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# Effects of channel confinement on pioneer woody vegetation structure, composition and diversity along the River Drôme (SE France)

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## Abstract

River embankments are one of the main causes of a loss in active channel movement. The knock-on effects of river channel stabilization include important shifts in the ecohydrological conditions in the protected zone behind embankments, which has already been well exemplified. However, few authors have attempted to investigate changes to pioneer units of vegetation colonizing the active channel following the construction of dikes. As a consequence we studied the structure, composition and diversity of pioneer vegetation units dominated by willow and poplar along the River Drôme in two adjacent, but contrasting, river reaches: an embanked reach and an unconstrained reach, each subject to the same flow regime, but offering very different hydrogeomorphological contexts for vegetation colonization. Our results clearly demonstrate that river embankments affect channel geometry. A reduction in channel width (from between 200 and 500 m to less than 100 m) leads to steeper elevational gradients with an overall coarser grain size and consequently drier overall conditions on colonizable landforms in the channelized reach. Pioneer vegetation responded by colonizing landforms at higher elevations above the low water mark and by occurring in smaller units within the channelized study reach. There was also a reduction in species diversity, a homogenization in vegetation unit structure and a predominance of more drought-tolerant ligneous species (*P. nigra*) in pioneer vegetation units in the channelized study reach. Copyright © 2007 John Wiley & Sons, Ltd.

**Keywords:** riparian pioneer vegetation; channel geometry; braided river; *Populus*; *Salix*; sedimentation; embankment

## Introduction

The nature conservation and socio-economic values of riparian forests have been increasingly recognized, since the 1970s, by both the scientific community and river managers. The services they provide and functional roles they play are multiple and include (i) flood buffering, (ii) landscape improvement, (iii) positive contributions to water quality, (iv) wood production, with related benefits for aquatic fauna, and (v) important contributions as a unique ecotone to both in-stream and riverside biological diversity (Décamps, 1996; Naiman *et al.*, 2005). Along many European rivers embankments are constructed to prevent arable and urbanized land from flooding. This leads to a loss in channel shifting and important environmental changes in the riparian zone, with notable consequences for the regeneration, growth and structural development of riparian forests.

Pioneer vegetation units colonizing the riparian zone are typically dominated by species that are well adapted to intermittent flood disturbances and most of these are members of the Salicaceae family (willows and poplars) (Karrenberg *et al.*, 2002). The successful recruitment and growth of these pioneer woody riparian vegetation species depend on very specific soil–water conditions that relate to their positions along a river. Successful colonization depends on

## Effects of river embankments on pioneer vegetation communities

riparian vegetation situation in relation to water levels, the frequency and intensity of water level fluctuations and also surface sediment grain sizes at any given location (McBride & Strahan, 1984; Bradley & Smith, 1986; Van Splunder *et al.*, 1995; Hughes *et al.*, 1997; Barsoum & Hughes, 1998; Shafroth *et al.*, 1998; Johnson, 2000; Rood & Mahoney, 2000; Kalischuk *et al.*, 2001; Barsoum, 2001; Guilloy-Froget *et al.*, 2002).

The appropriate conditions for the regeneration of pioneer woody riparian vegetation species tend to disappear behind embankments. Species replacing the willows and poplars (and occasionally, alder) in these embankment-protected areas are typical of later successional stages such as ash, maple and oak. These species have greater tolerance of drier conditions and do not rely on flood disturbances to create ideal conditions for regeneration (Bravard *et al.*, 1986; Pautou & Girel, 1994; Girel *et al.*, 1997; Mendonça-Santos *et al.*, 1997; Van Looy *et al.*, 2003). The construction of embankments leads, therefore, to a significantly reduced and much more spatially confined area along the river where pioneer woody riparian vegetation can regenerate under 'ideal' environmental conditions.

Moreover, between dikes, the concentration in river flow results in an increase in water depths and shear stresses across all flows. It also leads to an increased frequency of sediment entrainment (Ricks, 1995), which generates a higher turnover of bedform material (Shafroth *et al.*, 1998). Together, these act to significantly modify the channel geometry of embanked reaches compared with the unconstrained, unembanked situation (Brooks, 1988), with possible consequences for the structure and composition of pioneer vegetation colonizing the active channel areas. The channel planform in embanked reaches demonstrates a different pattern compared with the pre-embankment situation (Peiry, 1988; Poinsart, 1994; Landon, 1999). The channel can be expected to contain a succession of riffle features. Along dikes, deep pools are typically associated with gravel bars on the opposite bank (Richards, 1976; Thompson, 1986; Peiry, 1988).

