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# The biogeomorphological life cycle of poplars during the fluvial biogeomorphological succession: a special focus on *Populus nigra* L.

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**ABSTRACT:** Riverine ecosystems are recurrently rejuvenated during destructive flood events and vegetation succession starts again. Poplars (i.e. species from *Populus* genera) respond to hydrogeomorphological constraints, but, in turn, also influence these processes. Thus, poplar development on bare mineral substrates is not exclusively a one-way vegetative process. Reciprocal interactions and adjustments between poplar species and sediment dynamics during their life cycle lead to the emergence of biogeomorphological entities within the fluvial corridor, such as vegetated islands, benches and floodplains. Based on a review of geomorphological, biological and ecological literature, we have identified and described the co-constructing processes between riparian poplars and their fluvial environment. We have explored the possibility that the modification of the hydrogeomorphological environment exerted, in particular, by the European black poplar (*Populus nigra* L.), increases its fitness and thus results in positive niche construction. We focus on the fundamental phases of dispersal, recruitment and establishment until sexual maturity of *P. nigra* by describing the hierarchy of interactions and the pattern of feedbacks between biotic and abiotic components. We explicitly relate the biological life cycle of *P. nigra* to the fluvial biogeomorphic succession model by referring to the 'biogeomorphological life cycle' of *P. nigra*. Finally, we propose new research perspectives based on this theoretical framework.

**KEYWORDS:** biogeomorphology; biogeomorphological life cycle; fluvial biogeomorphic succession model; abiotic-biotic feedback; engineer species; Salicaceae; evolutionary geomorphology

## Introduction

In geomorphology and ecology, many research projects related to the role of organisms as geomorphological agents at the Earth surface have been carried out without an established link between the two disciplines. However, disciplinary concepts can help to establish an interdisciplinary understanding of functional connections between organisms and geomorphic forms and processes, as for example the concept of 'ecosystem engineers' developed in ecology. According to Jones *et al.* (1994), an engineer species is defined as a species that exerts a strong control over ecosystem function by way of creating or significantly modifying the habitat.

It is widely recognized that certain modifications induced by engineer organisms within their physicochemical environment provide positive feedback to ecosystem function (Wright and Jones, 2006; Fisher *et al.*, 2007; Hastings *et al.*, 2007). An illustrative example is the North American beaver (*Castor canadensis* Kuhl, 1820), which builds dams and modulates matter and energy fluxes into rivers (Dawkins, 1982; Naiman *et al.*, 1988; Gurnell, 1998; Odling-Smee *et al.*, 2003; Butler and Malanson, 2005), leading it to be defined as a 'keystone species' (*sensu* Paine, 1995) that controls riparian ecosystem structure and function (Wright, 2009). Jones *et al.* (2010) suggested that modifications of the physical environment by engineer organisms, if sufficiently durable (such as in the case

of the ones enhanced by *C. canadensis*), change selective pressures within the ecosystem (see also Wright *et al.*, 2012). It has even been hypothesized by Dawkins (1982) that beaver constructions, and related modifications in selective pressures, enhance their own fitness by selecting the most efficient engineer-alleles promoting niche construction (NC). Odling-Smee *et al.* (2003) defined such feedback as 'positive NC', synonymous to the notion of an 'extended phenotype' previously proposed by Dawkins (1982). Niche construction thus is a specific case of ecosystem engineering referring to the situation when selective pressures for the engineer species or others species in the ecosystem is modified through the creation or the modification of the habitat. By definition, according to Odling-Smee *et al.* (2003) NC operates with an evolutionary response within the biologically-modified ecosystem. Positive niche construction must be considered as a particular type of NC where the fitness of the ecosystem engineer is improved by the modification of the habitat.

Riparian plants also drastically modify their hydrogeomorphological environment through their interaction with water and sediment flow during floods (Corenblit *et al.*, 2009b; Gurnell, 2013). Over millions of years, aquatic and riparian plant species have developed efficient traits increasing their fitness in a fluvial environment (Lytle and Poff, 2004; Nakamura *et al.*, 2007; Nakamura and Inahara, 2007; Bornette *et al.*, 2008). Thus, the chances of riparian plants establishing and interacting with hydrogeomorphological processes within fluvial corridors have an evolutionary explanation (Niklas, 1997). The responses of riparian plants to flood events were affected, in the long-term, by past exposure to comparable hydrogeomorphological events. Specific life history, physiological, morphological and biomechanical adaptations improved their resistance and resilience within a disturbed, unstable and fluctuating environment (Lytle, 2001). As a consequence, certain morphological and biomechanical traits became 'active' from a geomorphological point of view. That is, through their ability to interfere directly with water flow and sediment dynamics during floods, those traits allowed plants to modify certain properties of the geomorphological environment, mainly by trapping and stabilizing sediment, organic matter, diaspores and nutrients (Osterkamp and Hupp, 1984, 2010; Hupp and Osterkamp, 1996; Tabacchi *et al.*, 2000; O'Hare *et al.*, 2012). It was also demonstrated that the evolution of plant traits, such as deep rooting systems and tall, lignified aerial structures, led to drastic changes in fluvial structure and dynamics during the Paleozoic period (Gibling and Davies, 2012).

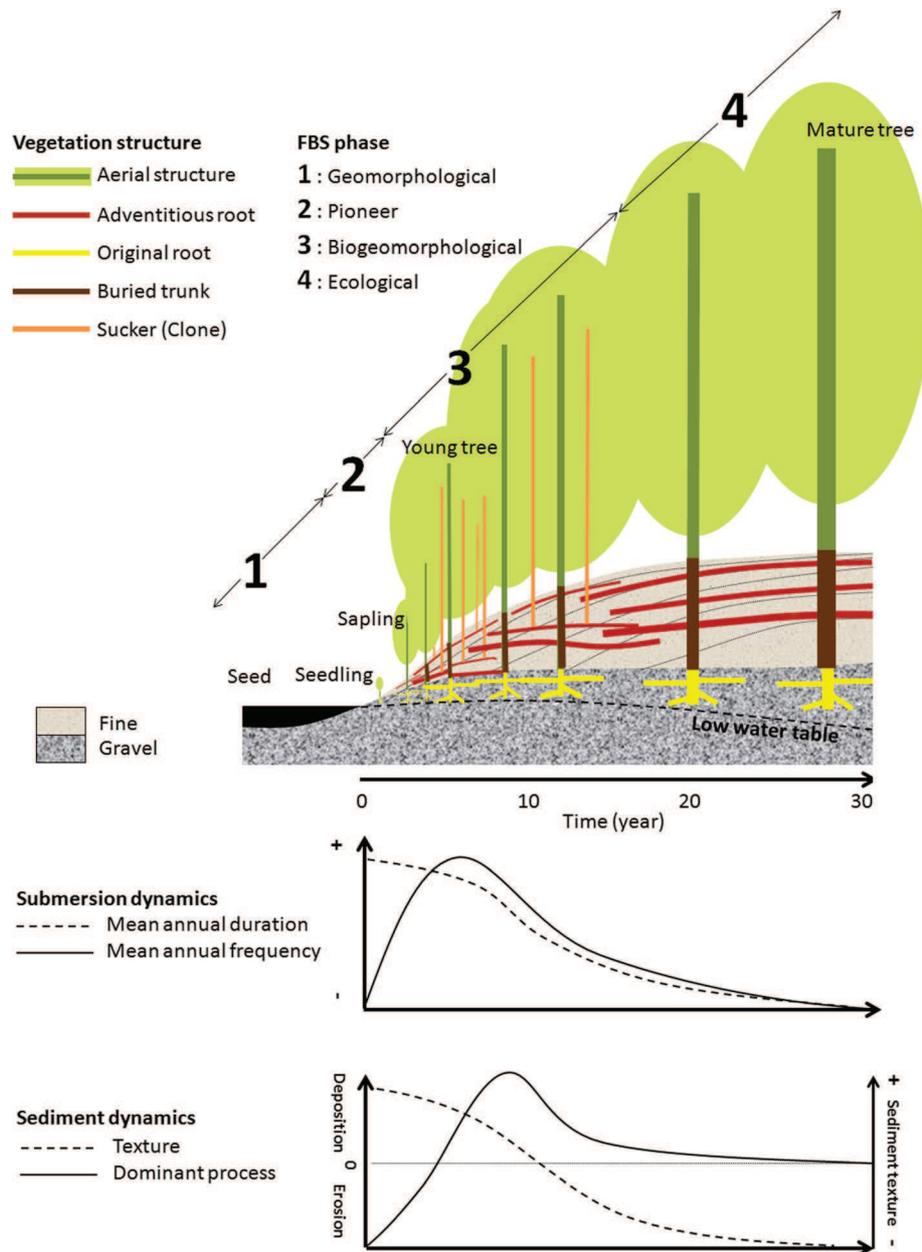
Many riparian plant species from temperate fluvial corridors have been identified as engineer species driving hydrogeomorphological processes, e.g. *Tamarix ramosissima* L., *Elaeagnus angustifolia* L., *Alnus incana* (L.) Moench, *Salix* spp. and *Populus* spp. (reviewed by Gurnell, 2013). Corenblit *et al.* (2009a) discussed the possibility of a form of specific evolutionary feedback that enhances riparian plant adaptations, not only to the original (unmodified) hydrogeomorphological conditions within river systems, but also to their own modifications of the hydrogeomorphological environment. The process of matter and resource accumulations within patches of pioneer vegetation was related to positive biogeomorphological feedbacks, providing optimized habitat conditions and resource allocation for engineer and co-occurring species (Edwards *et al.*, 1999; Gurnell *et al.*, 2005). Corenblit *et al.* (2009a) and Francis *et al.* (2009) suggested that engineered vegetated fluvial islands, benches and floodplains emerging from the positive feedback could essentially be extended expressions of genes (i.e. extended phenotypes) of the engineer organisms. Several field observations suggested that such biogeomorphological entities maintain and 'replicate' themselves within

the fluvial corridor (Edwards *et al.*, 1999; Gurnell *et al.*, 2001). The question of whether the emergence of biogeomorphological structures such as fluvial islands and floodplains can be related to a positive NC (*sensu* Odling-Smee *et al.*, 2003) is paramount to discerning whether these biogeomorphological entities do have an evolutionary basis (Corenblit *et al.*, 2011).

