James, 2009). As wind only acts over limited spatial scales, hydrochory is the main dispersal process (Johansson and Nilsson, 1993), and it affects the vegetation community to a great extent in terms of species composition (Greet et al., 2011a). Hydrochory depends on many factors, ranging from the morphological and hydraulic dynamics of the channel (Merritt and Wohl, 2002) to the floating characteristics of the seeds (Carthey et al., 2016).

In this scenario, the variability of the river flow plays a major role for several reasons (Greet et al., 2011a). First, the occurrence of floods is necessary for hydrochory to take place. High water stages are required to collect the seeds released by the vegetation that grows on the banks (Nilsson and Svedmark, 2002; Braatne et al., 2007). During the low water stage, the scoured seeds deposit in the new site where they then germinate. The hydraulic conditions (e.g., Froude, Reynolds and Shields numbers) that occur during the rising or falling limbs of the hydrograph determine how many seeds are scoured or deposited (see Merritt and Wohl, 2002; Goodson et al., 2003, for quantitative studies).

Second, the actual position of the water stage during and after a flood affects the zonation of the seed deposition/scouring processes (Merritt and Wohl, 2002). In fact, these two levels determine the range of elevations over which seeds can be dispersed (Stella et al., 2013). This, in turn, is crucial in determining the species composition and the germinability of the seeds (Goodson et al., 2003).

Third, the timing of flood events, with respect to the timing of the seed fall, determines the effectiveness of the hydrochory process (Braatne et al., 2007; Stella et al., 2013; Greet et al., 2011a). Floods that occur before seeds have fallen have no effect on the dispersion process, as there are no seeds to be transported. Likewise, floods that occurs long after than seed fall are also not so effective, as most of the transported seeds lose their germinability before they settle. A synchronization between the timing of a flood and seed-fall is therefore important to determine the rate of germination and the rate of growth of different riparian species (Greet et al., 2011a). These, in turn, are key processes that affect the community distribution of the riparian species (Greet et al., 2011a). The synchronization of the timing of a flood and seed-fall is so important in determining the reproductive success of riparian vegetation that some species have developed particular traits to take advantage of the river flow fluctuations (Karrenberg et al., 2002; Greet et al., 2011a).

Although seed hydrochory is the main process behind the colonization of river margins, RFFs are also important in dispersing other types of reproductive material. Vegetal litter, removed during high river flows, is an important source of nutrients and propagules that are effectively dispersed by floods (Stella et al., 2013). It should also be noted that the flow-induced sedimentation that occurs during high river flows is fundamental for the final establishment of the dispersed propagules (Steiger et al., 2005). Moreover, the seedling establishment that follows large floods may occurs weeks or months after the physical disturbances that have created the new colonization sites. Thus, there is a potential temporal disconnect between the hydrological conditions that induce the clearing of old vegetation and those that promote the establishment of the new vegetation.

Seedling recruitment. During seedling recruitment, the water stage plays a key role in determining the specific elevation of the transect plot in which different species will germinate and grow (Fraaije et al., 2015). A high water stage is a limiting factor for most species, as seeds cannot germinate in submerged conditions (Johnson, 2000). The random dynamics of the water stage determines the plot-specific substrate moisture, which, in turn, determines the germination and the rate of growth from the seed state to the seedling state (Trowbridge, 2007). Moreover, seeds of different species react differently to plot-specific environmental conditions (e.g., substrate moisture, nutrient availability, light and temperature) giving rise to *priority effects* (Bakker and Berendse, 1999; Trowbridge, 2007). In this picture, the time required to reach the seedling stage after the seed has been deposited is crucial. This is particularly important when the hydrological regime does not exert a strong selection on species composition. In this case, the species that first colonizes the site will remain the dominant species. Technically speaking, this behavior is referred to as the *priority effect*, and has been documented to last for years, until a new disturbance clears the site (Bakker and Berendse, 1999).

Seedling survival.

The survival of the recruited seedlings is affected to a great extent by the recessions and the rises in the water stage. A recession of the water stage entails that the level of the groundwater table and the position of the capillary fringe drop to a lower elevation. As a result, when the depth of the water source for seedlings changes, the roots have to adjust to the new conditions. If the re-allocation and the capacity of roots to expand more deeply is slower than the celerity of the groundwater to drop to a lower elevation, seedlings suffer from drought stress, and their survival depends on the recession rate of the water stage (Mahoney and Rood, 1992). Several experimental studies (at a laboratory and at a field scale) have demonstrated that a slow stage recession is required for seedling survival (Miao et al., 2009), and that an abrupt recession of the water table, after the peak of a flood, is likely to drought-kill all the seedlings (Rood and Mahoney, 2000). In very arid environments, a slow recession of the stage is often not sufficient to allow vegetation recruitment to occur. In these environments, it has been observed that summer droughts can kill all the seedlings (Johnson, 2000; Garssen et al., 2014), and that moderate floods that take place on late summer are necessary for their survival (Braatne et al., 2007).

Drought stresses exert a marked species selection. It has been shown that prolonged droughts induce species shifts (Garssen et al., 2014), and that the water stage regime has an important effect on the species that can colonize the river banks (Stella et al., 2010). As a consequence, species characterized by different levels of drought resistance colonize different elevations of the river transect (Karrenberg et al., 2002).

Drought stresses on seedlings of riparian species have been studied quantitatively in great detail. For example, Johnson (2000) found that drought is the main cause of mortality of large seedlings (older than 3 years), while other factors affect younger individuals. In their laboratory study, Amlin and Rood (2002) measured the physiological performance of young seedlings stressed by an imposed water table regime. They imposed a constant rate of water table reduction. Moreover, they observed that a decline rate of 1-2 cm/day induced mild, hard to detect, effects, but faster falling rates caused a marked negative effect that induced vegetation death. These data were confirmed in the studies by González et al. (2010) and by Stella et al. (2010). Interestingly, González et al. (2010) found that the best growth performance of seedlings took place for a water stage declining rate of 1 cm/day. Stella et al. (2010) detected that two critical thresholds for the water stage falling rate exist. Below (above) a declining rate of 1 (6) cm/day of the water table, 100 (0)% of survival occurs, irrespective of the considered species. In contrast, the survival response is very specie-specific for water stage falling rates between these thresholds. The picture depicted above is particularly important in dry climates In wet climates drought generally induces only a limited mortality in most species (Fraaije et al., 2015).

An increment in the river flow may cause the flooding of young seedlings. In this case, the main stresses exerted on the young vegetation are burial and scouring, and the disturbance of the latter is often magnified by the occurrence of floating debris or ice. It should be noted that, during flooding, seedlings do not have time to implement incremental adaptation mechanisms of resistance (e.g., the progressive increment of root length with the progressive deepening of the groundwater). As a result, their survival depends on their resistance to the flooding disturbance they have developed since their germination, and on the severity of the disturbance. The laboratory investigation conducted by Perona et al. (2012) has demonstrated that a flood with a given magnitude removes the part of the vegetation that has mechanical characteristics of the root apparatus below a flood-depth-dependent-threshold. Therefore, even small flow fluctuations can exterminate –by burial or erosion– young newly recruited seedlings (Johnson, 2000). In contrast, regulated rivers are often vegetated up to the margins of the flowing water (Braatne et al., 2007), since the destructive effects of floods have been mitigated.

Flood stress on riparian seedlings has been the subject of many studies. However, the complexity of the processes involved has led to less quantitative results than in the case of drought-stressed seedlings. It is well known that storm-induced, late summer floods are more significant for young seedlings (i.e., of an age of less than one year, and thus with a very limited root apparatus, Johnson, 2000). Moreover, it has been shown that seedling survival is affected to a great extent by the duration of floods, while the flood depth plays a minor role (Garssen et al., 2015). This is probably related to the results of Polzin and Rood (2006), who found that burial kills more seedlings than scouring. Therefore, the longer the duration of the floods, the greater the volume of discharged sediments, and hence, the higher the risk of burial. In contrast, high river flows may not be sufficient to increment the stream velocity and thus the bed shear stress to such an extent that mortality by scouring is increased.

The role of winter floods has also been elucidated. In the winter season, ice increases the scouring capabilities of streams, and causes seedlings to be frozen in ice blocks and then to be uprooted. As a result, winter floods can be responsible for the removal of a large amount of vegetation, especially large seedlings (older than one year) that have survived the summer floods. Flood driven ice was found to hinder colonization at very low sites (Johnson, 2000). Braatne et al. (2007) confirmed that the survival of seedlings may depend on winter floods. Only when the magnitude of winter floods is moderate, can the vegetation colonize the river margins.

In a similar way to the drought case, flood-induced stresses also exert a strong species selection. Flooding can induce very high mortality in all species (Fraaije et al., 2015), and it can therefore be effective in clearing river banks. It follows that the species that grow faster in the cleared sites will have the best chances of colonizing it (Garssen et al., 2015).

2.2. Effects on adult vegetation

Vegetal species can implement a large number of behavioral adaptations to withstand the hostile conditions they encounter during their life spans, such as water scarcity, soil slope, and wind (Zwieniecki and Newton, 1995; Danjon et al., 2005; Lombardi et al., 2017). In the riparian environment, the river flow fluctuations are the main cause of the onset of these hostile conditions. High river flows cause anoxia, burial, physical damage and uprooting, whereas low water stages cause drought stresses.

These RFF-induced behavioral adaptations, and their related processes, are discussed hereafter according to the effect that they exert on (see Table 2 for a synthesis): (i) the shoot- (or above-ground-) biomass, topology and, density, thus excluding the death of the plant, (ii) the root- (or below-ground-) biomass and topology, excluding also in this case the death of the plant, (iii) the ultimate survival of the adult plants, and (iv) the age spatial-distribution of vegetation.

Shoot biomass. The shoot biomass of riparian flora is affected to a great extent by the river flow dynamics.

Shoot biomass	
• Biomass reduction to keep optimal eco-physiological conditions	Williams and Cooper (2005)
• Drought stress causes a decay of biomass	Rood et al. (2003), Williams and Cooper (2005), Stella et al. (2013), Garssen et al. (2014)
• Anoxia causes a reduction of biomass	Garssen et al. (2015)
• Hydrodynamic stresses induce breaking of branches	Karrenberg et al. (2002), Stella et al. (2013)
• RFFs influence wood density	Lawson et al. (2015)
Root biomass	
• Root biomass increases with good levels of moisture and oxygen	Naumburg et al. (2005), Pasquale et al. (2012), Gorla et al. (2015)
• Roots die if substrate moisture is below threshold	Stromberg (2013)
• Roots die if oxygen is below threshold	Naumburg et al. (2005), Caruso et al. (2013), Gorla et al. (2015)
• Shear stress may scour roots	Stella et al. (2013)
• Flow variability determines the root morphology	Mahoney and Rood (1998), Williams and Cooper (2005), Merritt et al. (2010), Pasquale et al. (2012), Caruso et al. (2013), Holloway et al. (2017b)
Survival	
• Anoxia kills vegetation (duration of anoxic conditions crucial)	Friedman and Auble (1999), Vervuren et al. (2003), Kramer et al. (2008), Caruso et al. (2013), Garssen et al. (2015)
• Scouring kills vegetation	Friedman and Auble (1999), Edmaier et al. (2011), Perona et al. (2012), Stella et al. (2013), Kui et al. (2014), Pasquale et al. (2014)
• Burial kills vegetation	Johnson (2000), Mosner et al. (2011), Kui et al. (2014)
• Drought rarely kills vegetation	Amlin and Rood (2002), Francis et al. (2005), Williams and Cooper (2005), Reynolds et al. (2014)
Age spatial distribution	
• Early colonization stages at the river shore	Mosner et al. (2011), Cline and McAllister (2012), Egger et al. (2015)
• Old colonization stages at the upper floodplain	Cline and McAllister (2012), Egger et al. (2015)
• RFFs promote biodiversity	Karrenberg et al. (2002), Uowolo et al. (2005)
• Limitation of reproductive material and priority effects may alter the picture depicted by RFFs alone	Vervuren et al. (2003), Polzin and Rood (2006), Trowbridge (2007), Fraaije et al. (2015)

Table 2: Synthesis of the RFF-induced processes involved in the dynamics of adult vegetation.

When the vegetation is exposed (i.e., the water stage is lower than the plot height), riparian flora adjusts the shoot biomass through a number of mechanisms, with the aim of maintaining optimal eco-physiological conditions (Williams and Cooper, 2005). Different mechanisms act at different levels of the drought stress, and they generally cause a decay of the shoot biomass (Garssen et al., 2014). In order of increasing seriousness, these mechanisms are (Rood et al., 2003; Williams and Cooper, 2005; Stella et al., 2013): (i) the increment of the root growth to the detriment of shoot growth, (ii) the reduction of shoot elongation, (iii) the reduction of trunk expansion, (iv) the reduction of the leaf area, (v) the mortality of leaves, and (vi) the sacrifice of some branches. The lab experimental study conducted by Hughes et al. (2010) has demonstrated that shoot biomass is higher in fluctuating ground-water regimes. This is probably due to an increment of the root biomass during the low water stage periods (see point (i) in this paragraph), that can provide more water for the shoots when the substrate is made moist during the transient high water stages.

When the vegetation is flooded, two main processes threaten the shoot biomass: root anoxia and flow drag. The lack of oxygen at the root level greatly reduces the plant water uptake (Garssen et al., 2015). As a result, the physiological effects induced by flooding are very similar to those induced by droughts, and entail a great reduction of the biomass. It should be noted that when anoxia is the only factor that stresses the submerged vegetation (i.e., when the hydrodynamic drag is negligible), the duration of a flood is not a determinant factor (Garssen et al., 2015). In contrast, the depth of the flood influences the shoot biomass to a great extent (Garssen et al., 2015). In fact, the different flood adaptive mechanisms (e.g., adventitious roots or shoot elongation) are only effective up to a certain threshold flooding depth. If this threshold is not exceeded, the plant can convey oxygen to the roots, and the normal biological activity is preserved. If this threshold is exceeded, the plant has no means of conveying oxygen to the roots, and will quickly loose most of the shoot biomass. For example, submerged plant have a typical survival time of 20-60 days. Before this survival time, flood duration has little effect on shoots biomass alterations (i.e., shoot biomass reduction depends on the flooding depth only).