Predicting how vegetation might respond to shifting ecohydrological conditions is of interest not only to the conservationist, but equally to the river manager. Both seek to understand better not only how riparian forest species composition, structure and recruitment is affected by embankment construction, but also how hydrogeomorphological parameters influence vegetation in these riparian ecosystems, especially in terms of the implications these have for the production of large wood. Unfortunately, despite a good understanding of the conditions required by key riparian vegetation species for regeneration (which helps to explain species presence/absence), limited research attention has been focused on understanding shifts in vegetation community composition and structure (Merigliano, 1998; Kollmann *et al.*, 1999), particularly where hydrogeomorphic conditions have been altered by human pressures. Our understanding of shifts in the composition and structure of pioneer units of vegetation in channelized river reaches is especially limited (see Peeters and Tachet, 1989, for macro-invertebrates).

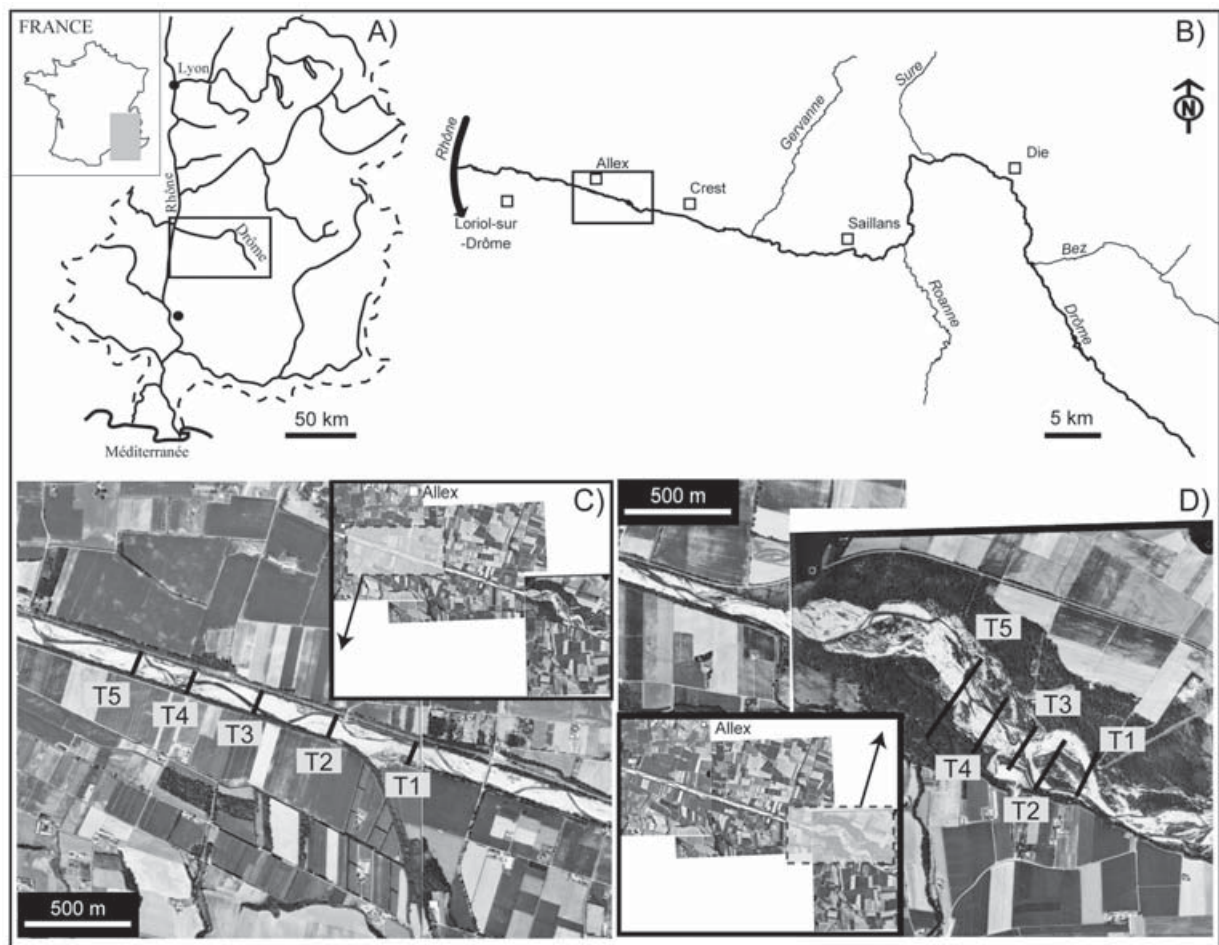
The main aim of this paper is to analyse the impacts of hydrological and sedimentological changes caused by channel confinement on pioneer vegetation community composition, structure and diversity. We investigated the impacts of an artificial narrowing of the river channel on water levels (for the same discharge) and cross-sectional geometry (and thus, elevational differences in patches of vegetation along the river). We tested the hypothesis that channel narrowing following the construction of embankments leads to (i) an increase in grain size, notably within vegetated patches, (ii) a decrease in sediment thickness within vegetated patches (following an augmentation of shear stress) and (iii) a decrease in pioneer patch sizes (due to the more dynamic context of the embanked reach). We studied two contrasting river reaches along the River Drôme: an embanked reach and an unconstrained reach. Each is subject to the same flow regime, but offers very different hydromorphological contexts for vegetation colonization. We, therefore, do not analyse the effect of inter-annual flow variability, but we focus on channel geometry as the main control factor.