We suggest that the consideration of this positive biogeomorphological feedback between an engineer plant and its physical environment requires revisiting its life cycle. Strictly speaking, the life cycle of a plant corresponds to its course of development through a series of different stages, from the time of inception to death. A riparian angiosperm life cycle begins with a seed that, in adequate hydrogeomorphological conditions, will germinate and produce a seedling that will grow to a mature plant over a few years. The mature plant will then eventually reproduce sexually, forming new seeds, and the next life cycle will start in the form of a new plant. In a fluvial context, specific ranges of hydrogeomorphological conditions control the successive phases of the life cycle of some ligneous plants, from seed release, germination and growth to sexual maturity (Braatne *et al.*, 1996). The objective of revisiting the life cycle of riparian species, especially engineer plants, is to relate their biological sequence of development to hydrogeomorphological conditions (such as sediment texture, deposition rate, relative elevation above the water surface and related exposure to submersion), since they are modifiable by the engineer plant during its life cycle (Figure 1).

Species related to the *Populus* (Salicaceae) genera (e.g. within the *Aigeiros* section: the black poplar *Populus nigra* L. in Europe, the Eastern cottonwood *P. deltoids* (Bartr.) Marsh. and Fremont cottonwood *P. fremontii* S. Wats. in respectively eastern and western North America; within the *Tacamahaca* section: the Narrowleaf cottonwood *P. angustifolia* James in central North America and the Ontario Balsam poplar *P. balsamifera* L. in northern North America) are commonly known within riparian ecosystems as 'poplar'. The term 'cottonwood' is used in North America for poplars from the *Aigeiros* section. Poplars are widely distributed throughout the northern hemisphere. They have been broadly studied in regard to their responses (e.g. seed dispersion and germination, seedling and sapling survival and growth) to hydrogeomorphological patterns and constraints (Johnson *et al.*, 1976; Stromberg and Patten, 1991; Shafroth *et al.*, 1995; van Splunder *et al.*, 1995; Rood and Mahoney, 1996; Scott *et al.*, 1997, 1999; Mahoney and Rood, 1998; Cooper *et al.*, 2003; Francis *et al.*, 2005; Lambs *et al.*, 2006; Stella and Battles, 2010), their effects on sediment and fluvial landform dynamics (Gurnell *et al.*, 2001; Rodrigues *et al.*, 2007; Corenblit *et al.*, 2009b) and their interactions with microorganisms such as nitrogen-fixing bacteria (Doty *et al.*, 2005) and mycorrhizal fungi (Beauchamp *et al.*, 2006).

This article is based on a literature review and aims to link the biological development of riparian poplars to the modifications they induce in their hydrogeomorphological environment. We have illustrated our theory with examples, mostly related to the European black poplar (*P. nigra*), which was identified by Gurnell and Petts (2006) as a keystone ecosystem engineer shaping western European fluvial systems. Here we focus on riparian poplars even though our theory and conceptual model may probably be transferred to a much wider range of riparian ligneous species from different genera, e.g. *Alnus*, *Salix* and *Tamarix* in temperate regions. We hypothesize about the existence of a specific biogeomorphological feedback mechanism between fine sediment deposition, landform construction and *P. nigra* development within fluvial corridors. That is, we suggest that the modification of the geomorphological environment by *P. nigra* may be functional



**Figure 1.** Spatiotemporal sequence of co-development between aerial and underground *P. nigra* structures and the main hydrogeomorphological parameters related to submersion and sediment dynamics. The different phases of the fluvial biogeomorphologic succession (FBS) are indicated in the figure. This figure is available in colour online at [wileyonlinelibrary.com/journal/espl](http://wileyonlinelibrary.com/journal/espl)

from a biological point of view (Corenblit *et al.*, 2010a). We discuss the possibility that these functional hydrogeomorphological modifications could be a form of positive niche construction (NC) improving the plant's chance to survive, reach sexual maturity and produce a maximum of viable seeds within a stabilized environment. All the successive conditions necessary to reach sexual maturity in an optimized niche are identified and articulated within the framework of the fluvial biogeomorphologic succession (FBS) model proposed earlier by Corenblit *et al.* (2007). Finally, research perspectives are proposed for testing the hypothesis of a positive NC by *P. nigra* and associated eco-evolutionary dynamics.

## ***Populus nigra*: Life History and Ecology**

### **Spatial distribution**

*Populus nigra* belongs to the *Populus* genus, which probably evolved in fluvial corridors at least 58 M years ago

(Eckenwalder, 1996). Its life history and ecology are thus specifically and closely related to river patterns and processes (Lytle, 2001; Karrenberg *et al.*, 2002). The spatial pattern of *P. nigra* fluctuated during the Quaternary in response to successive ice ages (Bennett *et al.*, 1991). Cottrell *et al.* (2005) showed that during the last ice age, between 100 000 and 10 000 BP, populations of *P. nigra* remained in southern Spain, southern Italy and the Balkans. The species recolonized North and Central European fluvial corridors during the Holocene. *Populus nigra*, and related *Populus* spp. from the *Aigeiros* or the *Tacamahaca* sections, are nowadays distributed within fluvial corridors in lowland, piedmont and mountainous zones of the northern hemisphere from North Africa and Ireland in the west, to Russia and China in the east (Zsuffa, 1974).

However, poplar and cottonwood populations have suffered greatly in the last 50 years due to increased human impacts within river catchments and fluvial corridors, and have almost become extinct in the north of America and Europe (Braatne *et al.*, 1996; Cottrell *et al.*, 2002; Muller *et al.*, 2002). A major

cause of this extinction is flow regulation and river channelization which drastically affect the critical phase of seedling recruitment (Mahoney and Rood, 1991). *Populus nigra* has thus become a target species for conservation and restoration (Lefèvre *et al.*, 1998; Villar and Forestier, 2006), and during the last two decades, several scientific projects (e.g. FLOBAR 2 (Floodplain Bioiversity And Restoration) and projects originating from the EUFORGEN program (EUropean FORest GENetic)) have aimed to better understand the current ecological and genetic dynamics of *P. nigra* and to propose targeted conservation strategies (Barsoum, 2001; Hughes and Rood, 2003; Rathmacher *et al.*, 2010).

## Specific adaptations to the fluvial environment

*Populus nigra* has evolved to take advantage of hydrogeomorphological flows within fluvial corridors through multiple adaptations related to these disturbances (Braatne *et al.*, 1996). Its seed morphology (extremely small with a readily detached coma of cottony water-repellent hairs) and biomechanics (strong buoyancy related to the hairs and a weight <0.8 mg; Karrenberg and Suter, 2003) optimize transportation by wind and water. Seeds are very abundant (>25 million per tree and year; Braatne *et al.*, 1996), non-dormant and short-lived, with disturbance-dependant germination on suitable, bare moist surfaces (Seiwa *et al.*, 2008). Its life cycle, from pollination, seed formation, dispersal and germination or vegetative propagation through mature growth is well synchronized with the natural flow regime, notably the frequency and timing of periodic and repeated droughts and floods (Hupp, 1992; Iwasa and Levin, 1995; Braatne *et al.*, 1996; Mahoney and Rood, 1998; Lytle and Poff, 2004; Stella *et al.*, 2006). Rapid germination and root elongation of *P. nigra* reduces drought mortality during the first summer and increases resistance to up-rooting during winter floods (van Splunder *et al.*, 1995, 1996; Barsoum and Hughes, 1998; Guillois *et al.*, 2002; Francis *et al.*, 2005; Francis and Gurnell, 2006). It is fast-growing and opportunistic with a good tolerance to submersion, sediment burial and high temperatures in summer, especially on bare alluvial bars (Chamaillard, 2011).

*Populus nigra* has a high phenotypic plasticity encompassing flood-induced changes and allocation of biomass to different parts of the plant according to prolonged submersions, mechanical stress, droughts or sediment burial. It is capable of vegetative propagation with root-borne sucker shoots (soboles) and it can regenerate from fragments after breakage as an alternative to sexual reproduction in highly dynamic hydrogeomorphic conditions (Barsoum *et al.*, 2004; Francis *et al.*, 2004). The size, shape and biomechanical properties of its root and aerial structures are also well adapted to cope with hydraulic constraints (Karrenberg *et al.*, 2003; Lytle and Poff, 2004).