Hydrodynamic stresses have been reported to induce the breaking of branches at preformed points (Karrenberg et al., 2002; Stella et al., 2013). This reduces the hydrodynamic resistance of plants and enhances their chances of surviving flow drag forces.

Finally, a very recent study (Lawson et al., 2015) has pointed out the importance of river processes in determining the wood density of trees growing in the riparian zone. The Authors first pointed out that plants with a high wood density are less prone to being damaged by floods, and are less exposed to the risk of xylem cavitation. As a result, flood and drought stresses are more likely to kill plants with low wood density. As a confirmation of this, the same Authors found that the mean wood density at the reach scale increased with the flow variability (which induced alternations of the flood and drought stresses), and with the magnitude of floods (which increased the flood damage). In contrast, they found that this flood-driven selection did not occur in river reaches characterized by a less variable flow regime. Hence, the vegetation density along the studied reaches spanned a wide range of values.

Root biomass. The water stage is a key driver of the root biomass, in terms of quantity, location and architecture of the roots. Root dynamics vary greatly as a function of the water and oxygen availability. When the substrate moisture at a fixed depth is below a species-specific wellness threshold, the roots at that depth lose their utility and die (Stromberg, 2013). In contrast, root density is increased in zones with sufficient moisture and oxygen (Gorla et al., 2015). If the stress conditions are sufficiently extended, the root system seeks new water resources in the deeper substrate layers (Naumburg et al., 2005; Pasquale et al., 2012). This deepening of the root apparatus is often flanked by an increment in the root diameter (Naumburg et al., 2005). This increment in diameter is believed to compensate for the increased hydraulic resistance that occurs when water is tapped from more distant sources (McElrone et al., 2004). The rate at which the substrate moisture concentration reduces also seems to be important for root elongation and deepening dynamics. However, contrasting results have been detected. For example, Gorla et al. (2015) found that a slow lowering of the water level promotes root deepening, while Hughes et al. (2010) reported that the root length was higher in fast drowdown regimes.

Moreover, when the substrate moisture exceeds a substrate-specific-threshold, the transport of oxygen from the atmosphere to the roots is inhibited. As a result, roots suffer from anoxia (Naumburg et al., 2005) and the water uptake capacity is reduced. If this condition persists, roots die (Naumburg et al., 2005; Caruso et al., 2013) and the root growth is limited to zones with sufficient moisture and oxygen (Naumburg et al., 2005; Gorla et al., 2015). Moreover, adventitious roots may form above-ground, and these can convoy oxygen to the anoxic zones (Caruso et al., 2013).

Finally, when roots are flooded and the hydrodynamic stresses are such that the bed sediment can be eroded, root scouring may occur (Stella et al., 2013).

The above picture shows that the flow variability and the elevation of the plot that hosts plants are crucial in determining the root morphology (Pasquale et al., 2012). Merritt et al. (2010) found that the root apparatus of plants living in zones with constant groundwater are not so elongated. Similarly, it has been found that vegetation growing close to a river (i.e., with a shallow water table) exhibits a shallow root system (Caruso et al., 2013) made up of short roots (Mahoney and Rood, 1998). In contrast, oscillating groundwater tables have been shown to gener-

ate very elongated root apparatus (Merritt et al., 2010) characterized by a high biomass (Hughes et al., 2010). In turn, root apparatus with a high vertical development have proved to have a much higher washing resistance than those characterized by a shallower development (Pasquale et al., 2012). Another interesting example of root dynamics has been reported in the field study by Williams and Cooper (2005). The Authors examined the case of a vegetation patch growing along a river that had undergone a strong reduction in the mean flow and regulation of the flow regime. After the reduction of the mean water stage and the WSFs, the shallowest root system was cut off from the groundwater, thus becoming useless and then dying. In order to prove this die-back, the vegetation patch was artificially flooded, and as a result the upper part of the substrate became wet and moist. The physiological status of the trees was assessed both before and after the flood. It was found that no changes in the physiological status of the trees occurred, as a result of the flooding. The only possible explanation for this behavior was the lack of roots that could have taken advantage of the additional provided water.

Finally, it is worth mentioning the field analysis conducted by Holloway et al. (2017b). They investigated the root distribution and pattern of some riparian trees and shrubs growing along an almost pristine, very dynamic braided watercourse. It has been shown that, in the most dynamic parts of the transect, the root apparatus is composed of grids of stems, shoots and roots that are vertically connected and that this peculiar root system is the result of RFF-induced deposition of very coarse sediments and the burial of tree shoots.

Survival. The survival of vegetation in river banks is closely related to the dynamics of the river flow. The occurrence of floods has been univocally associated with a reduction of vegetation abundance along channels (Crouzy and Perona, 2012; Miller et al., 2013). Two key processes are responsible for the vegetation removal and the death of vegetation: anoxia and geo-morphological/hydraulic mechanisms (Corenblit et al., 2009; Miller et al., 2013; Edmaier et al., 2015).

Anoxia is a death mechanism that is caused by the flooding of the roots, which induces a lack of oxygen at the root level. This, in turn, causes a reduction of the water uptake. As a result, the physiological activity of the vegetation during the flood (i.e., the water demand), the oxygen dissolved in the flooding water, and the duration of the stress conditions are key parameter that determine the chance of survival of a plant. In this regard, flooding is more harmful during the growing season, and cold flowing water (i.e., rich in oxygen) is less harmful than warm stagnant water (i.e., poor in oxygen) (Caruso et al., 2013). It has also been observed that water turbidity plays a role (Vervuren et al., 2003)

Several quantitative studies have found a positive correlation between plant mortality and flooding duration (Friedman and Auble, 1999; Kramer et al., 2008; Garssen et al., 2015). It has been found that mortality of some species increases with the depth of flooding (Kramer et al., 2008). The relations between flooding depth and plant survival are quite complex and species specific (Caruso et al., 2013; Garssen et al., 2015). Caruso et al. (2013) detected four stages of inundation severity: (i) the soil is not completely flooded, (ii) the soil is fully inundated, but the lower foliage is not underwater, (iii) the lower foliage is underwater, and (iv) the plant is fully submerged. Therefore, the damage and the death risk induced by inundations increase according to a multiple threshold process. The inundation effects becomes much more serious when a threshold is exceeded.

Geo-morphological and hydraulic mechanisms explain the removal of large amounts of vegetation. Pasquale et al. (2014) found that vegetation mortality is linearly proportional to shear stresses (see also Friedman and Auble, 1999). Moreover, they demonstrated that mortality is closely related to the elevation above the mean water table. They found that along a reach of the River Thur, Switzerland, the shoreline of the 55 days flood represented a clear threshold between poorly and richly vegetated banks. In this framework, the main geo-morphological and hydraulic mechanisms responsible for the death of adult vegetation are sediment scouring and the occurrence of drag forces (which induce vegetation uprooting), and sediment deposition (which causes vegetation burial).

Let us first focus on uprooting. According to Edmaier et al. (2011), two main types of uprooting are possible. Type I occurs when the drag force exerted by the flow instantaneously overwhelms the anchoring resistance. Type II is induced by sediment erosion around vegetation that decreases the anchoring resistance as long as the drag force prevails. Regardless of which uprooting mechanism is involved, several factors have been found to affect the final resistance of vegetation to uprooting: (i) the size and the flexibility of plants (the larger or stiffer the plant, the higher the drag forces, and therefore the higher the risk of uprooting, Stella et al., 2013). It should be noted that the flexibility of plants is important when the flooding depth is of the same order of the plant height or greater; (ii) the root structure (the longer the roots, the lower the risk of dislodgement, Stella et al., 2013; Holloway et al., 2017a); (iii) the sediment characteristics (the finer the sediment, the higher the risk of substrate washing, Stella et al., 2013); (iv) the obstacle-diameter-to-sediment-size ratio (the higher this ratio, the more pronounced the scour hole generated by the plant-stream interactions Edmaier et al., 2015); and (v) the sediment budget of the reach (the risk of dislodgement increases when there is a sediment deficit, Kui et al., 2014). It should be noted that such factors vary considerably in a vegetation community growing along a river reach (Perona et al., 2012). Therefore, a flood with a given magnitude will remove part of the vegetation that has characteristics (e.g., root length) below a minimum resistance threshold (Perona et al., 2012). It should be noted that the amount of removed vegetation

is a random variable. In fact, the physiological characteristics responsible of the uprooting resistance in a population (e.g., root length) exhibit a statistical distribution (Perona et al., 2012). Thus, the (random) portion of population with physiological characteristics not sufficient to withstand the flood is removed.

As far as the type II uprooting mechanism is concerned, the magnitude and the return interval of floods affecting the vegetation is crucial in determining the final outcome of the process. In fact, the type II uprooting mechanism is a delayed process, and its outcome depends on the balance between two factors. The first factor is the amount of substrate that is eroded during a flood (which reduces the anchoring resistance). The second factor is the root reinforcement and regrowth that occurs between two consecutive floods (which restores the anchoring resistance).

Let us now consider burial. Burial kills more than scouring (Kui et al., 2014), and a single deposition event, covering the vegetation with more than 0.40 m of sediments, can lead to complete mortality (Polzin and Rood, 2006; Pasquale et al., 2014). However, vegetation can recover during the time interval between two sediment-deposition events, and can adapt to the new plot elevation. As confirmation of this, Johnson (2000) observed some trees along the Missouri River, USA, that were able to withstand about 5-6 m of sediment deposition throughout their lifespan. Several factors affect the final resistance of vegetation to burial: (i) plant stiffness and the frontal area (the stiffer the plant and the larger the area, the higher the sediment deposition rate, Kui et al., 2014); (ii) sediment budget of the reach (the risk of burial increases when there is a sediment surplus Kui et al., 2014); and (iii) the density of the vegetated patch (Mosner et al., 2011; Kui et al., 2014) It should be noted that in the experimental configuration adopted by Kui et al. (2014) the occurrence of vegetation positively affected the deposition of sediments. However, in other circumstances (e.g., Edmaier et al., 2015) vegetation may induce localized erosion processes.

It should be noted that the high mortality that occurs in densely vegetated patches was interpreted by Johnson (2000) as a sedimentation-induced thinning. In fact, if a patch is too densely vegetated, the growth of young trees is hampered by the competition for nutrients and light. Therefore, the killing of a great number of trees by burial may help the few survived plants to reach adult life.

Drought stress plays a more marginal role in determining the survival of vegetation (especially for tree species). In fact, adult flora quickly adjusts the shoot biomass to restore optimal eco-physiological conditions (Williams and Cooper, 2005). Moreover, adult willows and cottonwood have been reported to develop very deep root apparatus, under the forcing of a falling water table (Amlin and Rood, 2002; Francis et al., 2005). As proof of this, Reynolds et al. (2014) studied abandoned floodplain plant communities along the Bill Williams River, a very regulated watercourse in Arizona, USA. These abandoned communities consist of vast patches of typical riparian trees that were recruited and then grew in the active zone of the river. The patches are now isolated from the active zone of the river, as the river regulation has made the groundwater table significantly deeper. However, during the change in the river flow regime, extensive and deep root systems developed to access water, and the riparian vegetation patches eventually survived.

Age and spatial zonation of vegetation population. The important effects exerted by RFFs on the recruitment, growth and survival of riparian vegetation shape the age and the spatial distribution of populations along the hydrological gradient (Mosner et al., 2011). The bank zone closest to the flowing water is characterized by frequent stage fluctuations, high shear stresses and shallow groundwater. This limits the vegetation age, so that only early colonization stages are supported (Cline and McAllister, 2012; Egger et al., 2015) in this zone. In contrast, a shallow groundwater table is fundamental for the recruitment of young flora (Egger et al., 2015). In contrast, the bank zone far from flowing water is seldom inundated, is stressed by low shear forces, and vegetation is only influenced by extreme events. This allows the vegetation to reach older colonization stages (Cline and McAllister, 2012; Egger et al., 2015). However, the groundwater in this location is at a great depth, and young colonization stages cannot be supported (Egger et al., 2015).

River flow fluctuations (and especially floods) are also fundamental for the removal of old vegetation (Braatne et al., 2007). In this context, nursery sites for younger individuals are created. Braatne et al. (2007) found that the almost constant river flow that occurred in regulated rivers caused the aging of cottonwood populations. This poses a significant environmental problem. In fact, as adult cottonwoods have short life, if no new nursery sites for younger individuals are provided by floods, no recruitment can take place. Hence, Braatne et al. (2007) highlighted the risk of the extinction of the cottonwood populations that vegetate regulated rivers over the next 100 years.

Interestingly, RFFs can also affect the distribution of male and female individuals of the same species along a transect, thus giving rise to a spatial segregation of sex (e.g., see Dawson and Bliss, 1989; Hughes et al., 2000; Dudley, 2006; Hultine et al., 2007, 2008; Hughes et al., 2010).

Finally, RFFs are a key driver in the promotion of biodiversity at the transect scale. In fact, different species colonize different zones of a transect, according to the species-specific differences in drought and flooding tolerance (Karrenberg et al., 2002; Uowolo et al., 2005).

The situations depicted above (i.e., young vegetation near the river and old vegetation far from the river) may be complicated by other processes. First, clonal suckers may extend the tree population to zones that would otherwise be impossible to colonize (Polzin and Rood, 2006). Second, the dispersal limitation of reproductive material may be a factor that limits colonization more than hydrological

forcing (Vervuren et al., 2003; Trowbridge, 2007). A slow colonization magnifies the effect of extreme floods, and it may last for decades and dictate the vegetation gradient along transects (Vervuren et al., 2003; Trowbridge, 2007; Fraaije et al., 2015).