## Methods and Materials

### Study site

The study was pursued in two adjacent downstream reaches of the River Drôme – a sixth order (Strahler, 1957) free-flowing piedmont river located in the south-east of France. The River Drôme is a tributary of the River Rhône and drains a catchment of 1640 km<sup>2</sup> (Figure 1(A)). Daily mean discharge is 18 m<sup>3</sup> s<sup>-1</sup> (Q<sub>2</sub> – 160 m<sup>3</sup> s<sup>-1</sup>; Q<sub>50</sub> – 370 m<sup>3</sup> s<sup>-1</sup>) as recorded at the Saillans station (20 km upstream of the study reaches, Figure 1(B)) over the 1910–2005 period. The combination of a steep slope (3–28 m km<sup>-1</sup>), abundant bed load and a hydrological regime characterized by high flood peaks (generally in the early spring and autumn), define the braided pattern of this gravel bed river. The summer months are generally periods of exceptionally low flow (2–3 m<sup>3</sup> s<sup>-1</sup>).

Fieldwork was undertaken 15 km upstream of the Drôme River's confluence with the River Rhône (Figure 1(B)). Two contrasting 2 km reaches were selected: (i) an unconstrained reach in which there is free lateral migration of the



**Figure 1.** Location of (A) the Drôme catchment in France as situated within the hydrographic network of the River Rhône, (B) the study reaches within the lower Drôme valley, (C) cross-sections in the embanked study reach (T1–T5) (photography: IGN) and (D) cross-sections in the unconstrained study reach (T1–T5) (photography: IGN).

river across the floodplain (Figure 1(D)) and (ii) an embanked reach, constrained along its entire length by dikes on both banks (Figure 1(C)). The major structures along the embanked reach were constructed gradually over a period of 49 years, as funds permitted, between 1775 and 1824 (Landon, 1999). The River Drôme was subject to intensive gravel mining and related channel degradation (Landon and Peigay, 1994). But gravel mining activities ceased in the 1980s and since then the river channel has settled into a new equilibrium state; gravel mining is thus no longer a relevant influence on current geomorphological conditions (Landon, 1999).

Along the two contrasting study reaches, surveys of vegetation units were confined to the active floodplain. In the embanked reach, the active zone extended from the inside edge of the dike on the left bank to the inside edge of the dike on the right bank, a distance of no more than 110 m. The maximum width of the active floodplain in the unconstrained reach was approximately 500 m in the 2005 field season and here the edges were defined by mature, established forest, or a major terrace (ground level  $\geq 3.0$  m above base flow river level).

### Physical and structural differences between study reaches

*Topographical survey.* Five cross-sections were surveyed under base flow conditions in the embanked and unconstrained study reaches in August of 2000, 2001 and 2005 (Figure 1(C) and (D)). Each cross-section ran in a straight line following a fixed compass bearing across the active floodplain from a marked point on the left bank to a marked point

on the right bank. Two of the five cross-sections in each reach were purposely set to run across the upstream and downstream tips of established pioneer vegetation units to include zones of island degradation and aggradation, respectively. Placement of the remaining three cross-sections was otherwise regular in an attempt to spread the points of cross-sections at regular intervals along each 2 km study reach.

Elevation along the transects was recorded using DGPS at 1 m intervals in the embanked reach and at 1 and 2 m intervals (according to rapid shifts in elevation) along the cross-sections in the unconstrained reach.