Furthermore, a high genotypic variability within *P. nigra* populations, and the ability to hybridize with other poplar species (e.g. *P. x canadensis* (*P. nigra* x *P. deltoides*); *P. x inopina* (*P. nigra* x *P. fremontii*)) with alternative life history traits, also contribute to increasing its ability to successfully become established in a highly fluctuating environment (Legionnet and Lefèvre, 1996). It has a high level of adaptive genetic variation within and among populations. Farmer (1996) noted that genetic variation of phenological traits occurs in different fluvial systems with different climatic and hydrological regimes. Tradeoffs between the timing and length of the growing season and the risk of frost, drought, and submersion damage led to different patterns of adaptive differentiation in *Populus* populations (Smit, 1988; Farmer, 1996). Thus, *P. nigra* genotypes originating from a given fluvial system may have a higher

fitness in that system than genotypes originating from other fluvial systems with different hydrogeomorphological conditions (Kawecki and Ebert, 2004).

## Combination of life history strategies

Under natural dynamic conditions (i.e. unchannelized and unregulated), the fluvial corridor is comprised of a shifting mosaic of different geomorphological patches subjected to contrasting habitat conditions, submersion frequencies and sediment scouring or depositional patterns (Pickett and White, 1985; Steiger and Gurnell, 2003; Bornette *et al.*, 2008). The stability of the fluvial environment differs in space and in time, and the place where *P. nigra* reaches maturity is generally much more stable than the place where it begins its life cycle, which is frequently disturbed during annual flood events.

*Populus nigra* combines ruderal 'r' and competitive 'K' traits and can express both r and K phenotypes according to its development stage and environmental constraints (Braatne *et al.*, 1996). Seed dispersal and seedling recruitment of *P. nigra* are based on an opportunistic r strategy. This strategy is well known to improve the chance of germination and survival in a disturbed and heterogeneous environment. It is a pioneer heliophilous species and its recruitment is closely related to fluvial dynamics and seed rain on bare alluvial bars and open abandoned river channels in full sun (Braatne *et al.*, 1996; Rood *et al.*, 2007; Stella *et al.*, 2011). Seedling recruitment locations are closely associated spatially with fine, moist sediment at the immediate margins of the low flow channel and vertically with the water table (Figure 1).

The physiology, morphology and biomechanics of *P. nigra* are adapted to resist hydraulic forces and prolonged submersions. Because of its high capacity to resist destruction during flood events, *P. nigra* generally enhances sediment and resource trapping and storage in its immediate vicinity during the first 10 years of its life cycle (Edwards *et al.*, 1999; Francis *et al.*, 2009). Matter accretion and vegetation growth, in turn, cause a progressive decrease in the hydrogeomorphic connectivity of the colonized patches, further limiting the risk of destruction during flood events and providing resources for additional root and canopy development. Mature cohorts (>10–15 years old) are generally located on the floodplain and on stabilized islands, which are both disconnected from hydrogeomorphological disturbances associated with annual flood events (González *et al.*, 2010) (Figure 1). Thus, habitat conditions (e.g. elevation in relation to the main channel; submersion frequency, magnitude and timing; sediment texture; supply of fine sediment and organic matter; ground water level) change drastically during the life cycle of *P. nigra*, with a progressive decrease of hydrogeomorphic disturbances. In the absence of external stress due to disturbance factors, Grime (1977) suggested that competition tends to emerge as an alternative strategy. Thus, with the decreasing frequency and magnitude of disturbance promoted by *P. nigra* itself, the role of inter- and intra-specific competition in the fluvial environment increases during the biogeomorphological succession (Corenblit *et al.*, 2007; Bornette *et al.*, 2008), and conversely to short lived opportunistic ruderal herbaceous species, *P. nigra* expresses competitive traits during its life cycle, improving resource acquisition (e.g. long life span, high size of its canopy for access to light, extended roots for access to ground water and nutrients). Because the phenotypic expression of *P. nigra* K traits requires a stabilized environment, these are only expressed during the mature stage of its life history cycle, after *P. nigra* has engineered its stabilized and hydrogeomorphologically disconnected habitat. We suggest that inherited genotypic

variations in engineer plants that have been recurrently exposed over multiple generations to changes in selection pressures, occasioned by the modification in the hydrogeomorphological environment, may explain the development and expression of the *K* traits in the adult stage.

## Key Phases of the *P. nigra* Biogeomorphological Life Cycle (BLC)

The life history of a species consists of a succession of key phases in its life cycle. Natural selection shapes this pattern, optimizing the chances of the organism producing the greatest number of viable seeds. The particularities of the life cycle phases (i.e. dispersal, germination, juvenile development until sexual maturity, reproduction, offspring number, senescence and death) partly depend on the organism's physical environment, which provides resources, dispersal possibilities and at the same time imposes development constraints. However, in the case of engineer species, and in particular in the case of *P. nigra*, life history theory needs to integrate feedback between the biological development sequence of the engineer organism and the environmental changes under its control (Figure 2; Table I).

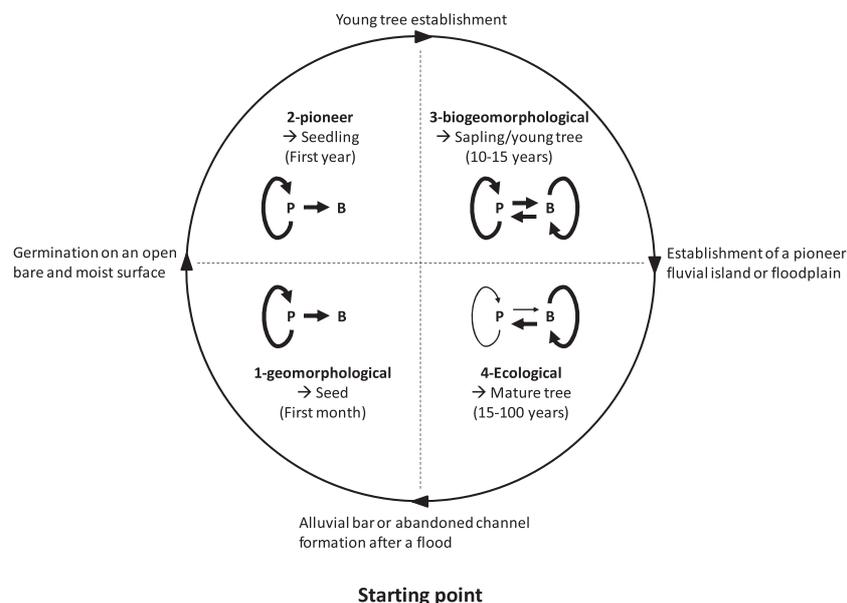
The fluvial biogeomorphologic succession (FBS) model proposed by Corenblit *et al.* (2007) is used here to describe (i) the different development phases of *P. nigra* within its biogeomorphological life cycle, and (ii) the pattern of abiotic-biotic interactions related to each development stage during the FBS. The initial FBS model describes reciprocal linkages between riparian vegetation succession and fluvial landform adjustments. It encompasses four main successive key development phases (i.e. geomorphological, pioneer, biogeomorphological and ecological), each with a specific pattern of interactions between abiotic and biotic components (for a full description see Corenblit *et al.*, 2007).

### The geomorphological phase of the FBS: critical for enhancing *P. nigra* seed dispersal and recruitment on suitable surfaces

During the geomorphological phase of the FBS, the enhancement of the biogeomorphologic life cycle of *P. nigra* requires the

formation of a bare surface or an abandoned channel potentially suitable for seed deposition and germination after a flood. These two kinds of fluvial landforms represent the main recruitment sites for riparian poplars (Stella *et al.*, 2011). Bare surface formation is often preceded by the destruction of vegetation on a pre-existing alluvial bar, by bank erosion and new sediment deposition, or also as a consequence of water recession during an extreme drought lasting some years. The initiation of the biogeomorphological life cycle of *P. nigra* thus depends on hydrogeomorphological (floods) or climatic events, which are not controllable by the plant at the beginning of the cycle. During this stage of the life cycle, the system is primarily driven by physical interactions between water flow and sediments (Figure 3(a)). Floods and associated natural geomorphological patterns of alluvial bar formation, bank erosion and channel avulsion thus remain essential for offering sites suitable for the recruitment of viable populations of this species (Naiman *et al.*, 2008).

During the geomorphological phase of the FBS, *P. nigra* produces seeds that are dispersed by wind and water, and deposited on the alluvial surfaces. The production of seeds by a mature female tree, located on the floodplain or on a stabilized and raised island, is the first step of the BLC of *P. nigra*. As a result of regional adaptations, the formation and release of seeds from the catkin during the geomorphological phase of the FBS is generally attuned to local climatic seasonality and the natural flow regime (Guilloy *et al.*, 2002; Karrenberg *et al.*, 2002; Stella *et al.*, 2006). The duration of seed release also varies according to the climatic context and to species life history (Johnson, 2000; Guilloy *et al.*, 2002). In the northern temperate zone, seed release generally occurs during spring and early summer. The high phenotypic plasticity and genotypic variability of *P. nigra* populations leads to a quasi-continual seed rain over approximately 2 to 2.5 months (Braatne *et al.*, 1996). Guilloy-Froget (2002) suggested that the temporal distribution of seed release may be mesokurtic with a peak located in late spring. For example, in south-western France it occurs from mid-April to mid-July (Guilloy *et al.*, 2002). This release period is timed to follow spring floods that produce bare, moist surfaces (Karrenberg *et al.*, 2002). Guilloy *et al.* (2002) reported 9 weeks of seed release on the River Loire and River Drôme (France) and 12 weeks on the River Garonne (France). Such a period of seed release increases the probability that some of the billions of seeds will meet the suitable 'recruitment box', as defined by Mahoney



**Figure 2.** Biogeomorphological life cycle (BLC) of *P. nigra* during the fluvial biogeomorphologic succession (FBS). The duration and the structure of interactions between physical (P) and biosocial (B) components are indicated for each phase (i.e. geomorphological, pioneer, biogeomorphological and ecological) of the FBS