2.3. Effects on the riparian environment

River flow fluctuations affect a number of environmental conditions that play key roles in vegetation dynamics. In the following, we will consider: (i) the geo-morphological dynamics of rivers; (ii) sediment deposition, in particular considering the effects on the substrate texture; (iii) the concentration of nutrients and salts; and (iv) the fate of wood debris (see Table 3 for a synthesis).

Geo-morphological dynamics. Floods continuously shape and rework the morphology of rivers (Latterell et al., 2006; Wang et al., 2016). This reworking is fundamental for the succession and recruitment of vegetation. The erosion and deposition processes that occur during major floods are in fact necessary to create barren nursery sites (Friedman et al., 1996; Merritt and Cooper, 2000; Fierke and Kauffman, 2005; Braatne et al., 2007), and new sites for recruitment rarely develop in regulated rivers where high spring flows are reduced (Braatne et al., 2007). It has also been observed that: (i) floods are not very effective in clear encroached zones (Miller et al., 2013) and (ii) a sediment deficit at the reach scale does not allow nursery barren sites to be formed (Merritt and Cooper, 2000). This suggests that the creation of nursery sites and the removal of old vegetation is related to large scale morphodynamical processes (Merritt and Cooper, 2000). The Authors associated floodplain morphological dynamics with the recruitment and colonization of cottonwood along the Willamette River, Oregon, USA. They found that optimal nursery sites were located in fresh sediment deposits due to: the migration of lateral point bars; the coalescing of central, multiple or lateral bars; and the narrowing or abandonment of channels. Moreover, they also observed that the erosion of old vegetation was mainly driven by: cut-bank erosion or bank scalloping, bar cut-off, and widening and expansion of secondary channels or re-opening of abandoned channels. The latter process was also observed along ephemeral sand rivers, where large floods, driven by storms, induced a significant channel widening (Friedman and Lee, 2002).

River flow fluctuations also play a key role in driving eco-morphodynamic processes. For example, vegetated patches promote sediment deposition (Mosner et al., 2011). It has been reported that the elevation of vegetated sand bars may increase by as much as 0.5 m in 2 years (Johnson, 2000). This elevation increment is crucial to increase the survival-chance of vegetation, and to complete the vegetation succession toward the adult stage.

Finally, it should be noted that, apart from the stream-driven morphological processes, other important morphological processes can originate from hillslope-driven disturbances, such as landslides and debris flows (Friedman et al., 2006). These processes are more frequent in mountainous zones, where bed mobility is often limited by the size of the sediments (Polzin and Rood, 2006).

Substrate texture. River flow fluctuations influence the substrate texture of the sediment deposits which, in turn, are a crucial driver of vegetation dynamics. Floods deliver large amounts of fine sediments (Stella et al., 2013) that are usually rich in nutrients, and promote substrate moisture conditions when they are deposited (Nilsson and Svedmark, 2002; Asaeda et al., 2015). This process creates an ideal environment for the recruitment and growth of vegetation, and is enhanced at the lower transect elevations (Goodson et al., 2003). Therefore, alterations of the natural fine sediment regime may have important consequences on vegetal communities: e.g., a surplus of fine sediments has often been associated with vegetation encroachment (Asaeda and Rashid, 2012), and the presence of large patches of fine sediment may favor certain vegetation species (Asaeda et al., 2015).

River flow fluctuations affect the stratigraphic architecture of river banks (Merritt et al., 2010). Different river flows generate sediment deposits that have a heterogeneous sediment size (Steiger et al., 2005). This, in turn, causes patches with different hydraulic permeability, different moisture retention capacity, and different resistance to sediment washing. As the stratigraphy of a plot is crucial for the recruitment and survival of different species, all these aspects have important ecological consequences (Robertson and Augspurger, 1999). For example, stratigraphic heterogeneity favors the co-existence of different species in the same locations along the hydrological gradient (Stromberg, 2001).

Finally, the understanding of sediment dynamics, and their effect on vegetation, is crucial for the correct management of the release of sediments from dams (see Asaeda and Rashid, 2012, for a detailed description of the phenomena).

Nutrient and salt dynamics. River flow fluctuations affect the transport of nutrients (mainly Nitrogen and Phosphorus) and salts, both of which are important for the life of vegetation (Asaeda and Rashid, 2014). This transport may occur along the river transect (i.e., from the stream to the banks, or *vice versa*) and/or along the vertical profile of the sediment deposits, as a result of groundwater fluctuations.

The transport of nutrients from the watercourse to the banks usually occurs through the deposition of fine sediments rich in Nitrogen and Phosphorus (Sparks and Spink, 1998; Stromberg, 2001; Nilsson and Svedmark, 2002; Asaeda and Rashid, 2012; Stella et al., 2013). These nutrient exchanges are closely related to the hydrological regime of the river, and any alteration of the hydrological regime causes changes of the nutrient dynamics (Asaeda and Rashid, 2012). Altered nutrient conditions have been reported to promote changes in the composition of vegetation species (Asaeda et al., 2015; Garssen et al., 2015).

The dynamics of salts in river bank soils is equally im-

Geo-morphological dynamics	
• Floods are not so effective in clear encroached zones	Miller et al. (2013)
• No formation of nursery barren sites with sediment deficit	Merritt and Cooper (2000)
• Nursery sites/removal of vegetation induced by large scale morphodynamical processes	Friedman et al. (1996), Merritt and Cooper (2000), Fierke and Kauffman (2005), Latterell et al. (2006), Braatne et al. (2007), Wang et al. (2016)
• Migration of lateral point bars; coalescing of central, multiple or lateral bars; narrowing or abandonment of channels create nursery sites	Dykaar and Wigington Jr. (2000)
• Cut-bank erosion, bank scalloping, bar cut-off, widening and expansion of secondary channels, re-opening of abandoned channels erode old vegetation	Dykaar and Wigington Jr. (2000), Friedman and Lee (2002)
• Vegetated patches promote sediment deposition	Johnson (2000), Mosner et al. (2011)
• Vegetated patches promote obstacle induced scouring	Edmaier et al. (2015)
Substrate texture	
• Floods deliver fine sediments (ideal for the recruitment)	Nilsson and Svedmark (2002), Goodson et al. (2003), Stella et al. (2013)
• Alterations of the fine sediment regime induces vegetation encroachment	Asaeda and Rashid (2012), Asaeda et al. (2015)
• RFFs determine the river bank stratigraphy	Stromberg (2001), Merritt et al. (2010)
• RFFs cause heterogeneity in sediment deposits (that promotes biodiversity)	Robertson and Augspurger (1999), Steiger et al. (2005)
Nutrient and salt dynamics	
• WSFs affect the transport of nutrients	Asaeda and Rashid (2014)
• Transport of nutrients is driven by fine sediments	Sparks and Spink (1998), Stromberg (2001), Nilsson and Svedmark (2002), Asaeda and Rashid (2012), Stella et al. (2013)
• Alterations of nutrient regime promote changes in species composition	Asaeda et al. (2015), Garssen et al. (2015)
• Floods remove salts from the surface	Stromberg (2001)
• WSFs may convey downward salts	Naumburg et al. (2005)
Wood debris	
• Large wood debris promote vegetation colonization in the active zone of the river	Edwards et al. (1999), Kollmann et al. (1999)
• Large wood debris promote extensive scour upstream their location	Edwards et al. (1999)
• RFFs remove combustible wood debris	Ellis et al. (1999), Stromberg (2001)
• RFFs promote the recycle of nutrients stored in wood debris	Ellis et al. (1999)

Table 3: Synthesis of the RFF-induced processes involved in the dynamics of the riparian environment, and which have a feedback on vegetation.

portant, and influences the species composition of the riparian community. First, the high stream velocities experienced during floods are the main drivers of the removal of salts from the substrate surface (Stromberg, 2001). Second, river WSFs drive the groundwater fluctuations in the river banks. Such fluctuations can play an important role on those vegetation species that are sensitive to salts (Naumburg et al., 2005). In fact, when the groundwater is high, salts are dissolved in the upper substrate layers. When the water table drops, the dissolved salts are conveyed downward. As a result, the health of the roots can be affected by salts also in deep substrate layers.

Wood debris dynamics. Wood debris dynamics, driven by river flow fluctuations, plays a major role in a number of situations. First, we discuss the role of wood debris dynamics on the colonization by vegetation of the active zone of the river (Edwards et al., 1999; Kollmann et al., 1999). Wood debris is removed by high-magnitude floods (see the *Geo-morphological dynamics* paragraph in this subsection), and conveyed downstream. During the receding limb of the hydrograph, this debris is deposited within the active zone of the watercourse. The fate of the deposited debris depends on its size and on the location along the hydrological gradient in which the deposition occurs. Small pieces of wood and large wood debris (LWD) deposited at a low elevation will likely be conveyed downstream during a new flooding event. LWD deposited on the top of bare bars, may instead promote the formation of vegetated islands within the active zone of the river (Edwards et al., 1999). In fact, LWD are massive obstacles to the flow, and affect the local dynamics of sediments to a great extent. A deep scour is usually promoted upstream of the obstacle, while the deposition of sediments, vegetative propagules of other plants and organic material takes place downstream of the wood debris. Such deposition zone is the ideal site for the successful recruitment and fast growth of riparian vegetal species. As a consequence, the resistance of the vegetated island to new floods, and its capacity of trapping new sediments increases.

A second key aspect is that periodic floods are fundamental for the removal of combustible wood debris. It has in fact been extensively reported that a lack of flooding promotes the accumulation of woody litter, which in turn can cause the inception (or facilitate the propagation) of wildfires (Ellis et al., 1999; Stromberg, 2001).

Finally, interactions between wood debris and flooding promote a nutrient cycle. First, floods redistribute the woody litter at a reach scale, thus helping nutrients to dispel in zones poor in nourishing substances (Ellis et al., 1999). Second, floods promote the decomposition of litter. Wet conditions are in fact necessary for a fast leaf decomposition (Ellis et al., 1999). In this framework, a key parameter is the timing of the floods that occur in the late spring/early summer. In fact, the earlier the flood, the earlier is the leaf decomposition and the related release of nutrients. Therefore, early floods make nutrients available before the growing season, with a consequent advantage for species that require nourishing substrates (Ellis et al., 1999). In contrast, a delay in the wetting of the wood debris may delay the release of nutrients until after the growing season (Ellis et al., 1999). This, in turn, may induce some advantages for the species that require substrates poor in nutrients. Finally, two important aspects should be pointed out: (i) the alternation of wet/dry conditions is necessary for the decomposition of logs and (ii) the flood-induced deposition of sediments that bury litter may alter this picture. In fact, it has been reported that litter burial may either accelerate or slow down the wood decomposition (Ellis et al., 1999).

3. Key characteristics of the river flow fluctuations

River flow fluctuations are driven by precipitation phenomena that span a wide range of spatial and temporal scales. The (strongly nonlinear) interaction between these precipitation phenomena, the catchment hydrology, and the river morphology give the river-flow time-sequence in a specific transect, $Q(t)$.

In the riparian vegetation studies, the focus is usually on the temporal behavior of the river stage, $h(t)$, rather than on the flow time-series, $Q(t)$ (e.g., Mahoney and Rood, 1998; Dixon and Turner, 2006; Benjankar et al., 2014; Doulatyari et al., 2014; Muneepeerakul et al., 2007; Perona et al., 2009). In fact: (i) the switching between flooded and dry conditions in a generic plot depends exclusively by the water stage; (ii) some key drivers of riparian vegetation dynamics (e.g., drought stresses) are more linked to the water stage than to the river flow; and (iii) the water stage alone is usually sufficient to give a first order estimation of the shear stress acting at the river bottom. The water stage time-series, $h(t)$, is evaluated from the flow rate time-series, $Q(t)$, by the rating curve of the river transect (i.e., the relation $h(t) = F[Q(t)]$).

River stage time-series, $h(t)$, exhibit fluctuations of different magnitudes, which can range from hour- to multi-year time-scales and which have to be described by statistical parameters. The ecological dynamics driven by RFFs were characterized by Richter (Richter, 1996; Richter et al., 1997) through five key hydrological parameters: magnitude, duration, timing, return interval, and rate of change in the water stage of the hydrological events.

In order to define the parameters listed above from a quantitative point of view, let us consider an exemplifying time-series of the water stage, $h(t)$, in a river transect (see Figure 1*a*). The water stage reference is set at the lowest point of the transect, and the focus is on a vegetated plot situated at elevation η from the reference level (see Figure 1*b*). In order to characterize the WSF-driven dynamics of vegetation, the elevation of the plot and the elevation of the deepest root should be considered (see Figure 1*b*). The vegetation is stressed by floods when the water stage exceeds the elevation of the vegetated plot. In contrast, a tree is drought-stressed when the WS is below the elevation of its deepest root.