*Hydrological survey.* Hydrological conditions in both reaches were compared during high flows through the collection of flood marks at 30 points in each study reach following a high flow event ( $89 \text{ m}^3 \text{ s}^{-1}$  recorded at the Saillans station in April 2005). The frequency of flows higher than this particular event is 1.9% over the 1990–2005 period (annual flood =  $120 \text{ m}^3 \text{ s}^{-1}$ ). The elevations of measured flood marks in the embanked study reach were confirmed by an automatic water monitoring level fitted with a pressure sensor (model CTD-Diver).

*Number and sizes of pioneer units.* Within the active floodplain, in both the embanked and unconstrained study reaches, distinct landform units were identified: a main low flow channel, secondary channels, unvegetated bars, bars occupied solely by herbaceous species and units occupied by a mixture of herbaceous and pioneer ligneous species such as willow, alder and/or poplar. Our study focuses on the last one of these identified landform units, which are referred to in this paper interchangeably as ‘pioneer vegetation units’ or ‘pioneer patches’. The pioneer vegetation units or pioneer patches are considered to be islands (‘pioneer islands’) where they (1) form a discrete patch of ligneous vegetation occupied mainly by willow and poplar and (2) are surrounded entirely by water and/or unvegetated bar surfaces (Osterkamp, 1998; Ward *et al.*, 2000). These islands correspond well to phase II island types described by Edwards *et al.* (1999) along the River Tagliamento, a similar gravel bed river located in northeastern Italy.

Pioneer patches were identified and surface areas measured at the reach scale in both contexts by using aerial orthorectified photos acquired in 2001 by the Institut Géographique National at the scale of 1/17 000;  $10 \text{ m}^2$  was used as a minimum size for pioneer patches.

## Characteristics of pioneer woody vegetation units

The characterization of vegetation communities in the embanked and unconstrained study reaches proceeded with field survey work in August 2001. Two of the largest ‘pioneer islands’ in each study reach were selected for assessment. These larger pioneer islands were considered to be among the longest-established woody pioneer vegetation units on the active floodplain. The surface areas of each island were determined using mapped points collected at regular intervals around the perimeter of each island.

The age of each island was determined through tree-ring analysis of the five tallest trees present in each of the pioneer islands studied (*P. nigra* cored 50 cm from ground level).

*Vegetation community characteristics.* In order to determine the degree of between- and within-patch variability, vegetation was surveyed in numerous widely placed quadrats within each unit. Vegetation was sampled along seven 2 m wide belt transects, each positioned in a direction that was perpendicular to the central lengthwise axis of each island. An initial measurement of island length guided the positioning of the seven belt transects at regularly spaced intervals across the lengths of each island. Within each island, floristic data were collected in  $4 \text{ m}^2$  quadrats placed at regular intervals along the length of the seven belt transects (Table I). The downstream and upstream extremities of each island were excluded over a length equal to 10% of the total island length. This was in order to avoid the disproportionate influences on vegetation composition of recently heavily disturbed areas, significant piles of large wood at the upstream tips of islands and aggradation at the downstream ends of the islands.

**Table I.** Characteristics of vegetated islands that were surveyed

	A	B	C	D
Reach type	unconstrained	unconstrained	embanked	embanked
Length (m)	215	188	46	68
Island surface ( $\text{m}^2$ )	6800	8700	300	1000
Elevation above summer baseflow river levels (m)	0.9–1.4	0.8–1.2	2.0–2.2	1.9–2.2
Number of quadrats (vegetation survey)	34	37	13	24
Number of sediment cores	22	26	6	10



The number of quadrats sampled along each belt transect depended on transect length. That is, vegetation was sampled in one quadrat where the transect length was 6 m or less, in two quadrats if transects were 10 m or less, in three quadrats if 20 or less, in five quadrats if 50 or less and in six quadrats if more than 50 m. Each quadrat measured 4 m<sup>2</sup> (2 m × 2 m). For ligneous species, stem diameters were measured 5 cm above ground level ( $n = 2240$  stems). The presence/absence of other species (mostly herbaceous) was also noted within each quadrat. The ecological preferences of individual species were determined based on available descriptions in the scientific literature and notably the work of Rameau *et al.* (1989) and Girel and Manneville (1998).