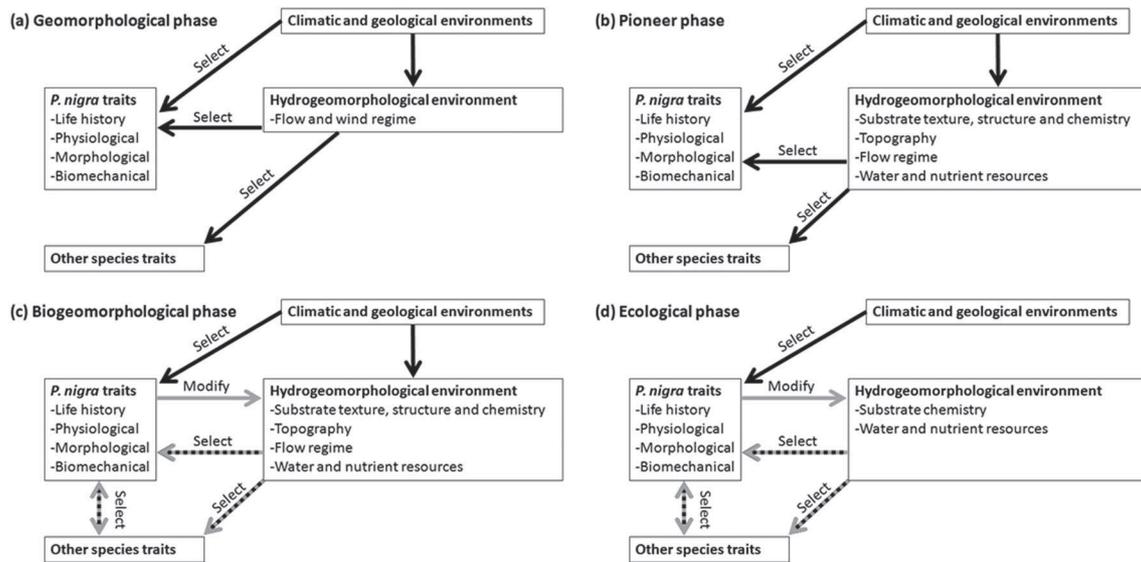
**Table 1.** Biogeomorphological life cycle (BLC) of *Populus nigra* during the fluvial biogeomorphologic succession (FBS). The main processes acting in the biotic compartment are listed chronologically and are related to the main processes co-acting in the hydrogeomorphological (abiotic) compartment for each phase of the FBS (i.e. geomorphological, pioneer, biogeomorphological and ecological)

FBS phase	Duration	<i>P. nigra</i> development stage	Main processes in the biotic compartment	Main related process in the abiotic compartment
Geomorphological	First month	Seed	1. pollination 2. seed formation 3. release 4. dispersal by wind and water 5. deposition	1-3. alluvial bar or abandoned channel formation after a flood 4-5. high flows/flood event
Pioneer	First 2 years	Seedling	6. germination 7. strong vertical elongation of roots according to water table recession (summer survival)/limitation of stem growth	6-7. water table recession in summer/ high flows and flood events in winter (submersion, sediment erosion, transportation and deposition)
Biogeomorphological	From 2 to 10–15 years	Sapling/young tree	8. strong and rapid increase in stem growth rate after the first 2 years 9. development of lateral roots and the first generation of adventitious roots and clonal shoots (suckers) 10. root colonization by ruderal endomycorrhizal fungi (improvement of water and nutrient uptake) 11. potentially roots grafting (improvement of resource uptake at the patch/cohort scale) 12. strong development of adventitious roots and suckers	8. first generation of fine sediment depositions and nutrient accumulations 9. increase of surface roughness and sediment stability 11. increase of sediment stability and nutrient storage 12. maximization of fine sediment, organic matter and nutrient trapping during annual floods/ establishment of a pioneer fluvial island or floodplain/hydrogeomorphological disconnection (reduction of submersion and duration frequency)
Ecological	From 15 to 30–50 years (max of 100 years in certain conditions)	Mature tree	13. sexual maturity 14. loss of numerous suckers/resource allocation to main stems 15. shift from generalist ruderal endomycorrhizal fungi to specialized, competitive ectomycorrhizal fungi (improvement of water and nutrient uptake in a stabilized environment) 16. strong release of organic matter and exudates from roots and canopies 17. senescence and death or destruction during a flood.	14. decrease in surface roughness 16. modification of soil physicochemical properties and micro- and macro-organism assemblages 17. landform remobilization during a large flood or evolution of the riparian community toward hardwood terrestrial formations

and Rood (1998). However, it is the conjunction between multiple fluctuating hydrogeomorphological parameters, and the number, location and height of adult *P. nigra* reproducers that will or will not lead to a suitable recruitment box within a given year and a given area.

Seeds are generally transported by wind, frequently followed by flowing water and floods. Seeds transported by wind can disperse upstream and downstream. The distances that seeds are transported by wind are not well established, but, based on general observations, Braatne *et al.* (1996) suggested that most seeds are deposited within a few hundred meters of the

mother tree. Imbert and Lefèvre (2003) noted on the Drôme River (France), that upstream and downstream migration rates can in some cases be almost symmetrical, allowing wind transport to attenuate the downstream accumulation of gene diversity by flowing water. Conversely, Pospíšková and Šálková (2006) noted a significant spatial genetic pattern according to pollen dispersion distance ranging from 10 to 230 m on the Morava River (Czechoslovakia). Only 20% of the local population originated from relatives growing beyond this distance range. Based on a literature review, Villar (2012) concluded that the spatial genetic structure of *P. nigra* populations within



**Figure 3.** Hierarchy of interactions during the four phases of the FBS: (a) geomorphological; (b) pioneer; (c) biogeomorphological; and (d) ecological

the fluvial corridor is not systematically correlated with distance between populations. Indeed, the spatial genetic structure of populations reflects complex interactions and fluctuations between multiple intrinsic and extrinsic factors (e.g. phenology and seed dispersal, location and morphology of mature male and female individuals, wind intensity and direction, flood regime, topography).

### The pioneer phase of the FBS: critical for seedling establishment of *P. nigra*

During the pioneer phase of the FBS, *P. nigra* seeds germinate on the alluvial surface and seedlings need to survive during the first two years (Figure 4). This phase is characterized by a strong, unidirectional control of *P. nigra* by hydrogeomorphological patterns (i.e. river channel morphology, sediment texture and moisture retentiveness) and meteorological and hydrogeomorphological

processes (i.e. atmospheric precipitation, temperature, alluvial water table regime, flow variability, sediment erosion, transport and deposition) (Figure 3(b)). The abiotic control of the atmosphere and the river system is critical throughout this stage from germination to establishment (Mahoney and Rood, 1991).

Seeds transported by water accumulate downstream at different locations and elevations on alluvial surfaces, according to channel morphology/topography and river discharge. A different water level usually corresponds with each seed release, reflecting a combination of flow pulses and gradual summer water level recession. Over the last 20 years, a large body of literature has established the hydrogeomorphological conditions suitable for poplar seedling recruitment (e.g. van Splunder *et al.*, 1995, 1996; Braatne *et al.*, 1996, 2002; Guilloy *et al.*, 2002; Stella and Battles, 2010; Guilloy *et al.*, 2011). When habitat conditions are suitable, a large number of seeds germinate, often forming successive strips of seedlings parallel to the water's edge. Poplar seedlings can germinate in large numbers (e.g.  $>4000 \text{ m}^{-2}$ ; Braatne *et al.*, 1996), but only a



**Figure 4.** *Populus nigra* seedlings (4 months old). The photograph was taken in September on an alluvial bar at the river Tech (France). At this stage, root length can exceed a third of the stem height; here, they are developing on a sandy gravel substrate. Photography D. Corenblit. This figure is available in colour online at [wileyonlinelibrary.com/journal/espl](http://wileyonlinelibrary.com/journal/espl)

few of these seedlings usually survive the first year (Johnson, 2000; Karrenberg *et al.*, 2002; Dixon and Turner, 2006). Some seedlings are located too high on the alluvial surface and thus cannot maintain root contact with the receding water table and capillary fringe. It has been shown that the connection between roots and the alluvial water table is critical during the first summer because poplar seedlings are obligate phreatophytes (Mahoney and Rood, 1998). Guillooy *et al.* (2002) and Stella and Battles (2010) review and report experimental observations concerning cottonwood seedling growth and survival according to progressive water table recession. They showed that successful recruitment requires a root growth rate of between 0.4 and 1.3 cm day<sup>-1</sup>. Guillooy *et al.* (2011) noted that *P. nigra* seedlings generally do not survive abrupt water level drops >40 cm and that the chances of seedling survival also depend on sediment texture. This was supported by experimental work by Barsoum (2001) which showed that water table recession should not exceed 0.5 cm day<sup>-1</sup> in coarse sands and 2.5 cm day<sup>-1</sup> in gravels. However, Guillooy *et al.* (2002) showed that small summer discharge fluctuations (flow pulses) or even some rain events can be sufficient to enhance *P. nigra* summer seedling survival.

Other intrinsic and extrinsic factors affect seedling survival during the summer period. Barsoum and Hughes (1998) and Guillooy *et al.* (2002) showed that small differences in the age of the seedling can influence their survival; older seedlings appear to be more tolerant to sediment burial, drought and abrupt water level drops (see also Guillooy *et al.*, 2011). *In situ* and experimental analyses have also indicated that temperature may not significantly affect seedling survival during the first summer (Moggridge and Gurnell, 2009; Chamailard, 2011).