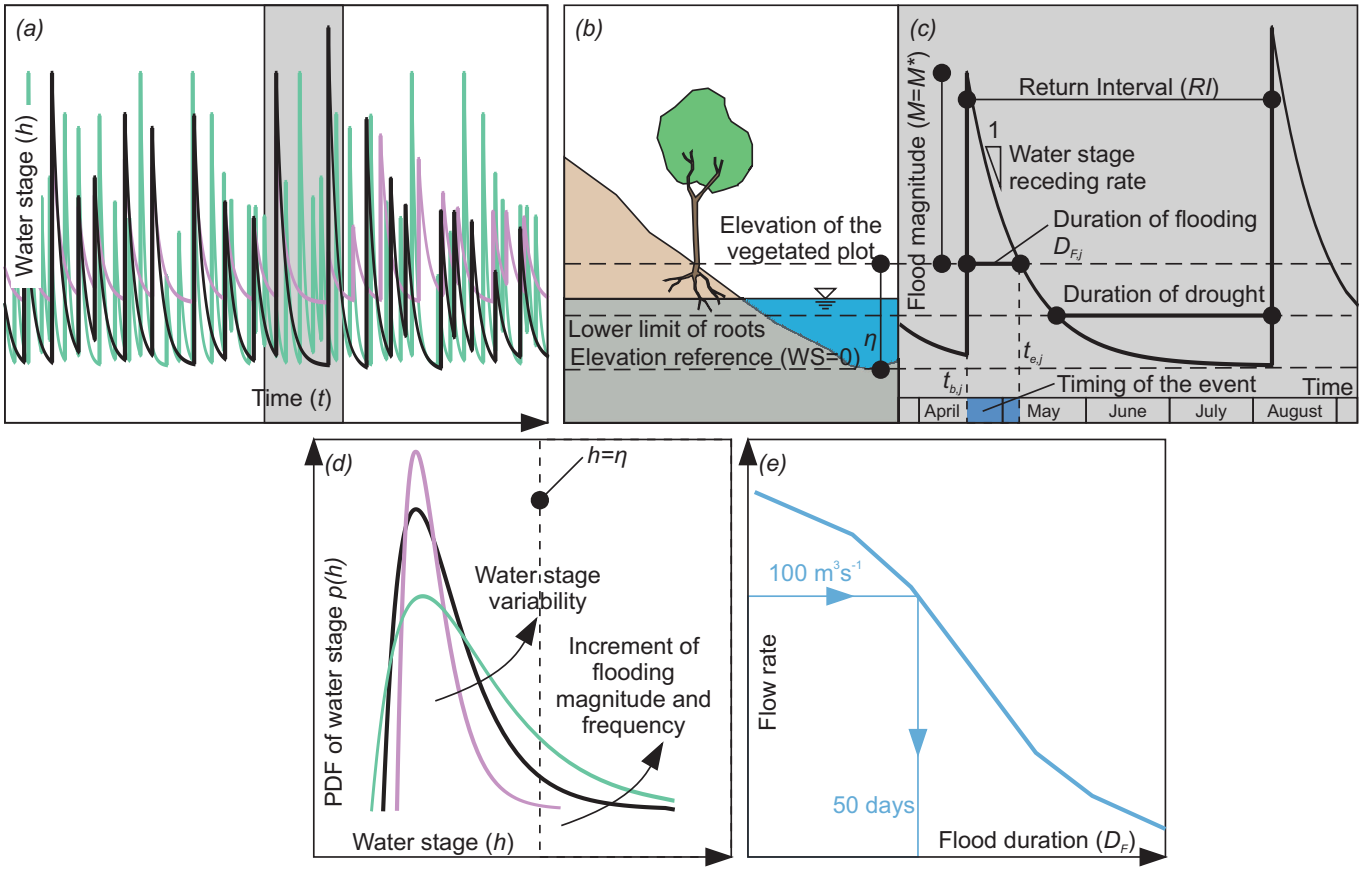

Figure 1: (a) Exemplifying time-series of the water stage, $h(t)$, in a river transect. The pink-black-green colors denote increasing water stage variability. (b) Illustrative example of a vegetated river transect. The reference level above which elevations and the water stage are evaluated is set at the lowest point of the transect. The elevation of the vegetated plot, η, and the elevation of the deepest root are considered, to characterize the vegetation dynamics driven by water stage fluctuations. (c) Illustrative example of a single hydrological event of magnitude $M = M^*$ (enlarged view of the gray area in the panel a). It is possible to observe the magnitude of the flood, M, the duration of the flooding, the duration of the drought, the return interval, RI, and the water stage receding rate. (d) Exemplifying PDF of the time-series reported in the panel a. (e) Illustrative flow duration curve. The reported example shows that the 100 $m^3 \cdot s^{-1}$ flow rate is exceeded for 50 days a year.

Characterization of floods. Floods can be conveniently characterized by the following parameters:

- flood magnitude. The flood magnitude (or flooding depth), $M(t)$, is defined as the difference between the water stage that occurs at time t, $h(t)$, and the elevation of the vegetated plot, η (i.e., $M(t) = h(t) - \eta$, see Figure 1c). The bed shear stress exerted by the flowing water, which is responsible for substrate washing, grows linearly with the flooding depth;

- return interval. The return interval (or mean first passage time), RI, is on average the time that passes between two events of magnitude M^* or higher (see Figure 1c). From an eco-hydrological point of view, the return interval is a proxy of the time that passes between two hydrologically stressing events (Surian et al., 2015). The magnitude and the frequency of the hydrological disturbances in a transect are tightly connected, and are well described by the PDF (probability density function, $p(h)$) of the time-series $h(t)$ (see Figure 1d). In fact, the return interval of a flood of magnitude M^* can be evaluated as

$$RI(M^*) = \frac{1}{1 - P(\eta + M^*)}, \qquad (1)$$

  where $P(\eta + M^*)$ is the cumulative probability of occurrence of a water stage $h^* = \eta + M^*$ (i.e., a flood of magnitude M^*, at plots with elevation η). The evaluation of $p(h)$ provides a good characterization of the flow variability. Let us consider river regimes with different water stage variability (e.g., green and pink curves in panels 1a and 1d) and with the same mean value. Increments in the water stage variability (green curve) promote a higher probability of flooding, and thus a reduction in the return interval of floods of a given magnitude. The opposite occurs if the water stage variability is reduced (pink curve).

- flood duration. The flood duration is the time interval during which the site is submerged (i.e., $h(t) > \eta$, see Figure 1c). Formally, the flood duration $D_{F,j}$ of the $j-th$ flood that affects a plot of elevation η reads

$$D_{F,j} = t_{e,j} - t_{b,j}, \qquad (2)$$

  where $t_{b,j}$ and $t_{e,j}$ are the instants at which the flood began and at which the flood ended. This parameter plays a key role, as the detrimental effects of floods on vegetation grows as the duration of the flooding period increases. One of the standard tools for the analysis of flood duration is the flow duration curve (see Figure 1e), i.e., the number of days in a year in which a given flow rate is exceeded. It should be pointed out that transects with the same flow duration curve may exhibit very different behaviors (e.g., frequent floods of short duration or rare long-lasting floods). A key tool to differentiate transects with the same flow duration curve and gain an indication about the duration of flood events is the auto-correlation function (Bras, 1990; Maidment, 1993). This function reads $\rho_h(s) = \overline{h(t)h(t+s)}/\overline{h^2(t)}$, where s is the time delay and the bar denotes time averaging, and can be summarized by the correlation time $\tau_h = \int_0^\infty \rho_h(s)\mathrm{d}s$. This last metric is a proxy of the (linear) memory of the water stage time-series: a high value of the correlation time is an indication of long-lasting flood events.

It should be noted that the flooding depth $M(t)$, the return interval RI, and the duration $D_{F,j}$ are dependent to a great extent on the plot elevation, η. As a result, a "hydrological gradient" can be observed along river transects: the magnitude, duration and frequency of floods reduce, while the elevation of the vegetated plot increases.

Characterization of drought stresses. Substrate moisture is influenced by the position of the groundwater table which, in turn, depends on the river stage. These two values are almost coincident for very coarse sediments. However, delays and frequency cutoffs occur between river stage rising and falling and the groundwater table, when bank substrates have medium or low permeability. Moreover, atmospheric factors and the vegetation itself affect the substrate moisture content (Polzin and Rood, 2006).

For the above reasons, the following approximations are usually assumed, when the characteristics of droughts are analyzed: (i) the groundwater and the river water stage coincide, (ii) no atmospheric factors influence the substrate moisture (i.e., substrate moisture dynamics are groundwater-driven), and (iii) the width of the capillary fringe is constant.

The previous assumptions are usually somewhat representative of the alluvial sediment deposits that make up river banks. In this framework, drought stresses can be characterized from an hydrological point of view by means of two parameters:

- duration of the drought period. Analogous to the duration of floods, it is the time interval during which the groundwater table is below the deepest root (see Figure 1c);

- rate of decline in the water stage. The rate of decline in the water stage over the falling limb of the hydrograph (i.e., after the flood has passed, see Figure 1c) is measured as the change in the water stage elevation Δh that occurs during the time interval Δt, namely $\Delta h/\Delta t$. Many quantitative studies have found that a meaningful time interval for studies about riparian vegetation is $\Delta t = 1$ day (e.g., Gorla et al., 2015).

It is worth stressing that the response of vegetation to droughts or floods depends to a great extent on the

physiological (e.g., water demand) and reproductive (e.g., seed dispersal) activities of plants. As vegetation activities are basically seasonal, the timing of hydrological events is crucial (Greet et al., 2013).

4. Modeling of vegetation dynamics forced by river flow fluctuations

4.1. Seedling recruitment models

Seedling recruitment is the most fragile and threatened process of riparian forest regeneration (Mahoney and Rood, 1998; Amlin and Rood, 2002; Dixon and Turner, 2006; Benjankar et al., 2014). It is well known that flow regimes altered by river regulation or climate changes prevent successful seedling recruitment. For example, river regulations that limit geomorphic disturbances hinder the creation of the bare surfaces needed for seedling recruitment (Rood and Mahoney, 1995; Scott et al., 1997). Moreover, man-induced drought stress may increase the mortality of newly recruited seedlings (Amlin and Rood, 2002; Stella et al., 2010). In this scenario, models capable of simulating the recruitment of seedlings have been developed. The main objective of these models is to assess whether the hydrological conditions that follow seed release are appropriate for the germination of seeds and for the survival of young seedlings. Table 4 reports a synthesis of the RFF-induced processes considered in the different seedling recruitment models.

Recruitment box model (RBM). Mahoney and Rood (1998) tackled this issue for the first time through a quantitative approach, and developed the celebrated "recruitment box model". This model predicts whether seedlings that grow at a given elevation will survive during the summer that follows germination and establishment. The prediction considers a single river transect, and it is based on the behavior of the 3-day moving averaged water stage (see the black thick curve in Figure 2*a*), where the elevation reference is set at the shoreline of the minimum flow rate observed during the summer. Three thresholds determine the survivability of seedlings. First, seedling recruitment is only possible in the [50-150] cm elevation range (see the horizontal dashed lines in Figure 2*a*). Second, the seed release season lasts from the middle of June to the end of July. As a result, locations in the [50-150] cm range that are flooded at the end of this season (e.g., the orange area) are not suitable for recruitment. These two thresholds delimit an area on the stage-time plane which is called 'recruitment box" (thick box). Only the points that fall within this box and that are located above the curve of the 3-day moving averaged water stage may be suitable for recruitment (gray area). The third threshold for recruitment is that the water receding rate must not exceed 2.5 cm/day (thick dashed line in Figure 2*a*). When the receding rate is faster (e.g., the red curve), recruitment is not possible, as seedlings are drought stressed and therefore die. The opposite occurs when the receding rate

	Mahoney and Rood (1998)	Dixon and Turner (2006)	Benjankar et al. (2014)
Formation of sites for recruitment			
Creation of barren sites	–	–	✓
Removal of former vegetation	–	–	✓
Deposition of fresh alluvial substrate	–	–	–
Dispersal of reproductive material			
Dispersion of seeds by hydrochory	–	✓	–
Scouring and transport of seeds	–	✓	–
Deposition of seeds	–	✓	–
Zonation of seed deposition	–	✓	–
Seedling recruitment			
No seed germination in submerged zones	✓	✓	✓
Germinability depends on substrate moisture	–	✓	–
Seedling survival			
Killing of seedlings by drought	✓	✓	✓
Killing of seedlings by burial and scouring	–	✓	✓
Selection of vegetal species	–	–	–

Table 4: Synthesis of the key RFF-induced processes listed in Table 1 and considered in the seedling recruitment models. The marks ✓and – indicate that the corresponding process has been considered or not considered, respectively.

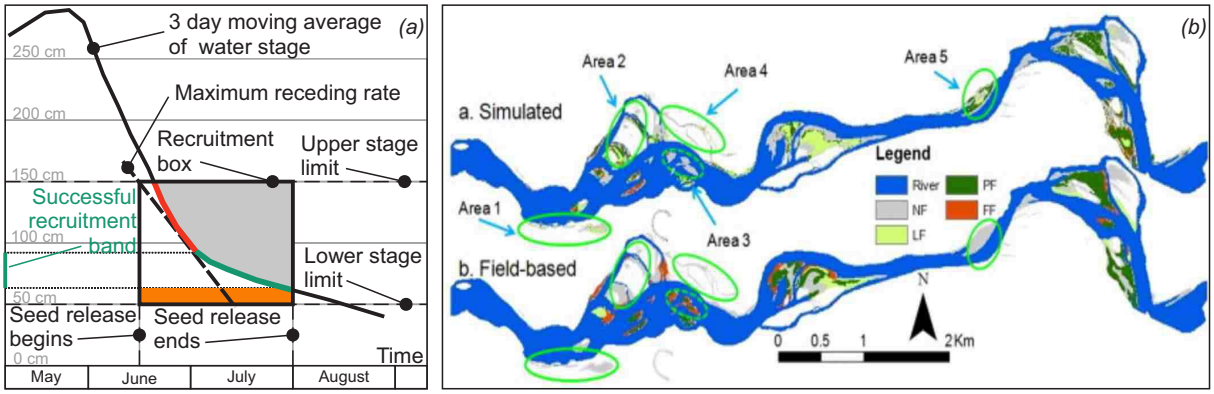

Figure 2: (a) Recruitment box model (Mahoney and Rood, 1998). The horizontal dashed lines delimit the upper and lower stages within which seedling recruitment is possible. The vertical dashed lines delimit the seed release season. These four lines delimit the "recruitment box" (thick box) in the stage-time plane. In this box, (i) locations that are flooded at the end of the seed release season (orange area) are not suitable for recruitment; (ii) points located above the curve of the 3-day moving averaged water stage may be suitable for recruitment (gray area). The thick dashed line denotes a water receding rate of 2.5 cm/days. The red curve highlights when and where the receding rate of the hydrograph is faster than 2.5 cm/days, hence recruitment is not possible. The green curve shows when and where the receding rate of the hydrograph is slower than 2.5 cm/days, thus recruitment is possible. The green segment on the vertical axis marks the elevation band where recruitment may be successful. (b) Simulated and field-based recruitment favorability classes in the braided reach of the Kootenai River, Idaho, USA in the year 2006 (Figure reproduced from Benjankar et al., 2014)

is slower (green curve). These three thresholds delimit an elevation band (the green segment on the vertical axis) where recruitment may be successful.