The next critical step during the first year of the pioneer phase occurs in the autumn–winter period when floods can uproot or bury the seedlings. Seedlings that were located relatively high on alluvial surfaces generally die during the summer, whereas seedlings located relatively low may not survive because of their high exposure to flood scouring, ice jams, prolonged submersion, and sediment burial (Mahoney and Rood, 1998). Thus, seedlings located at intermediate elevations are most likely to survive the first year after germination. Moggridge and Gurnell (2009) also found that the upstream presence of an obstacle, such as a patch of established Salicaceae, provided open but hydraulically sheltered sites that were particularly suitable for sexual regeneration along the dynamic Tagliamento River (Italy). This illustrates that vegetative regeneration from wood fragments or buried trunks may help to facilitate seedling establishment downstream. A similar concept is proposed in the review by Gurnell *et al.* (2005), which suggests a ‘nursing’ effect on seedlings by large wood accumulations that create and preserve suitable micro-sites for recruitment.

As proposed by Cooper *et al.* (2003), interactions between numerous and non-stationary climatic and hydrogeomorphological parameters lead to multiple pathways of seedling recruitment. For example, the authors noted on the Yampa and the Green Rivers (USA) that sexual recruitment of poplar can occur on (i) alluvial bars in unregulated river sections, (ii) alluvial floodplain surfaces during infrequent large flood events, (iii) channel margin benches in canyon pools and eddies, (iv) secondary and abandoned channels, (v) low elevations on alluvial bars during multi-year droughts, and (vi) alluvial bars formed prior to flow regulation on dammed rivers during controlled flood events. Sexual reproduction can also fail for several consecutive years if all the suitable conditions are not met (Stromberg, 1993; Mahoney and Rood, 1998). Ultimately, the recruitment pathway will define the zones where vegetation will engineer the fluvial corridor during the biogeomorphological phase (Gurnell *et al.*, 2012).

## The biogeomorphological phase of the FBS: critical for the development of young trees and the construction of a mature biogeomorphological entity

After 2–3 years of development, *P. nigra* saplings (young trees) begin to interact significantly with water and sediment flows, triggering the biogeomorphological phase of the FBS. During the first year of seedling development vertical growth of shoots is limited because energy is preferentially allocated to roots to improve resource acquisition and anchorage (Braatne *et al.*, 1996). When, after 2–3 years, the sapling has become established and the roots are well developed (often penetrating to 60 to 100 cm depth in fine grained substrates), vertical shoot growth becomes much more rapid and individuals can easily reach 10 to 15 m within 8–10 years (reviewed by Braatne *et al.*, 1996).

During the FBS biogeomorphological phase, *P. nigra*'s biogeomorphological life cycle encompasses extensive feedbacks between biological and geomorphological components (Figure 3(c)) leading to the emergence of post-pioneer and mature biogeomorphological entities such as vegetated islands (Figure 5) and floodplains (Edwards *et al.*, 1999; Gurnell, 2013).

It is primarily the strong anchorage of young individuals within the river's gravel bed that rapidly enhances their resistance to shear stress during floods. Initial roots extend quickly after germination and a major tap root develops vertically in the coarse sediments of alluvial bars until it eventually reaches the water table, which limits its extension because of a lack of oxygen. After the first two years of growth, *P. nigra* are firmly anchored and have generally developed sufficient aerial biomass to interfere with hydrogeomorphological processes (Figure 6). The rapid development of aerial structures increases surface roughness and thus leads to the trapping of fine sediment (Gurnell and Petts, 2006), organic matter and nutrients (Francis *et al.*, 2009) and diaspores (Corenblit *et al.*, 2009b) downstream of isolated individuals or within the cohorts (for a more detailed explanation see Gurnell *et al.*, 2005; Corenblit *et al.*, 2007). In turn, the impact of *P. nigra* on the geomorphological structure strongly modulates its growth rate, biomass and architecture (number of shoots, suckers, and adventitious roots) until it reaches sexual maturity at 10–15 years (Stanton and Villar, 1996). For example, lateral roots grow near the surface providing stability and an extensive rhizosphere that favours water and nutrient uptake; the length of these lateral roots can reach 30 m at the adult stage (Buell and Buell, 1959; Drénou *et al.*, 2004).

Rood *et al.* (2011) observed positive feedback between vegetation growth and sediment aggregation in the Snake and the Salmon Rivers (USA). The authors argue that fine sediment deposition favored the establishment and clonal expansion of another Salicaceae species: *Salix exigua* Nutt., locally known as sand bar willow. In return, the adventitious roots and canopies protected and trapped more sand. The authors suggested that this bidirectional process sustains the co-existence of surface sand and sand-bar willows. Comparable feedbacks between vegetation growth and sediment accretion were also described by Hupp and Simon (1991). Furthermore, in six study sites along two Californian rivers, Douhovnikoff *et al.* (2005) used fingerprinting markers (AFLPs) to observe that clones of *S. exigua* could occupy a surface as large as 325 m<sup>2</sup> and an average of six clones per sites occupied 75% of the vegetated area, suggesting that prolific clonal growth supports long-term colonization of alluvial bars.

As in many Salicaceae trees, vegetative regeneration (i.e. clonal) is an important method of reproduction for *P. nigra* (Rood *et al.*, 1994; Stromberg *et al.*, 1997; Arens *et al.*, 1998; Barsoum *et al.*, 2004). Clonal expansion can occur in different



**Figure 5.** Development of a pioneer island within the active tract of the River Tagliamento (Italy). This landform represents a cohesive point within the braided channel. Here, young individuals of *P. nigra* enhance sediment and organic matter trapping and stabilization. At this stage, the roots of the young trees are already well developed and provide the landform with strong resistance to erosion. Such an island can keep growing for many years and ultimately become connected with the adjacent floodplain (Gurnell *et al.*, 2001). Photography A.M. Gurnell. This figure is available in colour online at [wileyonlinelibrary.com/journal/espl](http://wileyonlinelibrary.com/journal/espl)

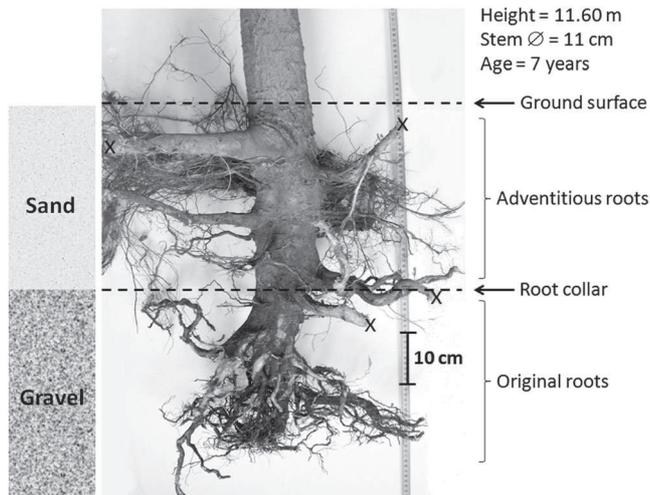


**Figure 6.** *Populus nigra* cohorts (4–7 years old) established on an alluvial bar on the River Garonne (France). The photograph was taken in winter after annual flood events. The water level during the flood is well marked on the trees; it illustrates the high degree of hydrological connectivity of the young cohorts of *P. nigra* with the active river tract. Photography J. Dousseau. This figure is available in colour online at [wileyonlinelibrary.com/journal/espl](http://wileyonlinelibrary.com/journal/espl)

ways and from different parts of an individual (e.g. from branches, broken and partly buried trunks, excavated roots). Barsoum *et al.* (2004) suggested that vegetative reproduction of *P. nigra* ensures regeneration and propagation within highly disturbed fluvial contexts. Vegetative propagation represents a defense mechanism to mechanical constraints, submersion and sediment burial. Fragments can be dispersed by water flow in a very similar way to seeds throughout the year and can enhance the clonal expansion of an individual many kilometers downstream, even on elevated surfaces not suitable for seed germination (Barsoum, 2002; Barsoum *et al.*, 2004; Mogggridge and Gurnell, 2009). The molecular mechanisms of *Populus* vegetative responses to physical and chemical constraints are currently the subject of an increasing number of studies. *Populus* has

indeed become a target model for studying the cellular and molecular processes that underlie the biology of trees since its full genome sequence was published (Tuskan *et al.*, 2006). Recent proteomic analyses have shown that poplars have developed complex biochemical mechanisms to detect mechanical constraints such as those imposed by water flow and sediment burial and to induce specific responses improving their anchorage (Scippa *et al.*, 2008; Trupiano *et al.*, 2012).

Each sediment deposition around the main stem of an individual tree leads to the formation of successive levels of adventitious roots (Foussadier, 2003) (Figure 7). Alestalo (1971) noted that along unchannelized rivers, riparian trees are excellent indicators of the site's age, signifying the minimum age of alluvial bar formation. It was shown in different



**Figure 7.** Root architecture of a young (7 years old) individual of *P. nigra*. This root system was excavated by the authors on a pioneer fluvial island on the River Garonne (France). Crosses denote points where the roots were cut during root extraction. Recurrent flood events generally lead to high rates of sand deposition caused by high vegetation roughness. It is during this phase that a young *P. nigra* produces the most adventitious roots and suckers. In the case of the sampled individual, the mean annual sedimentation rate was approximately  $5 \text{ cm yr}^{-1}$

river systems that adventitious roots and tree ring growth patterns of poplar and also willow species, are markers of spatio-temporal patterns of sedimentation on floodplains (Hupp and Morris, 1990; Friedman *et al.*, 2005; Piégay *et al.*, 2008). The root collar and initial root zone corresponds to the germination zone and indicates the position of the original ground surface. After several years, *P. nigra* root dynamics lead to the formation of a dense and extensive rhizosphere, i.e. the critical zone influenced by root exudates and associated symbiotic microorganisms such as nitrogen-fixing bacteria and mycorrhizal fungi (Doty *et al.*, 2005; Gryta *et al.*, 2006). Bormann and Graham (1959) suggested that at this stage, roots from the same riparian tree species can even merge together (i.e. natural root grafting) forming a network of connected trees (for a review see Graham and Bormann, 1966). Jelinkova *et al.* (2009) noted that the poplar genus is affected by such dynamics, and Lev-Yadun and Sprugel (2011) indicated that natural root grafts lead to significant physiological and mechanical benefits: for example, when trees become connected they share the same physiological processes related to resource uptake and storage. This provides some benefits for water and nutrient uptake and redistribution at the scale of the cohort during stressful periods; whereby certain individuals may benefit from older individuals with greater absorption capacities. Root grafting also increases mechanical resistance to destruction by water flow during floods or by wind at the scale of the cohort, and energetic reserves stored in broken trees can become usable by surrounding individuals.

Suckers generally grow from poplar lateral roots, forming new stems that increase surface roughness and consequently sediment trapping and stabilization, primarily during the FBS biogeomorphological phase. This in turn enhances the formation of new adventitious roots on the clones. Barsoum *et al.* (2004) used five simple sequence repeat (SSR) markers on the River Garonne (France) to show that asexual reproduction in *P. nigra* frequently occurs through flood training, i.e. new shoot emergence from young shoots that had been toppled and buried during flood events (Rood *et al.*, 1994). Replicated genotypes were identified by Barsoum *et al.* (2004) in two-thirds of all stands sampled, and were most

often found to occur within the middle-aged stands as nearest neighbors, forming units of 2–4 trees growing in close proximity.

*P. nigra* clonal expansion enhances fine sediment and nutrient trapping, and landform stabilization, ultimately favoring vegetative development until sexual maturity (Francis *et al.*, 2009). According to Jones *et al.* (2010), an abiotic feedback occurs when the engineer is affected only by the abiotic modifications it induces. But, in the case of *P. nigra*, there is evidence of both abiotic and biotic feedbacks related to co-occurring species responding to *P. nigra* engineer effects that, in turn, also affect the engineer species. It has been demonstrated that specific symbiotic interactions take place between endo and ectomycorrhizal fungal species and *P. nigra* during its life cycle (Harner *et al.*, 2010, 2011). Gardes *et al.* (2003) and Gryta *et al.* (2006) observed a significant variation in mycorrhizal community assemblage and type diversity according to the *P. nigra* development stage and the degree of hydrological connectivity. Arbuscular endomycorrhizal fungi were found on the roots of young (1–4 years) *P. nigra* individuals located on disturbed and highly disturbed patches on the River Garonne. However, ectomycorrhizal fungi were found on the roots of the older (25–50 years) trees in less disturbed patches. A combination of endo- and ectomycorrhizal fungi was observed in intermediate situations. The pattern of clonal colonies established in the disturbed patches showed a ruderal strategy with generalist species such as *Tricholoma scalpturatum* (Fr.) Quél. reproducing sexually and forming small colonies that did not persist over time, as a result of the recurrent disturbances. Within the less disturbed patches, a tendency towards clonal propagation, mainly by the host specialist *Tricholoma populinum* J.E. Lange was observed. *Tricholoma populinum* clones have a competitive strategy in order to enhance the local persistence and interaction with their host (it has been demonstrated that mycorrhizal fungi enhance phosphorus recovery by plants from their environment, e.g. Allen, 1991).

### The ecological phase of the FBS: critical for optimizing sexual reproduction of mature trees

The positive feedback system of matter accretion, vegetative growth, biochemical transformation of the substrate and mycorrhizal inoculation leads to the emergence of functional biogeomorphological entities at the landscape scale approximately 15 years after plant germination on a bare gravel surface. These functional entities correspond to raised and stabilized vegetated fluvial islands, benches and floodplains (Figure 8).

During the ecological phase of the FBS, nutrient accumulation reaches such a state that the internal cycle of resources can satisfy the biotic needs of the mature riparian trees (Fisher *et al.*, 2007) and related symbiotic species (e.g. Gryta *et al.*, 2006). The stabilized landform and soil community structure also increases the persistence of mature trees within the fluvial corridor. At this time, the biogeomorphological entity has achieved maturity and nutrient input equals nutrient output; only infrequent (i.e. exceptional) and very high energy floods may bypass the biotic demand or cause vegetation and landform destruction at the scale of the fluvial corridor. Thus, at the mature stage, landforms engineered by *P. nigra* optimize the survival of adult trees, the uptake of resources (Lamb and Berthelot, 2002) and, ultimately, improve their chances of producing as many seeds as possible during their life (Gurnell *et al.*, 2012).

From an ecological point of view, the ecological phase is dominated by autogenic ecological processes (Figure 3(d)). It is characterized by a reduction of clonal expansion (Barsoum



**Figure 8.** Post-pioneer *P. nigra* trees (20–25 years old) on the floodplain of the River Garonne (France). The photograph was taken on a vertically aggrading fluvial island of the River Garonne. Photography L. Lambs. This figure is available in colour online at [wileyonlinelibrary.com/journal/espl](http://wileyonlinelibrary.com/journal/espl)

*et al.*, 2004), with many suckers dying and being eliminated during floods at the end of the biogeomorphological phase. It also encompasses powerful feedbacks on herbaceous plants (Bendix and Hupp, 2000; Corenblit *et al.*, 2012) and mycorrhizal (Gryta *et al.*, 2006; Harner *et al.*, 2010, 2011) community structure and function, with regard to hydrogeomorphological disconnection and physicochemical changes in the soil and at the surface.

The duration of the FBS ecological phase depends on the disturbance regime that can reinitiate the cycle due to lateral migration of the river channel or floodplain stripping, and on the autogenic succession that can drive the evolution of the riparian community toward hardwood terrestrial formations (replacement of the phreatophyte species by *Quercus* spp., generally commences after 30–50 years, e.g. Pautou *et al.*, 1997; González *et al.*, 2010).

Gurnell *et al.* (2005) and Collins *et al.* (2012) showed, respectively, on the River Tagliamento (Italy) and on river valleys of the Pacific coastal temperate rainforest of North America, that at the end of the riparian tree biogeomorphological life cycle, large trunks that are eroded and deposited during floods, greatly enhance the BLC of the next generations of riparian trees. The authors noted that large deposited trunks resist fluvial transport and remain in river channels long enough to initiate and stabilize wood jams. These accretion points, in turn, contribute to the creation of new alluvial patches and protect them from erosion. In highly dynamic river systems (braided and island-braided types), these patches provide suitable sites for trees to establish and mature in areas where the cycle of floodplain turnover is rapid, thus providing a future source of large wood and reinforcing the cycle of biogeomorphological regeneration.

### Fluvial biogeomorphologic succession turnover dynamics

At the scale of the fluvial corridor, the biogeomorphological life cycle of *P. nigra*, described here according to the four phases of the fluvial biogeomorphologic succession model, leads to a spatiotemporal transverse partition of the fluvial corridor between a highly connected and unstable area concentrating water flows and driven by physical processes, and a

disconnected and stabilized area in which mineral and organic matter accumulates and trophic and non-trophic autogenic ecological interactions such as competition tend to dominate. Consequently, by modifying its physical environment, *P. nigra* also affects the whole riparian community structure, function, and resistance and resilience.

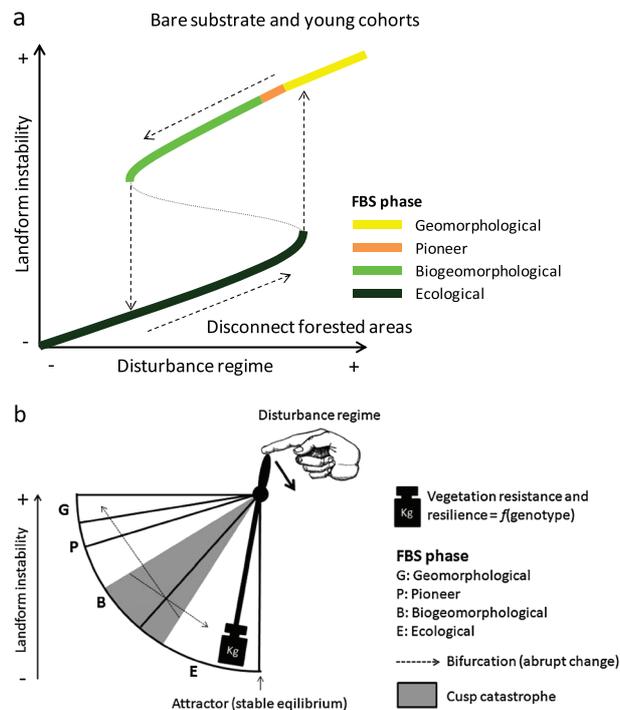
The relative (statistical) proportion and turnover of highly connected areas dominated by bare substrate or young cohorts (<10 years), and engineered areas dominated by sexually mature cohorts (>10–15 years), vary along the longitudinal and transverse gradients according to stream power, the natural flow regime and topography (Bornette *et al.*, 2008). Feedback between *P. nigra* and its hydrogeomorphological environment varies in frequency, duration and intensity according to the submersion regime and the gradient of energy. It also varies according to the quantity and texture of sediment transported along the longitudinal gradient from areas with intermediate to high stream power (approximately 30 to 300 W m<sup>-2</sup>). Outside this energy range, the hydrogeomorphological regime may be too weak or too strong to maintain a durable abiotic-biotic reciprocal linkage (Francis *et al.*, 2009; Corenblit *et al.*, 2011). The relative proportion of highly connected and engineered areas also varies longitudinally and transversally in relation with anthropogenic alterations (Surian *et al.*, 2009) and bioclimatic changes such as the one that operated during the last 10 000 years of the Holocene (Lespez *et al.*, 2008).