Improved description of seed dispersal, deposition, and germination in the RBM. Dixon and Turner (2006) improved the original model by Mahoney and Rood (1998) by introducing a more refined description of the seed dispersal and deposition, germination, and survival processes. In order to test the model against field data, 30 sandbars in the Wisconsin River (Wisconsin, USA) were considered. Three transects were surveyed for each bar, and each transect was made up of 1 meter wide segments (plots). Real hydrographs with daily resolution were used to evaluate (numerically) the water stage position and the shear stresses acting at the bottom. As a result, the daily time-series of the fluctuating water-stage and shear-stress were made available for all of the transect plots. In order to assess the recruitment dynamics, the number of seeds and seedlings in all the plots was simulated daily. Four eco-hydrological and morphological processes were considered: (i) seed dispersal, (ii) seed deposition, (iii) seed germination, and (iv) seed survival.

Seed dispersal determines the maximum number of seeds available per plot, SA, in a given day. SA depends on the the species considered and is a function of the calendar day of the simulation. Seed deposition processes determine the number of seeds that are actually deposited, SD, in a given plot on a given day, and depends on SA and on the water stage dynamics. The algorithm developed by the Authors is a good model of hydrochory processes. In fact, it considers that the deposition of SA is more effective in plots that are emerging (see the original work for further details). Seed germination determines the number of deposited seeds, SD, that become seedlings, SE, in a given plot on a given day. Germination success depends on the number of days the seed is in dry conditions, and on the position of the water stage. Finally, the survival of seedlings is determined by the evaluation of the drought and scouring stresses. The position of the water stage and the shear stress at the bottom determine (through a mechanistic approach) the percentage of survival of seedlings I (see the original work for the approach adopted to evaluate I). As a result, the number of seedlings on the following day will be $SE(d+1) = I \cdot SE(d)$ with I in the [0,1] range, and where d stands for the day of the simulation. The Authors considered a three year long hydrograph to calibrate and validate the model parameters, and found a very good match with the results of field surveys and measurements.

This approach shows a key improvement, compared to the original model by Mahoney and Rood (1998). Mahoney and Rood (1998) considered that seedling recruitment was only possible in the $[50-150]$ cm elevation range. Although this has in fact been widely observed, there is no mechanistic reason for the adoption of this rule. Dixon and Turner (2006), instead, did not refer to any empirically-derived rule. They determined the realistic distribution of seedlings along a river transect only through the modeling of mechanistic processes.

Finally, it should be pointed out that the model by Dixon and Turner (2006) may be an important tool to assess the effects of river discharge fluctuations or hydrological-alterations on the dynamics of riparian forest recruitment. Dixon and Turner (2006) performed some preliminary analysis on this issue in their work. In particular, they focused on the seedling dynamics that occurred over a large time span, that is, 1935-2000. Two scenarios were considered: the real hydrograph of the river (i.e., subject to river regulation) and a hypothetical hydrograph in which any human

impacts had been artificially removed. They found that alterations of the hydrological regimes were responsible for up to 90% of the modifications of the seedling dynamics, and that river regulation promotes the survival of seedlings (and thus vegetation encroachment of the active floodplain zones).

Modeling of recruitment processes at a reach scale. Benjankar et al. (2014) improved the original model by Mahoney and Rood (1998) by considering the recruitment processes at a reach scale rather than at a transect scale. To this aim, they considered DEMs (digital elevation models), with a cell resolution of 5×5 meters, of real reaches of the Kootenai River (Idaho, USA). A real one year long hydrograph with a daily resolution was adopted to evaluate the water stage and the shear stresses time-series in all the DEM cells. In order to assess the fate of the seedlings, a fuzzy-logic approach was adopted (i.e., logical rules and sharp thresholds were used to determine the evolution of the system, rather than rigorous equations). Four key hydrological and morphological processes that promote recruitment were accounted for in each DEM cell: (i) the shear stress had to be be sufficiently high to remove old vegetation and create barren sites, (ii) the water stage had to recede sufficiently slowly, to allow the growth of seedling roots, (iii) the elevation above the minimum water stage observed during the summer had to be in the [60-200] cm range, and (iv) the duration of winter floods did not have to exceed the flooding tolerance of the seedlings. Each process was quantified with scalar values, and deemed to be a good (G), fair (F) or poor (P) condition for seedling recruitment (e.g., a water receding rate below 0.5 cm/days was considered a good condition for recruitment). Fuzzy rules were then adopted to classify the DEM cell as fully favorable (FF), partly favorable (PF), less favorable (LF) or non favorable (NF) (e.g., if the four considered processes give good conditions, the FF conditions were met). Some typical results of this model are reported in 2*b*, together with a field-based analysis that was performed by the Authors to validate their model.

This approach introduces at least two key improvements, with respect to the original model by Mahoney and Rood (1998). First, the model does not assume that all the banks are bare and suitable for recruitment. Instead, the model evaluates the zones in which the shear stress is sufficient to remove old vegetation and create barren sites. Second, the simulations also consider the winter season, and can therefore give a prevision of the zones where seedlings are expected to survive the first year of their life.

4.2. Minimalistic stochastic models

Over the last few years, it has been demonstrated that the probabilistic structure of river flow time-series plays a key role in determining the dynamics of riparian vegetation (Shafroth et al., 2002; Greet et al., 2011b). Randomness is a crucial feature of the riparian environment, since its dynamics depends on the intensity, frequency and duration of the river flow fluctuations. In order to elucidate the key role of the river flow stochasticity, a number of studies have adopted a minimalistic approach in which realistic but, at the same time, mathematically manageable stochastic models have been developed. These models describe the essential physical and biological processes, and the key role of stochastic fluctuations is explicitly embedded in the mathematical framework. The analytical solvability of the equations is preserved, computationally demanding numerical simulations are avoided, and the role of the probabilistic characteristics of flow randomness emerges in a clear way (see Table 5 for a synthesis of the model, and for a comparison with other approaches). For this reason, the minimalistic approach has been used successfully over the last few years to elucidate a number of eco-morphological processes (Camporeale and Ridolfi, 2006, 2007; Muneepeerakul et al., 2007; Perona et al., 2009; Tealdi et al., 2011; Crouzy and Perona, 2012; Tealdi et al., 2013; Doulatyari et al., 2014; Tron et al., 2014, 2015; Vesipa et al., 2015, 2016).

Approach. The first minimalistic stochastic approach to riparian vegetation was developed by Camporeale and Ridolfi (2006), and it focused on the vegetal biomass that can be observed in a river transect plot. In this approach, the biomass is used as proxy of more detailed features of vegetation (e.g., the number of individuals or the total dry mass of vegetation in a plot, etc.). In order to understand the rationale behind the minimalistic approach, let us consider the illustrative river transect reported in Figure 3*a*. Riparian vegetation is found on the banks, and its dynamics is driven by the river stage, h, and by the depth of the phreatic surface, δ. As riparian substrate permeability is usually high, the position of the groundwater table is assumed equal to the stream stage. Both inundated and exposed zones occur in the transect, for any stage h. In the submerged zone (zone I in Figure 3*a*) the detrimental aspects of floods are assumed to be dominant over the positive aspects, and the biomass of the plot reduces. When the plot is exposed (zones II-IV in Figure 3*a*), the (phreatophyte) vegetation biomass dynamics only depends on the depth of the groundwater table, δ. If δ falls into a species-specific range $[\delta_1, \delta_2]$, the vegetation can take up water and grow (zone III). When $\delta < \delta_1$ (or $\delta > \delta_2$), root anoxia (or the weak capillary fringe) halts the growth of biomass (zones II and IV).

As water stage fluctuates randomly (see Fig. 3*b*), each plot undergoes exposure and flooding periods of random intensity and duration. It therefore results that the phreatic surface depth (during the exposure phases) and the water depth (during inundations) are random variables. The plot-dependent random sequence of exposure/inundation periods affects the vegetation dynamics to a great extent, and gives rise to plot-specific biomass time-series. Degradation and growth phases switch randomly, and the vegetation biomass, v, exhibits stochastic dynamics (see Figure 3*d*). This dynamics can conveniently be described by means of plot-specific PDFs (see the curve $p(v)$ in Fig. 3*e*).

Model Class	Approach: Vegetation dynamics	Approach: Vegetation succession	Approach: River flow variability	Key results	References
Minimalistic stochastic models	• Vegetation growth depends on groundwater depth • Vegetation removal depends only on flood depth • Morphodynamics - vegetation interactions considered in a simplified manner	• No explicitly considered • Inter-species facilitation-competition mimics reed-shrub succession	• Explicitly considered • River flow is described by statistical parameters (average flow, standard deviation, temporal correlation)	• Analytic plot-specific PDF of vegetation biomass • The variability of vegetation due to river flow fluctuations is considered	Camporeale and Ridolfi (2006), Camporeale and Ridolfi (2007), Muneepeerakul et al. (2007), Tealdi et al. (2011), Tealdi et al. (2013), Doulatyari et al. (2014), Tron et al. (2015), Vesipa et al. (2015), Vesipa et al. (2016)
Dynamic vegetation models	• Vegetation growth and removal depends on many variables (e.g., watertable depth, shear stress exerted by the stream at the bottom, etc...) • Morphodynamics - vegetation interactions can be considered in a detailed manner	• Never considered in existing works, but an extension seems straightforward	• The numerical approach allows the analysis of one hydrograms at a time • Idealized hydrogram have been adopted • Simulation of river flow stochasticity requires a Monte Carlo approach	• Time-series of vegetation abundance at the reach scale	Bertoldi et al. (2014), Miyamoto and Kimura (2016)
Successional models	• Vegetation growth and removal depends on many variables (e.g., substrate moisture, stream shear stress, etc...) • Morphodynamics - vegetation interactions never considered in the literature	• Explicitly considered. Most of the models consider the successions occurring in wetlands, reed grasslands and softwood forests	• The analysis of only one hydrogram at a time is possible by numerical simulations • Real hydrograms have been adopted • River flow stochasticity has never been considered	• Temporal evolution of the riparian vegetation population at the reach scale	Benjankar et al. (2012), Benjankar et al. (2012), Egger et al. (2012), García-Arias et al. (2013), Rivaes et al. (2014), Benjankar et al. (2016), García-Arias and Francés (2016)
Structured population models	• The abundance of individuals of different age classes is considered • Individuals can either die or switch to the following age class • Death/Switching between classes is regulated by river hydrology • Morphodynamics - vegetation interactions are not considered	• Explicitly considered for cottonwood population	• The numerical approach allows the analysis of one hydrogram at a time • Synthetic hydrograms derived from real hydrological data have been adopted • Simulation of river flow stochasticity requires a Monte Carlo approach	• Time-series of abundance of different age classes at the reach scale	Lytle and Merritt (2004)

Table 5: Synthesis of the approaches adopted in the main models of adult vegetation dynamics and the corresponding key results obtained.