Fisher *et al.* (2007) and Tabacchi *et al.* (2009) suggested that the resilient and resistant patterns of the fluvial biogeomorphological system emerge from feedback loops between the hydrogeomorphological and biological processes. Biogeomorphological resistance and resilience determine the proportion of bare substrate and young and mature cohorts within the fluvial corridor. In natural conditions, the proportion of these three elements remains relatively constant at the level of the fluvial corridor, despite vegetation growth and geomorphological adjustments at smaller scales. Gurnell and Petts (2006) suggested that engineer plants such as *P. nigra* modify the location of the boundaries between different fluvial types along the upstream–downstream gradient of energy. Engineer plants also modulate the rate and types of habitat turnover as plant growth or hydrogeomorphic disturbance conditions change (see also Bertoldi *et al.* 2010; Gurnell *et al.*, 2012). The biogeomorphological turnover does indeed decrease in natural (i.e. non-impacted) conditions along the longitudinal gradient of energy,

from island-braided types dominated in terms of relative proportion by young individuals reproducing dominantly by vegetative means, to more stable wandering and meandering types dominated by mature cohorts reproducing sexually. In torrential headwaters the occurrence of *P. nigra* individuals in the fluvial corridor is primarily related to its ability to regenerate rapidly from fragments (Francis *et al.*, 2004; Gurnell *et al.*, 2005; Moggridge and Gurnell, 2009). Braided reaches are characterized by a high turnover of gravel bars and small islands. Van der Nat *et al.* (2002) reported that almost 30% of vegetated islands developing within the active tract of the River Tagliamento are renewed every 2.5 years. Arscott *et al.* (2002) showed that habitat turnover was close to 60% in upstream reaches of the River Tagliamento, compared with only 20% in downstream reaches. Zanoni *et al.* (2008) observed from a diachronic study (a 60-year period between 1944 and 2005) on the same river (in reaches corresponding to the island-braided type) that fluvial island turnover took between 12 and 24 years. The authors pointed out that during the study period the location of islands changed rapidly but that the island-braided form persisted within the same river section, with a constant proportion of islands and open gravel areas.

Furthermore, Corenblit *et al.* (2010b) noted a non-linear behavior of biogeomorphological resistance/resilience on the Mediterranean River Tech, in the southeastern Pyrenees (France). In response to a major flood that occurred in 1940 the fluvial landscape of the River Tech demonstrated high resilience, emphasizing the existence of positive feedback driven by pioneer riparian vegetation. The feedback corresponded to fluvial island and floodplain accretion, vegetation succession and to an increase in biogeomorphologic stability under current hydrogeomorphologic and bioclimatic conditions. The spatial analysis of the evolution of the biogeomorphological system toward stabilization revealed a metastable dynamic with a threshold occurring 30 years after the major destructive flood event, which corresponded to the abrupt reinforcement of biogeomorphologic cohesive forces driven by engineer plants during the fluvial biogeomorphologic succession.

Strong biogeomorphological positive feedbacks can thus lead to abrupt 'catastrophic' (*sensu* Thom, 1975) changes between alternative stable states (*sensu* Scheffer *et al.*, 2001) (Figure 9(a)). We suggest that engineer plant species such as poplars drastically modify physical equilibrium conditions within fluvial corridors, depending on disturbance and recovery. A cusp catastrophe (cf. Thom, 1975) emerges during the fluvial biogeomorphologic succession related to poplar BLC, defining abrupt non-linear transitions and hysteresis cycles between the different biogeomorphologic alternative stable types (i.e. highly connected areas dominated by bare substrate and young cohorts, and disconnected forested areas) (Figure 9(a)). Abrupt transitions occurring at the boundaries are related to (i) the threshold of vegetation physiological and mechanical resistance to destruction during floods; and (ii) the resilience properties of vegetation related to interactions between species life history, the geomorphic structure and the natural flow regime. The biogeomorphological system shifts to an unstable state dominated by the geomorphological/pioneer phases locally along meander banks during moderate floods leading to translation of channels, or at the scale of the fluvial corridor during large, high energy floods (Figure 9(a)); the biogeomorphological system shifts during the biogeomorphologic phase toward a stabilized state dominated by the ecological phase (i.e. the attractor domain) where vegetation resistance overpass destructive forces imposed by water flow (Figure 9(a)). As shown on the River Tech (French Pyrenees), the biogeomorphologic phase is an instable transition state between the two possible biogeomorphologic domains (i.e. the one



**Figure 9.** Non-linear dynamics of landform instability during engineer plants biogeomorphological life cycle: (a) hysteresis cycle (see Scheffer *et al.*, 2001) of landform instability according to the BLC of riparian engineer plants during the fluvial biogeomorphologic succession; (b) conceptual model illustrating the non-linearity of landform instability according to the disturbance regime and to vegetation resistance and resilience. This figure is available in colour online at [wileyonlinelibrary.com/journal/espl](http://wileyonlinelibrary.com/journal/espl)

dominated by the geomorphological/pioneer phases and the second dominated by the ecological phase) (Corenblit *et al.*, 2010b). The non-linear dynamics of the FBS is illustrated in Figure 9(b) with an analogical conceptual model. Intermediate patchy biogeomorphologic landscapes, corresponding to island-braided and wandering rivers, may be indicators of the imminence of a catastrophic (abrupt) change toward a state dominated in relative terms by bare sediment or by riparian forest. Corenblit and Steiger (2009) stressed that the overall evolution of riparian vegetation traits favoring resistance and resilience to hydraulic constraints may have led to major modifications, not only in fluvial types, sediment dynamics and river morphology but also in ecosystems functioning along ecosystem-engineered longitudinal and transverse gradients.

## Positive Niche Construction by *P. nigra* and Associated Eco-evolutionary Dynamics: a Testable Hypothesis?

### Niche construction and eco-evolutionary dynamics: definition

The biogeomorphological life cycle of engineer plants such as *P. nigra* may be viewed as an emergent property originating from feedback between engineer organisms and the hydrogeomorphological environment on an evolutionary timescale. The framework of 'evolutionary geomorphology' specifically associated with biological processes was proposed by the authors in order to consider such feedbacks on an evolutionary timescale (Corenblit and Steiger, 2009; Steiger and Corenblit, 2012). Based on this framework, we suggest that the reciprocal coupling

between the life cycle of poplar and its hydrogeomorphological environment needs to be considered in the light of evolution.

Dawkins (2004) and Matthews *et al.* (2011) pointed out that there may be various responses of populations to engineer activities within an ecosystem. The variety of modalities of reciprocal interactions and adjustments between organisms and their biological and physical environment, and the lack of a clear distinction between main concepts (e.g. ecosystem engineer, foundation and keystone species, positive and negative NC, niche changing, extended phenotype) have resulted in debates concerning the range of application of the concept of NC (Dawkins, 2004; Post and Palkovacs, 2009). As defined by Odling-Smee *et al.* (2003), we consider that the principle of NC may be that engineer organisms modifying the environment can change the selective pressure for themselves and for other organisms. Thus, NC operates with an evolutionary response within the engineered ecosystem (see also Laland *et al.*, 1999). Therefore, two basic conditions define NC: (i) the physical environment must be modified by an engineer species; (ii) the modified environment must induce an evolutionary response (e.g. selection and evolution of life history traits) of the engineer species, or of other organisms within the ecosystem (i.e. eco-evolutionary dynamics; Erwin, 2008; Post and Palkovacs, 2009).

The first criterion of NC is met in the case of riparian poplars. Indeed, submersion frequency and duration, sediment scouring or deposition, sediment texture, organic matter and nutrient content are largely and durably modified by riparian poplars along the transverse gradient of hydrogeomorphological connectivity (for a review see Gurnell, 2013). However, the functional linkages among plants and specific landform modulations need to be established and certainly represent a crucial challenge for the sciences of geomorphology and ecology (Steiger and Corenblit, 2012). At the current stage, the second criterion of NC and associated eco-evolutionary dynamics remains to be validated formally.

Fisher *et al.* (2007) pointed out that the modifications of the fluvial environment by engineer plants may certainly act as a selective force driving ecological strategies along longitudinal and transverse hydrogeomorphological gradients. We suggest that the engineered environment components probably benefit engineer species, both directly, as suggested by Francis *et al.* (2009) in the case of fluvial islands, but also indirectly through eco-evolutionary interactions between the engineer species and co-occurring (e.g. symbiotic) organisms that also benefit from NC. Gardes *et al.* (2003) noted that the fluvial habitat engineered by *P. nigra* leads to fundamental modifications in the interactions of mycorrhizal species and community traits along the transverse gradient of connectivity. The authors suggested that each mycorrhizal type (specialist *T. populinum* and generalist *T. scalpturatum*) and association play a different role in *P. nigra* nutrition during its development. Gryta *et al.* (2006) suggested that *P. nigra* differentially rewards the two types of fungal species through modulation of the amount of photosynthates allocated to the growth and reproduction of genets colonizing roots. As a result of a co-evolutionary process, *T. populinum* clones would have performed better on *P. nigra* than clones of *T. scalpturatum*. Cooperation is indeed a relevant evolutionary innovation (Morris *et al.*, 2012). This may be possibly the case for *P. nigra* and related ectomycorrhizal fungi with a modulation of cooperative interactions during the construction of the niche.