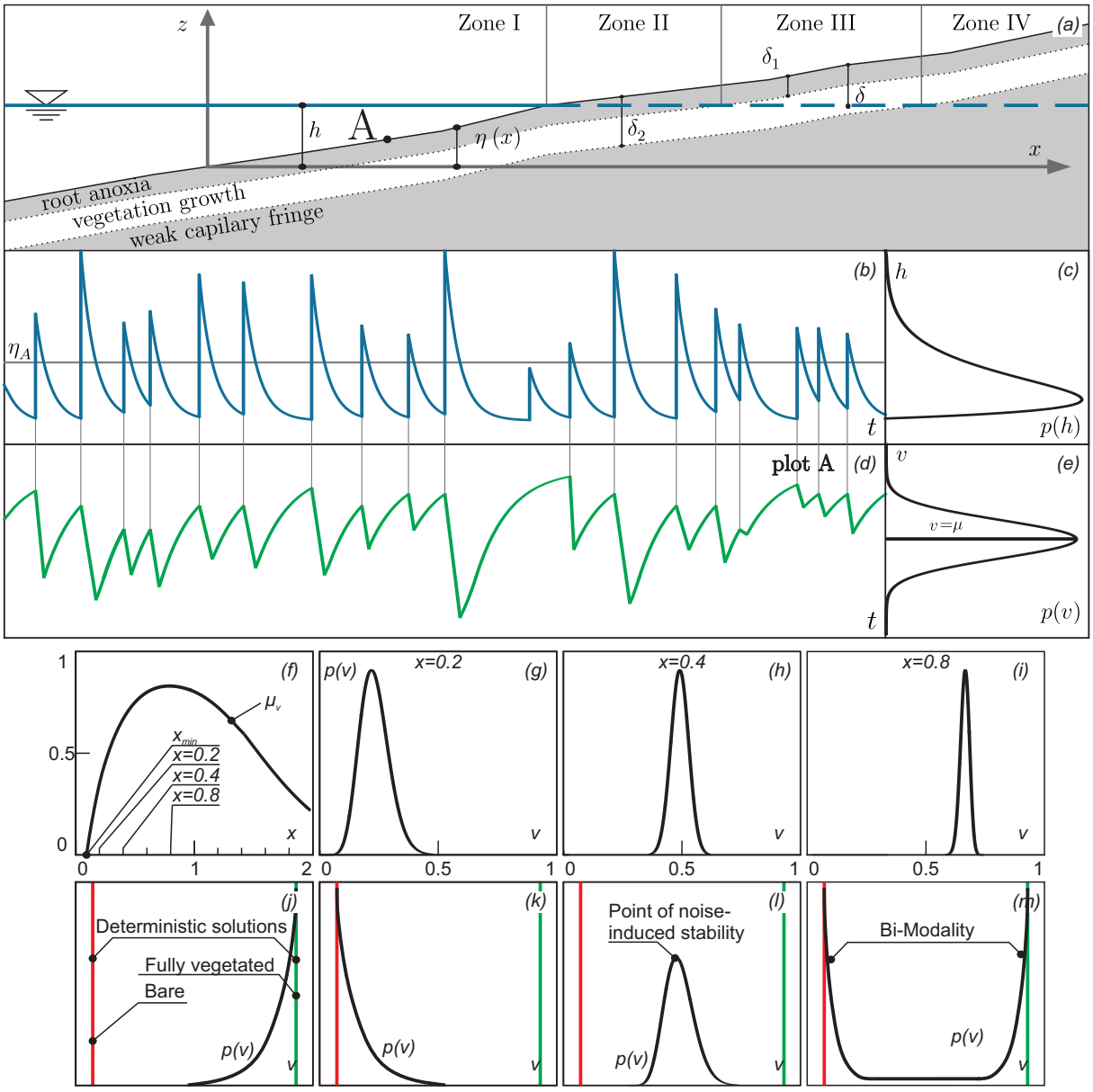

Figure 3: (a) Scheme of a river transect. The thick blue line represents the water stage and groundwater table. The gray regions delimit the position of the phreatic surface that hinders vegetation growth in the corresponding surface plots. The white layer between the gray areas denotes the locations of the phreatic surface that are suitable for vegetation growth. Panels (b, c) report the qualitative time-series and PDF of the water stage. Panels (d, e) show the time-series and PDF of the vegetation biomass at plot A. (f) Behavior of the plot-specific mean value of the biomass along the transect. $(g - i)$ Plot-specific PDFs of the biomass at three selected locations. $(j - m)$ Disturbance-induced changes in the biomass PDFs.

In order to deduce the plot-specific PDF of vegetation biomass, the stochastic dynamics of vegetation are modeled at a generic plot of coordinate x by means of the piecewise stochastic differential equation

$$\frac{\mathrm{d}v}{\mathrm{d}t} = \begin{cases} g(v) & h \geq \eta \quad (a) \\ f(v) & h < \eta \quad (b) \end{cases} . \tag{3}$$

In (3), the functions $g(v) < 0$ and $f(v) \geq 0$ model the degradation and growth of the vegetation biomass that occur when the plot is flooded (i.e., $h \geq \eta$) and exposed (i.e., $h < \eta$), respectively. Only three eco-hydrological parameters (calibrated on real rivers) characterize the resistance to floods and the growth performance (i.e., the functions $f(v)$ and $g(v)$). Model (3) is stochastic, as the degradation and growth rate, as well as the switching between equations are forced by the random variable, h. A usual choice (Doulatyari et al., 2014; Tron et al., 2015) is to model the water stage time-series as a random sequence of exponentially distributed jumps (i.e., a white shot noise), and exponential decays. In this case, $h(t)$ can be defined by two simple hydrological parameters: the coefficient of variation of the water level, C_h, and the correlation time of the water stage time-series, τ. With this assumption, the plot-specific probability density function of the vegetation biomass, $p(v)$, can be analytically evaluated (see Camporeale and Ridolfi (2006) for further details).

Plot-specific PDF of vegetation biomass. The main result of the minimalistic stochastic approach is the plot-specific probability density function of the vegetation biomass, $p(v)$. This PDF: (i) can be evaluated knowing the three eco-hydrological parameters that define the flow-vegetation interactions, and the river hydrological parameters (C_h and τ); and (ii) quantifies (in a given plot) the variability of the vegetation biomass, induced by the unpredictable and stochastic dynamics of the river. It should be pointed out that the PDF strongly depends on the elevation above the mean water stage of the considered plot (see Figure 3f that reports the mean value of biomass, μ_v, along the river transect). Four typical behaviors can be observed: (i) plots close to the river ($x = 0.2$) are weakly vegetated and v exhibits a high variability; (ii) in plots with moderate elevation (e.g., $x = 0.4$, where the hydrological forcing is not particularly severe) the banks are well vegetated on average and the biomass variability reduces; (iii) at high elevations (x=0.8) inundations are rare and weak, the plot is always well vegetated ($\mu_v \sim 0.7$), and $p(v)$ is markedly peaked around its mean value; and (iv) far from the river ($x > 1$), the plot elevation becomes a limiting factor for the tapping of the phreatic surface. The vegetation suffers and its biomass decreases. In this case, the effect of inundations is marginal and $p(v)$ is peaked around μ_v.

Role of flow randomness on riparian vegetation dynamics. The stochastic system (3) admits two deterministic solutions (Camporeale and Ridolfi, 2007). If the water stage h is always lower than η, only equation (3b) holds, and degradation of the biomass never occurs; hence the plot is fully vegetated (green Dirac-δ in the biomass PDFs in Figures 3$j - m$). Vice versa, if h is always higher than η, only equation 3a holds, growth of the biomass never occurs, and $v = 0$, i.e., the plot is bare (red Dirac-δ in the biomass PDFs in Figures 3 $j - m$). When h fluctuates above and below η, three scenarios are possible, as a function of the disturbance characteristics (i.e., the amplitude and frequency of the fluctuations). In the first scenario, the system fluctuates around one of its deterministic solutions. In this case, the PDF of the biomass is no longer the Dirac-δ, but a monotone curve with a maximum at the deterministic solution (see Figure 3$j - k$). In the second scenario, random external forcing prevents the ecosystem from reaching any of the deterministic states. As a result, the ecosystem fluctuates around a state that is somewhere between these two deterministic states (see Figure 3l). Water stage fluctuations induces the occurrence of a statistically stable configuration between the two deterministic states. This phenomenon is also referred as "noise-induced stability" (D'Odorico et al., 2005; Ridolfi et al., 2011). Finally, in the third scenario, disturbances induce the coexistence of two distinct preferential states (Porporato and D'Odorico, 2004). The PDF of vegetation biomass becomes bimodal. This entails the ecosystem switching between the two possible deterministic states with rapid transitions. As a result, intermediate states are highly unlikely (see Figure 3m).

The "noise-induced stability" phenomenon may explain the occurrence of the widely observed bell-shaped biomass distribution along riparian transects. The effect of hydrological fluctuations displays a gradient along the river transect, with more devastating effects in locations closer to the river. As a result, the hydrological forcing deviates the biomass of a plot from a "fully vegetated" deterministic status to an extent that depends on the distance from the river, and also gives rise to a gradient of the vegetation biomass. The occurrence of the bimodal PDFs may explain the spatial patchiness of vegetation along rivers. The actual state depends on how the river flow dynamics allows one of the two preferential states to dominate. Finally, it should be pointed out that the occurrence of noise-induced stability phenomena and bimodal PDFs is related to the coefficient of variation of the water level, C_h, and to the correlation time of the water stage, τ.

Effect of damming. Tealdi et al. (2011) adopted a minimalistic stochastic model to quantify the effect of damming on vegetation dynamics. They assessed the modifications of the mean biomass along a transect (e.g., the curve $\mu_v(x)$ in Figure 3f) as a result of hydrological alterations. This quantitative study found that hydrological alterations may induce changes in the total biomass of more than 100%. Moreover, the elevation of the boundary between vegetated and bare plots ($x_{\min}$ in Figure 3f) can undergo alterations of the same order as that of the mean river water depth. This analysis allowed the role of the different components of the hydrological alterations

to be quantified. For example, alterations of the mean water discharge were found to be the main driver of narrowing/widening processes. In contrast, the total biomass is affected to a great extent by the coefficient of variation of the river flow. Quite surprisingly, a reduction in the mean water discharge induces an increment in the transect biomass, if a reduction of the river flow variablity also occurs.

Effect of river regime on vegetation dynamics. Minimalistic models have been used to study the dynamics of the vegetation that grows along rivers that have different hydrological regimes (Doulatyari et al., 2014). According to Botter et al. (2013), river flow regimes can be classified as persistent or erratic. This classification is based on the ratio between the mean inter-arrival of rainfall events that can produce a flow in a river and the mean response time of the catchment. Doulatyari et al. (2014) considered two real rivers with different types of hydrological regimes. They showed that, in persistent regimes (low flow variability), groundwater access is the main driver of the spatial distribution of vegetation along transects. They also showed that zones with a high inundation frequency and a long flooding time are clearly separated from dryer zones. Therefore, in these conditions, a sharp transition between the aquatic (bare) and the terrestrial (well vegetated) zone can be observed. In contrast, in erratic regimes (high flow variability) the spatial distribution of vegetation is impacted to a greater extent by inundations. As a result, the aquatic and the terrestrial zone are not so clearly separated, and a gradient of species with increasing flooding (drought) resistance can be observed toward (outward) the watercourse. Finally, the Authors found that the riparian biomass growing along rivers with an erratic regime is more prone to reduce in a climate change scenario.

Recovery time of riparian vegetation after disturbances. The recovery time is defined as the time that vegetation requires to recover from a low biomass value to a higher value. This metric is an important element to help understand the riparian vegetation dynamics. Several field studies (Beschta and Ripple, 2006; Marshall et al., 2013) have shown that understanding how the recovery of biomass is related to the hydrological and biological characteristics is a key point. In order to analytically study this issue, Vesipa et al. (2016) applied the results of the mean first passage time obtained by Sancho (1985) to the stochastic model (3), and evaluated the time required for vegetation to grow from a lower threshold to a target value. The fifth percentile of the biomass PDF was chosen as a lower threshold that represents the vegetation status after a major disturbance (e.g., a large flood or a wildfire). The mean value of the biomass PDF was instead chosen as the target value, namely the biomass of vegetation that, on average, can be observed in a plot. It was found that the recovery of riparian vegetation in disturbed conditions (e.g., a vegetated plot close to the river) is delayed by orders of magnitude, with respect to undisturbed conditions (e.g., a vegetated plot in the upper floodplain). The magnitude of the delay is closely related to the hydrological characteristics of the river and, in particular, to the coefficient of variation and to the correlation time of the water stage. Finally, it was shown that the recovery time of vegetation is an important feature that may promote or hamper the invasion of alien species after major disturbances, especially when hydrological alterations or climate change are considered.

Effect of river-network topology on vegetation dynamics. This topic was tackled by Muneepeerakul et al. (2007). To this end, they first modified the model (3) to consider also the drought stresses and the degradation that vegetation undergoes when the groundwater table is deep. With this approach, they evaluated the threshold elevation $x_{\max}$ above which the phreatotype vegetation cannot be sustained by the river. This information is complementary to the lower threshold $x_{\min}$ (Figure 3f), below which vegetation colonization is hampered by floods. In fact, the knowledge of the thresholds $x_{\min}$ and $x_{\max}$ allows the width of the river transect vegetated by riparian species to be evaluated. Second, the geometric and hydrological parameters that have to be used in (3) were derived from geo-morphic relations. In particular, the stream magnitude (a scalar parameter that describes the topology of river networks) was adopted. Muneepeerakul et al. (2007) found that: (i) the stream magnitude is a crucial parameter to define the width of the riparian zone; and (ii) the precipitation pattern and river flow have an important effect on riparian vegetation width. In particular, when the variance of the river flow increases, the biomass of the vegetation and the width of the riparian zones reduce. This is a key point, as increments in hydrological fluctuations and extreme events (especially extreme precipitations and river flows) are likely to be observed in the current ongoing climate change scenario. In this scenario of increased flow variability, the analysis conducted by Muneepeerakul et al. (2007) suggests the possibility of a dramatic depletion of riparian habitats.

Facilitation/competition dynamics between different species. Tealdi et al. (2013) has recently developed a stochastic model to study the facilitation/competition dynamics that occurs between two riparian species. The first species (e.g., riparian shrub) is dominant in the long term. It grows slowly, but it is able to better exploit nutrients, light, and water. As a result, it will eventually displace most of the other species. The second species (e.g., riparian reed) is sub-dominant. It grows very fast, and develops a thick cover, thus it provides armoring to the alluvial sediments and protection against floods to the dominant species. It was found that, under adverse hydrological conditions (e.g., high water stage variability, low elevation above the river), the protection provided by the sub-dominant species significantly increased the biomass at the transect scale and reduced the elevation of the boundary between vegetated and bare plots (i.e., the plot $x_{\min}$ in Figure 3f). Coherently, the role of the sub-dominant species

was less important in plots with milder hydrological conditions.

Feedback between vegetation and geo-morphological dynamics. Vesipa et al. (2015) has recently studied the feedback between vegetation and geo-morphological dynamics in a context of stochastic fluctuations of the water stage. When vegetation colonizes a bare plot, it induces an increment in the plot elevation (Steiger et al., 2001; Abbe and Montgomery, 2003). As a result of this elevation-increment, the flood-induced damage to vegetation is reduced, when the plot is flooded. The developed model is able to capture the following process: the presence of vegetation induces a (biomass-dependent) increment of the plot elevation, that protects the vegetation from floods, and, in turn, promotes a further growth of the biomass. This additional biomass promotes a new plot elevation increment, which further protects the vegetation from floods, and thus further promotes the growth of biomass. Hence, a positive feedback promotes the increment of the biomass.

Again in this case, the adopted quantitative approach allowed the Authors to quantify the effect of the vegetation-induced increments of plot-elevation. When the hydrological forcing is strong (e.g., a plot with a low elevation and high water stage variability) the protection provided by the elevation increments reduces the elevation of the boundary $x_{\min}$ (see Figure 3f) and increases the biomass at the transect scale to a significant extent (about 30%). The protection provided by the elevation increments is less critical when the hydrological forcing is weaker (e.g., high plot-elevation and low flow-variability). It should be noted that this model does not consider the occurrence of scour processes induced by vegetation (e.g., Edmaier et al., 2015).

Quantification of bare sediment areas. Perona et al. (2009) and Crouzy et al. (2013) focused on the probabilistic quantification of bare sediment areas, an important metric for engineering and river restoration projects. They developed a similar stochastic framework to model (3), with the aim of studying the sediment-vegetation dynamics driven by stochastic flood disturbances that occurs at the floodplain scale. They assumed that vegetation is eroded in the inundated part of the floodplain, and bare sediment surfaces are exposed. These surfaces are recolonized when the water stage reduces. In a similar way to the approach by Camporeale and Ridolfi (2006), in this approach the stochastic nature of the flooding events is described by a Poisson process, whereas the rates of vegetation colonization or erosion are modeled as deterministic processes. The key result was an analytical PDF of the exposed sediment area in the river reach.

Roots. Tron et al. (2014) and Tron et al. (2015) developed a minimalistic framework to assess the effect of the stochastic variability of the river stage on the root distribution of phreatophytic plants. The growth/decay dynamics of root biomass at a specific depth z were modeled through a mechanistic approach, according to the following rules: (i) root biomass is removed (due to drought stress) when the water table is too deep; (ii) root biomass reduces (due to anoxia) when the water table is too close; and (iii) root biomass grows when the water table is within an optimal range of distances. As the groundwater table fluctuates randomly, the root biomass at a depth z undergoes a random sequence of growth and decay phases, and a depth-specific time-series of root biomass occurs. In the same way as in the case of the shoot biomass, this stochastic root dynamics, characterized by randomly switches between degradation and growth phases, can be conveniently described by depth-specific PDFs. It has been found that rivers characterized by a high hydrological variability induce the rooting system of riparian vegetation to be spread over larger depths and to exhibit a shallow mean root depth. In contrast, rivers with a low hydrological variability are characterized by vegetation with deeper roots. The results of the model were compared with two root data sets obtained from from field and from controlled experiments, and a very good matching was found.

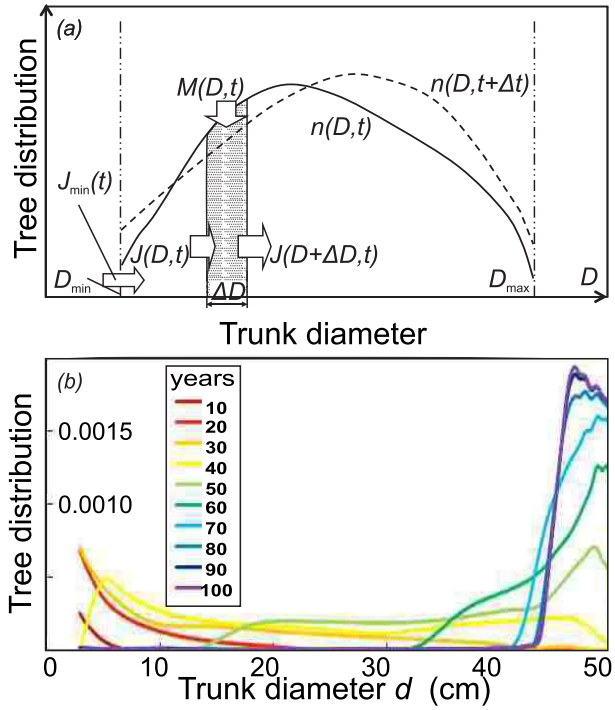

Figure 4: (a) Sketch of the temporal change of the tree distribution density in a floodplain due to tree growth, mortality due to flood impacts, and seedling recruitment. (b) Result of a stochastically generated realization from Monte Carlo simulations. The tree distribution density is reported after every 10 years.

4.3. Detailed mechanistic dynamic vegetation models

Approach. The dynamics of vegetation that colonizes river banks depends on a great number of processes that are induced by water stage fluctuations (Hughes, 1997; Bendix and Hupp, 2000; Glenz et al., 2006; Corenblit et al., 2007). Among others, these processes include the geomorphological evolution of the river topography, the dynamics of the substrate moisture and nutrients, and competition

between individuals of the same species and between different species. These processes act over a wide range of spatial and temporal scales. They often interact with each other in a non-linear manner, and give rise to complex feedbacks. In this scenario, it is of utmost importance to understand and quantify the effect of the different characteristics of the hydrological regimes on the involved processes and feedbacks. To this aim, the use of mechanistic dynamic vegetation models plays a key role. Mechanistic dynamic models are used to estimate the abundance (e.g., number of individuals) and, possibly, the characteristics (e.g., trunk diameter) of riparian vegetation at the reach scale (Ye et al., 2013; Bertoldi et al., 2014; Miyamoto and Kimura, 2016). These characteristics are obtained by simulating the growth and decay of vegetation. These, in turn, are taken into account in a detailed mechanistic manner, considering the key (possibly non-linear and with feedbacks) processes that contribute to vegetation dynamics. Thanks to these types of models, the response of vegetation to flow regimes that have different hydrological characteristics can be studied. This may help to unveil and, more importantly, quantify, the connection between vegetation dynamics (e.g., biomass at the reach scale) and a particular characteristics of the hydrograph (e.g., the return interval of floods). It should be pointed out that this modeling approach requires numerical simulations, and that a representative description of the river flow stochasticity may require the evaluation of a very large number of Monte Carlo simulations (Miyamoto and Kimura, 2016). A synthesis of the approach is reported in Table 5.

Vegetation-morphodynamics interactions. Bertoldi et al. (2014) studied riparian vegetation under a fluctuating water stage, and considered the morphodynamics of the river. To this aim, an idealized watercourse, with the typical hydrological and geo-morphological characteristics of a medium-sized Italian Alpine river, was considered. Two-dimensional depth-averaged shallow water equations were introduced to model the flow field that resulted from a prescribed flow discharge. The morphological evolution of the sediment bed was modeled through Exner's equation, whereas the corresponding sediment fluxes were evaluated from simulation of the flow field. The presence of vegetation increased the local roughness and the critical Shields number, thus contributing to reducing the sediment fluxes. Vegetation was assumed: (i) to exhibit an equilibrium configuration along the river banks that depends on the plot elevation and on the optimal groundwater depth for root tapping, for a fixed non-fluctuating water stage; (ii) to approach such equilibrium according to a logistic growth; and (iii) to be instantaneously and completely washed away where the critical Shields number was exceeded. Finally, a series of four floods with constant discharge, stream power and return interval were considered to flush the braided reach. The main result of the work (in the perspective of the present review) is that two scenarios may emerge from vegetation-dynamics and morphodynamics interactions: the sediment bars can either be vegetated or completely bare after a flood. The first scenario arises when the hydrological forcing is not sufficient to remove all the vegetation from the sediment bars. In the second scenario, the opposite occurs. Bertoldi et al. (2014) found that these two scenarios depend to a great extent on hydrological forcing (e.g., return interval of the events) and on the ecological and hydraulic characteristics of the vegetation (e.g., growth rate or vegetation-induced roughness).

Size and age distribution. Miyamoto and Kimura (2016) have recently proposed a stochastic approach to assess the number of individuals and their corresponding size in a tree population along a river transect. The tree population dynamics were studied by focusing on the distribution density of the trees $n(D,t)$ (Figure 4*a*) over a unit area of the floodplain, where t is the time and D is the trunk diameter (used to characterize the tree size). As time passes, this distribution density is modified by three processes: (i) an increment in the tree size (term J in Figure 4*a*); (ii) the recruitment of new trees (term $J_{\min}$); and (iii) the death of some trees (term M). A shot noise model was used to generate the time-series of the daily mean flow discharge for a 100 year period. A one-dimensional momentum conservation equation, which includes the roughness induced by trees, was introduced to evaluate the hydrological characteristics that affect the recruitment, growth and death processes. In order to work with a realistic topography, the floodplain of a reach of the Kako River (Japan) was considered as a test site. Finally, 2000 realizations with different hydrograms randomly generated by Monte Carlo techniques were run in order to consider the hydrological stochasticity. The main result of the model was the size distribution of the tree population resulting from each single realization (see Figure 4*b*). It was found that a reduction in the flood disturbances promoted an increment in the number of trees and in the tree size. At the same time, an increment in the variability of the trunk diameter was also observed. Moreover, an increment in the flood disturbances led to a significant reduction in the number of trees, and only trees with large trunks were able to resist the new hydrological conditions.

4.4. Successional models

Approach. Over the last few years, several studies have demonstrated that riparian ecosystems are characterized by complex succession and retrogression processes, which are also known as vegetation recycle (Tockner et al., 2000; Naiman et al., 2005; Formann et al., 2014). During the succession phase, the vegetation types replace each other in a sequence that culminates in a stable vegetation configuration (Johnson and Miyanishi, 2007). In contrast, environmental stresses change the community structure in a reverse succession, and give rise to the so-called retrogression process. The outcome of this recycle process depends to a great extent on a number of environmental factors (e.g., nutrient availability, substrate properties, mois-

ture conditions, climate characteristics, etc.) and on the type and level of the external disturbances. In this framework, it is clear that the understanding and the quantification of the role of water stage fluctuations in driving a succession or a retrogression is a key point, and several models have been developed for this purpose (Benjankar et al., 2011, 2012; Egger et al., 2012; García-Arias et al., 2013; Rivaes et al., 2014; Benjankar et al., 2016; García-Arias and Francés, 2016). These models explicitly describe all the succession phases of vegetation, from the colonization of bare surfaces to the development of a mature hardwood forest (see Table 5, where a synthesis of the model and a comparison with other approaches are reported).

CASiMIR. The Computer Aided Simulation Model for Instream Flow Requirements (Benjankar et al., 2011) is a grid-based numerical model that simulates the vegetation dynamics at the reach scale and at the annual timescale. The dynamics of vegetation depends on the type of vegetation that is present in a grid cell. Five types of vegetation cover can be included in the model: gravel sand bar, pioneer vegetation, a cottonwood series, a reed series, a wetland series (see colored box in Figure 5*a*). Cottonwood, reed and wetland covers have been defined as "series" because these types of cover could undergo different growth stages (e.g., a cottonwood forest is composed of four stages, see the brown box in Figure 5*a*). Different herbaceous and woodland species have been considered in the vegetation types or phases described in the model. For example, the "Young cottonwood forest" stage in the cottonwood series (YCF in Figure 5*a*) represents a cover composed by any of the following species: Black cottonwood, Great plains cottonwood, Common snow-berry, Red osier dogwood, Red top, Quack grass, and Reed canary grass. A generic vegetation cover can undergo two possible evolution scenarios. The first scenario is called "succession"; it occurs when the hydrological conditions are favorable and entails that the vegetation will grow to the successive maturation cover stage (the blue dashed arrows in Figure 5*a*). For example, a "Young cottonwood forest" evolves into an "Old cottonwood forest" in the cottonwood series. The second scenario corresponds to "retrogression"; it takes place during harsh hydrological conditions and entails a degradation to less vegetated cover states (the red continuous arrows in Figure 5*a*). For example, a "Young cottonwood forest" degrades to a "gravel sand bar".

The model is based on the Boolean logic, in which the succession, or retrogression, of vegetation depends on the crossing of suitable thresholds. The model considers different hydrological parameters as input. These parameters are evaluated in all the cells of the grid starting from the hydrograph at the reach and the floodplain topography. The model output is the cell-specific type of vegetation (see Figure 5*b*).

The core of CASiMIR is the dynamic module that evaluates the cell-specific vegetation as a function of the initial vegetation (i.e., the previous year's vegetation) and the hydrological parameters. The dynamic module is divided

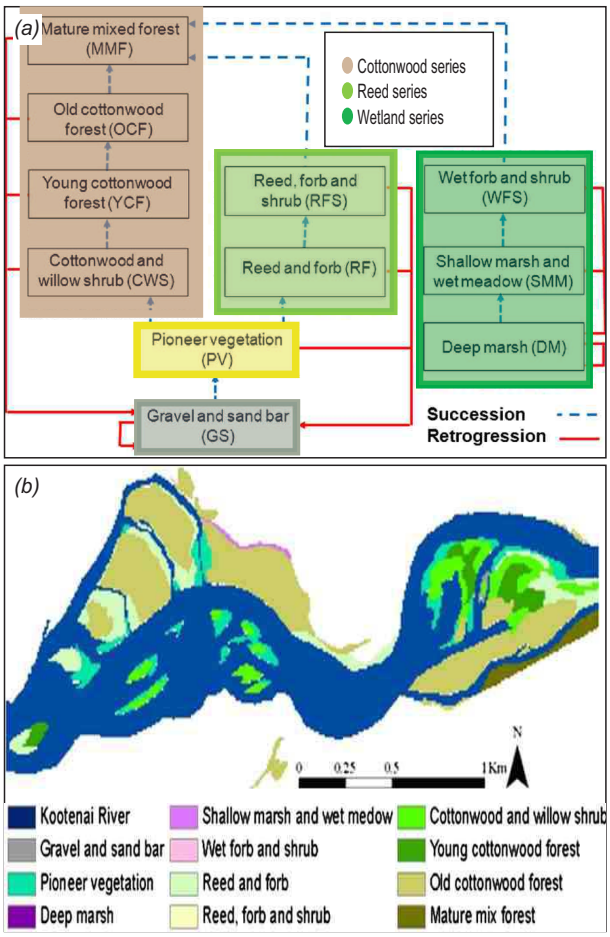

Figure 5: (*a*) Succession and retrogression pattern of vegetation (see text for description). (*b*) Illustrative vegetation maps of the Kootenai River (Idaho, USA) obtained from CASiMIR. The figures are taken from Benjankar et al. (2011).

into three sub-modules. (i) The recruitment sub-module delimits the zones that are suitable for the recruitment of cottonwood and willow shrub, reed and forbs, or deep marshes. This sub-module predicts the vegetation type mainly on the basis of the cell elevations above the river base flow. (ii) The succession sub-module relies on hard thresholds. If the maximum shear stress and the flood duration experienced in a cell over a year are both below the retrogression threshold, vegetation takes a step toward the maturation stage. When the cell age exceeds a maximum, the vegetation enters the following stage (see Figure 5*a*). (iii) The retrogression sub-module evaluates whether the maximum shear stress exceeds the retrogression threshold, and the vegetated plot turns into a bare bar.