We suggest that each of the phenotypes (i.e. individuals) and potentially extended phenotypes (*sensu* Dawkins, 1982) constituting the mature biogeomorphological entity (e.g. the vegetated fluvial island) may be viewed as a functional component of a complex adaptive system (*sensu* Levin, 1998). From a

biogeomorphological perspective, Phillips (2009) described such an interplay between multiple genomes and a soil as an 'extended composite phenotype' capable, to a certain extent, of self-regulation and self-replication.

## Suggestions for testing the hypothesis of *P. nigra* positive niche construction

The existence of *P. nigra* positive NC and the associated eco-evolutionary dynamics within fluvial corridors may be validated by providing answers to three fundamental questions: (i) How and to what spatiotemporal extent does *P. nigra* modify the hydrogeomorphic environment along different river sections and river systems? (ii) How and to what extent do these modifications affect ecosystem structure and function? (iii) How and to what extent does the engineered hydrogeomorphic environment affect the fitness for the engineer species and for other co-occurring species? Thus, the validation of the hypothesis of a positive NC and associated eco-evolutionary interactions between *P. nigra* and other co-occurring species needs to combine geomorphic, ecological and biological methods. In addition, this hypothesis will have to be validated *in fine* at the gene level.

First, it is essential to estimate to what degree the hydrogeomorphological environment is modified by *P. nigra* during the FBS. *In situ* experiments comparing manipulated patches (e.g. artificial inhibition of *P. nigra* recruitment, control of the number, diameter, architecture and height of stems) and unmanipulated control patches (with young establishing cohorts of *P. nigra*) may be useful to quantify the effects of *P. nigra* on sediment, organic matter and nutrient storage and landform dynamics. Such *in situ* analyses may be linked with *ex situ* semi-controlled experiments for understanding the expression of the morphological traits of *P. nigra* saplings according to the genotype and unmodified (initial) environmental conditions. Controlled experiments in flumes may also be used in order to quantify sediment and topographic changes associated with the presence of calibrated saplings.

Second, we need to define the degree to which the engineered environmental components (e.g. sediment, topography, and hydrogeomorphological connectivity) control specific phenotypic responses on target populations of the engineer species, and potentially feed back at the community level. In order to understand if the local modifications in the hydrogeomorphological environment are biologically useful (functional) for the engineer species, and thus may have potentially an evolutionary basis, we need to test (i) if they improve resource acquisition, biomass production and the chances of reaching sexual maturity; (ii) if they recurrently follow a similar succession pattern within the same river reach; and (iii) to what extent these environmental modifications are specific and vary between different hydrogeomorphological and bioclimatic contexts and according to variations in poplar life history, morphological and biomechanical traits. In particular, the morphological, biomechanical and physiological responses of riparian plant engineer species to mechanical stress, and more specifically to sediment burial, can be investigated through *ex situ* manipulations in controlled conditions using rhizotrons (Guilloy *et al.*, 2011) and the use of hydraulic flumes with sediments. High resolution *in situ* analyses of root and aerial structure architecture may help to establish the morphological, biomechanical and physiological responses attesting a functional linkage between the engineer species, sediment deposition, nutrient and water table dynamics. *In situ* root excavation needs to be performed using a non-destructive technical device (e.g.

high pressure washer). Chemical ecology or ecological stoichiometry (Sternler and Elser, 2002) and metagenomics (Marco, 2010) may also become useful in the near future to identify respectively characteristic chemical (e.g. C:N:P ratio) and DNA signatures at the scale of the community (i.e., metagenome) associated with juvenile, post-pioneer and mature biogeomorphological entities.

At the molecular level, the role of intraspecific genetic variability of *P. nigra* populations related to engineer traits must be defined in order to quantify the variability in abiotic responses (e.g. sediment accretion rates and resulting topography) and biotic responses (e.g. aerial and below-ground biomass allocation). This will require a formal examination of how and to what degree organism fitness is affected by the specific biotically-driven modifications in the hydrogeomorphological environment. We believe that the genetic aspects associated with the experiments proposed in this article are now accessible for *Populus* because many of the trait loci of related species, such as the black cottonwood (*Populus trichocarpa* [Torr. & Gray]), have now become target models for studying cellular and molecular processes (Tuskan *et al.*, 2006). Many of these trait loci have already been mapped (Yin *et al.*, 2004), for example, those related to the response of poplar roots to mechanical stress imposed by bending (Scippa *et al.*, 2008; Trupiano *et al.*, 2012). The following points may be addressed for specific effects and response traits: (i) the chromosomal location of trait loci controlling the response traits to hydrogeomorphic constraints (i.e. water flow, sediment burial and water table variation); (ii) the range of effects of each identified trait locus on the phenotype and extended phenotype; (iii) the chromosomal location of trait loci controlling the response traits to the engineered habitat; (iv) the modality of gene action at each trait locus; (v) the effect of interaction among the loci of different traits (see Bradshaw, 1996).

However, the potential for genetic complications associated with the combination of genomes between multiple poplar species through hybridization has also to be considered. Indeed, hybridization can be a source of new life-trait adaptations and thus it could complicate the validation of the hypothesis that niche modification is species specific. Another source of possible complication that must be considered is that phenotypic variation (e.g. morphological and biomechanical) can be related to the genotype, to the environment or the combination of the two components (Riemenschneider *et al.*, 1996).

The molecular studies may be coupled with studies at the landscape scale. Dietrich and Perron (2006) suggested that the frequency distribution of measurable landform properties (e.g. altitude, channel width and sinuosity) may differ between abiotic and biotic systems. Bouma *et al.* (2013) showed, using a flume experiment, that specific hydrogeomorphological structures are related to specific plant traits of three marsh species (*Spartina anglica* C.E. Hubbard, *Puccinellia maritima* Huds. Parl. and *Salicornia procumbens* Sm.). Van Hulzen *et al.* (2007) showed how the short-range (local) modification of the physical environment increased the fitness of engineer marsh-plant species. These findings indeed suggest that the effects of vegetation on landscape patterns can be functional and species specific. As pointed out by Thorsten *et al.* (2012), the understanding of the conditional ecological and geomorphological outcome of ecosystem engineering is highly relevant. Bertoldi *et al.* (2011) quantified the signature of riparian vegetation in the topography of the fluvial landscape, illustrating that the skewness and kurtosis of the river bed elevation frequency distribution showed a strong correlation with vegetation height, and thus with the plant development stage on the River Tagliamento (Italy). This kind of analysis can help support the first criterion of NC by testing the statistical significance of the

relationship between the biomass of an engineer plant and the variation in the modifiable components of the hydrogeomorphological environment. The recent development of terrestrial and aerial LIDAR and stereoscopic and multi-images photogrammetric methods may enable such studies to be carried out with great accuracy. The use of such technical devices may help testing if different topographic signatures are associated with different poplar species, such as *Populus alba* L., which produces root suckers and can also construct biogeomorphological entities (i.e. vegetated fluvial islands and floodplains) that could possibly reach a specific state that optimizes its fitness related to the natural flow regime. Other genera, such as *Salix* and *Tamarix*, which are also able to colonize gravel bars and expand their ecological phase to produce stable biogeomorphological entities representing sources of offspring, are also concerned (Birken and Cooper, 2006; Rood *et al.*, 2011).

## Concluding Remarks

Investigations related to riparian poplars at the interface between hydrogeomorphology and riparian ecology have progressed significantly over the last two decades. The original concept of a biogeomorphological life cycle (BLC) proposed in this article originates from this corpus of recent knowledge (see reference list). Here, the model was applied to riparian poplar species, with a particular focus on *P. nigra*. The BLC emerged from the model of fluvial biogeomorphologic succession (Corenblit *et al.*, 2007) and is integrated into the framework of evolutionary geomorphology (Corenblit *et al.*, 2011; Steiger and Corenblit, 2012). We still need to learn more about the reciprocal linkages between small scale phenomena (selection and expression of biological traits) and patch-scale geomorphological form and processes. Furthermore, most *in situ* studies related to interactions between riparian species and fluvial dynamics have focused on humid temperate and semi-arid fluvial corridors (for a review, see Gurnell, 2013). We stress the importance for also considering the variety of bioclimatic systems and their related riparian species in the near future. For example, tropical fluvial corridors are more bioclimatically stable regions than the temperate hemisphere. These fluvial systems contain many specific flood-adapted species (Junk *et al.*, 1989) because they have had much more time since the Tertiary to adapt in various ways to hydrogeomorphological constraints.

A huge research effort remains to be undertaken to integrate the evolutionary dimension within the existing models, such as the FBS (Corenblit *et al.*, 2007) and recruitment box (Mahoney and Rood, 1998). We believe that the framework of evolutionary geomorphology and the related BLC model presented in this article may be a useful theoretical basis for the formulation of new questions, hypotheses and experimental designs at the interface between geomorphology, ecology and biology.

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