Effect of damming and hydraulic works. CASiMIR has proved to be a useful tool to understand the role of water stage fluctuations on the dynamics of vegetation. Benjankar et al. (2012) applied CASiMIR to study the effect of damming and hydraulic works in the Kootenai River (Idaho, USA). Three different scenarios were considered. The "Historic" scenario represented the pristine condition. The "Pre-dam" scenario considered the network of levees that modified the Kootenai floodplain, while the river regime was considered unaltered. Finally, the "Post-dam" scenario considered topographic modifications of the floodplain and that the river regime had been altered by the Libby Dam. The analyses were particularly significant because it was possible to quantify the effects of different human alterations (topographic and hydrological) with respect to the pristine (Historic) scenario (e.g., the colonizing vegetation significantly decreased in the post-dam scenario and reed and grassland always became the dominant vegetation in altered river systems).

Effect of climate change on the riparian habitat. Rivaes et al. (2013) and García-Arias et al. (2013) applied the CASiMIR to three European rivers. In order to consider the main hydrological regimes that occur throughout Europe (nival, pluvial and nivo-pluvial regimes) three hydrologically different case studies were considered. More recently, they studied on the same sites the effect of climate change on the riparian habitat (Rivaes et al., 2014).

The hydrological alterations induced by climate changes were modeled as follows. First, climate change scenarios were selected from the climatological analysis of Nakicenovik and Swart (2000). Second, precipitation scenarios were determined, in accordance with the Global and Regional Circulation Models (Stanzel and Nachtnebel, 2010). Finally, the hydrological regimes at the considered reaches were obtained by means of precipitation-runoff models. A common alteration that was observed for all the hydrological regimes is that climate changes threaten the young and water-dependent vegetation phases the most. However, other alterations in the vegetation dynamics were found to depended to a great extent on the considered hydrological regime. This demonstrates that climate changes exert an hydrological-regime-specific pressure on the riparian habitat. In the nival regime, a reduction in the magnitude of the summer floods that promoted the succession of vegetation was observed. In the pluvial regime, the severe reduction in the discharge from spring to fall induced retrogression in large zones near the river. Finally, in the nivo-pluvial regime, the decreased discharge throughout the hydrological year seriously threatened some succession phases, with the risk of endangering the survivability of the vegetation populations in the long term.

Riparian Vegetation Dynamic Model. The basic concepts of the successional model for the vegetation dynamics adopted in CASiMIR have recently been expanded in the Riparian Vegetation Dynamic Model (RVDM) by García-Arias and Francés (2016). This model is based on the succession/retrogression scheme used in CASiMIR, but a number of key improvements have been introduced. First, the vegetation status in CASiMIR is only based on the successional stage that occurs in a grid cell. In RVDM, this information is completed with the vegetation biomass. In this way, cells at the same stage, but with different biomass, can be differentiated. Second, the succession toward more mature cover stages is only based on the cover age in CASiMIR. In RVDM, the succession also depends on the biomass (i.e., a sufficiently high biomass has to be reached before the successive successional cover stage can be attained). Third, the retrogression to less vegetated covers in CASiMIR is only based on the exceeding of critical thresholds (shear stress and flood duration). When thresholds are not exceeded, full growth of vegetation is considered. This is quite a heavy assumption, as hydrological stresses exert damage to vegetation over a gradient that ranges from full removal to no effect. In RVDM, partial damage, due to shear stress, drought and anoxia, can be evaluated. In this way, a more realistic modeling is obtained.

The evolution of vegetation is evaluated on a daily time-scale and with a fine spatial resolution (0.5-2m). Four modules are adopted to evaluate the daily biomass evolution and thus the possible succession/retrogression to different covers. The first module evaluates the local substrate moisture. To this aim, the evapo-transpiration model based on the work by García-Arias et al. (2014) is adopted. The second module evaluates the loss of biomass due to: (i) mechanical damage induced by floods (the biomass loss depends on the local shear stress), (ii) anoxia caused by flooding, and (iii) wilt caused by droughts (the biomass loss depends on the local substrate moisture). The third module models the recruitment, growth and succession/retrogression of vegetation. The recruitment considers the presence and germination of seeds, and the seedling dynamics. Vegetation growth is evaluated in terms of biomass increase, and depends on the local substrate moisture and on the availability of light. Succession to the successive cover stages of the series occurs when a threshold age and minimum biomass are exceeded. The last module considers competition between different riparian succession series and between riparian and the terrestrial vegetation. RVDM has been calibrated and tested

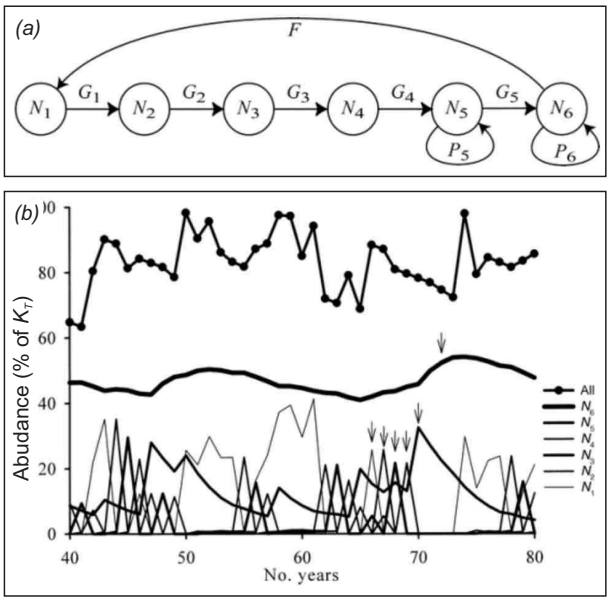

Figure 6: (a) Life cycle considered in the cottonwood structured population model. N_1 are seedlings, $N_2 - N_4$ are 2−4 year-old individuals, N_5 are sub-adult trees, and N_6 are reproductive adults. (b) Example of the individual abundance of cottonwood stages over years. The abundance is expressed as the percentage of K_T, the total area of the floodplain suitable for cottonwood growth. The figures are taken from Lytle and Merritt (2004).

along a reach of the Mijares River (Spain), and very satisfactory results have been obtained.

4.5. Structured population models

It has widely been observed that the age of cottonwood stands (or other riparian softwood trees) varies considerably along a river transect (Stromberg et al., 1997; Karrenberg et al., 2002). This wide variety of ages is mainly induced by the occurrence of river disturbances, which favor the colonization of new plants to the detriment of older stages of established forests. Considering the age of a riparian vegetation patch is important for a number of reasons. First, patches of different age show different resistance to hydrological forcing (the older the vegetation, the higher the resistance to floods and droughts). Second, patches of different age play different ecological roles (e.g., young seedlings are crucial for site colonization while adults tree are required for the production of seeds). In order to understand the role of the hydrological regimes (and possible alterations) in shaping softwood forests, it is crucial to consider the age-specific response of vegetation to disturbances and their ecological role. In this framework, structured population models are key tools.

Approach. The variables in structured population models are the abundance (number of individuals) of the distinct age classes in which the whole population is classified. In turn, environmental and ecological factors drive the transition to older stages and the survivability within a stage. It should be mentioned that considering the different ecological roles of different age classes is crucial to correctly model the survival or extinction of a population. In the field of riparian vegetation, Lytle and Merritt (2004) developed a structured population model for cottonwood (see the synthesis of the model and the comparison with other approaches in Table 5). The main point of their approach is that trees with different ages experience different growth and mortality rates. The dynamics of seedlings, second to fourth-year individuals, non-reproductive juveniles, and reproductive adults were considered individually in their model (see Figure 6a). The model was written as $\mathbf{n}(t+1) = \mathbf{A}(t)\mathbf{n}(t)$, where $\mathbf{n}(t)$ is a vector that lists the abundance of the six stages, and $\mathbf{A}(t)$ is the matrix that models the transitions between stages. Simulations are run starting from the initial population $\mathbf{n}(0)$, and considering discrete annual time steps. Stages 1 to 5 are characterized by the probability G_i of growing to the following stage (see Figure 6a). Stages 5 and 6 have the probability P_i of remaining in the current stage. Finally, stage 6 could generate new seedlings (stage 1 individuals) according to the fecundity rate F. All these rates, that is, G_i, P_i and F are assumed to depend on the hydrological conditions experienced by the river reach over the year. Years are scored as flood, drought or growth year as a function of the spring flood flow rate. A different set of G_i, P_i and F is applied for each hydrological-type of year. It follows that the transition matrix $\mathbf{A}(t)$ stochastically varies year to year, according to the hydrological-type of that year. The hydrological scenarios considered were derived from a real 83 year long discharge dataset.

Time-series of the individual abundance. A typical result of the model simulation is the time-series of the individual abundance (see Figure 6b). The key results were the extreme variations observed in seedling abundance and establishment, and the more regular behavior of the older stage classes. Additionally, it was observed that the greatest deviations from dynamic equilibrium (e.g., see the low abundance at 60 years in Figure 6b) were induced by sequences of multiple years with harsh hydrological conditions. This seems to confirm some field evidence (Auble and Scott, 1998) according to which sequences of years that exhibit specific hydrological characteristics are more important than single year events.

Role of the hydrological regime. Lytle and Merritt (2004) considered altered hydrological regimes. In particular, they altered the flood frequency and the autocorrelation between hydrological-type of years. They found that: (i) the natural flow regime induced the greatest adult population; (ii) a reduction of the flood frequency (e.g., due to flow regulation) entailed a significant decrease in population size, coupled with a strong increment in population variability. It has often been found that the high variability and low population size led to extinction of the population; and (iii) an increment of the flood frequency induced a reduction in the population size and variability. The auto-correlation between the hydrological-type of year was considered zero in the unaltered regime. This means that the occurrence probability of one type of

hydrological-year (i.e., flood, drought or growth year) is not linked to the hydrological-type of the previous year. Adding auto-correlation between the hydrological-type of years entails the occurrence of a multi-year-sequence of the same hydrological-type being more probable. It has been found that the size of the adult population reduced, when this auto-correlation was added. According to Lytle and Merritt (2004), this happened because the probability of a sequence of unfavorable years increases with the autocorrelation between years.

5. Conclusions

Over the last few decades, many field works have elucidated the importance of river flow fluctuations on the dynamics of riparian vegetation. River flow fluctuations have a direct effect on the plant communities, determining the recruitment-removal of new-old trees, the survival of seedlings, and the growth rate of adult trees. Moreover, they trigger morphological processes that have an important effect on vegetation. The main aim of these field works was to link the intensity of the biological and biomorphological processes to the hydrological characteristics of rivers. However, this is a very complex task and it is made particularly hard by two difficulties.

One difficulty concerns the selection of a sufficient number of hydrological indexes to describe the involved phenomena completely. In fact, key RFF-induced feedbacks may not be detected when the measures of hydrological variability are combined in too few indexes (Puckridge et al., 1998). Therefore, future researches should be dedicated to verifying whether the five hydrological parameters that are considered in studies about riparian vegetation are sufficient to fully characterize vegetation-RFF relations.

A further challenge is that the morphological evolution of river beds and vegetation dynamics can take place at similar temporal scales (Bendix and Hupp, 2000; Ye et al., 2013). Hence, the elevation of a vegetated plot is not constant throughout the life-span of the vegetation. However, hydrological parameters depend to a great extent on the plot elevation. Thus, the quantification of the processes that affect vegetation and the relation between these processes and the plot-specific hydrological parameters should consider this variability of the plot elevation. In this context, two complementary approaches have recently emerged. The first approach (e.g., Pasquale et al., 2014) entails the effect of water stage fluctuations being quantified at time-scales during which the bed elevation can be considered constant. The second approach (e.g., Wang et al., 2016) calls for the quantification of the feedback between modifications of the bed morphology and alterations of the vegetation cover. Through the combined use of these approaches, it may be possible to obtain a comprehensive knowledge of vegetation response to the hydrological forcing.

From a modeling point of view, the complexity of the adopted approaches is constantly growing: an increasing number of RFF-induced processes are described in a mechanistic way (e.g., García-Arias and Francés, 2016), and accurate and realistic topographies are adopted as case studies (e.g., Benjankar et al., 2014; García-Arias and Francés, 2016). The drawback of these refined models is that the investigation of the role of river flow stochasticity requires a great number of long-lasting numerical simulations (Monte Carlo approach, see Miyamoto and Kimura, 2016). Since this approach is usually not implemented, the variability of the vegetation dynamics induced by flow stochasticity is lost. As a result, it is difficult to generalize the results by disentangling how stochasticity works in the riparian environment and which phenomena stochasticity can induce.

In our opinion, the great challenge of the next few years will be to properly consider flow stochasticity in the framework of existing mechanistic models that describe vegetation dynamics and riparian species succession. Moreover, more efforts should be made to focus on all the relevant measures of hydrological variability (*sensu* Puckridge et al., 1998) to explore, recognize and catch disturbance induced phenomena in the riparian environment.

Acknowledgments

The Authors are grateful to the Editors for the invitation to write this review.

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