*Patterns of sedimentation.* Patterns of sedimentation were described through measurements of over-bank sediment (sand and finer sediment) thickness at 64 points located every 5 m along transects (the same points that were selected for placement of the vegetation quadrats). At each measurement point, sediment cores were collected to a depth of 10 cm. Grain size was then evaluated by measuring the relative proportions of sand (%) and finer sediment (sediment finer than 0.5 mm) (Dufour, 2005). Rates of sedimentation were derived by dividing overbank sediment thickness by pioneer island age (an estimate based on dendrochronological cores and a chrono-sequence of aerial photographs).

## Statistical analyses

Descriptive metrics and statistical tests of independence were applied to datasets using *StatView* software (Version 5) (Baron and Vang, 1996). In those instances where data sets were 'small' (less than 20), or where data sets did not have a normal distribution, non-parametric tests were used. Significant differences in the species composition of vegetation between quadrats were tested using a non-parametric analysis of similarity (ANOSIM) available through PAST software (Version 1.27). This test of similarity is based on rank comparisons of quadrat distances (Sorensen index) (Clarke, 1993; Hammer *et al.*, 2004). PAST software was also used for detrended correspondence analysis (DCA) and calculations of floristic similarities (Sorensen index).

## Results

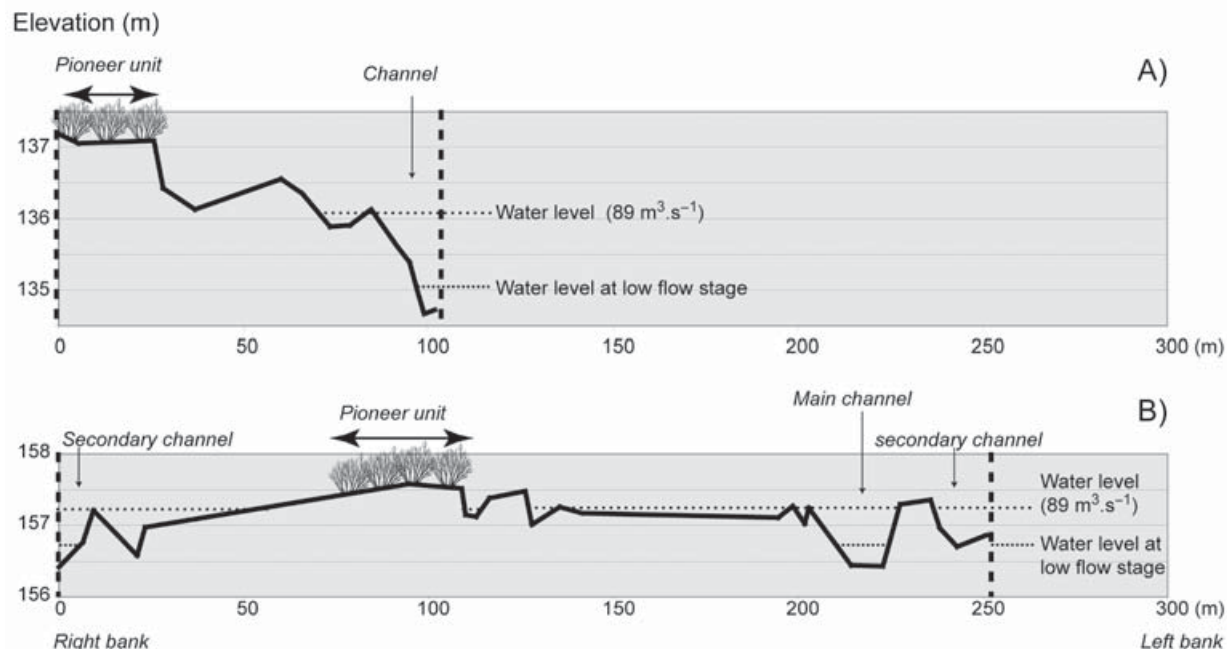
### Physical and structural differences between study reaches

Channel geometry differed between the embanked and unconstrained study reaches principally in terms of active channel width. In the embanked reach, active channel width ranged from 70 to 110 m, while in the unconstrained reach active channel width ranged from 200 to 500 m. In the embanked reach there was typically a pool on one side of the transversal cross-section, always complemented by a high sediment bar in the remaining portion of the cross-section (Figure 2). This configuration is a pattern that has developed since engineering works were completed 200 years previously (Landon, 1999). Pioneer units of vegetation were thus always located along the right or left bank rather than in the middle of the channel. In the unconstrained reach, erosion and the location of pioneer units of woody vegetation demonstrated a scattered distribution across profiles. In some cases there were many side-channels in addition to the main channel, contributing to several localized areas of erosion along each of the transversal cross sections.

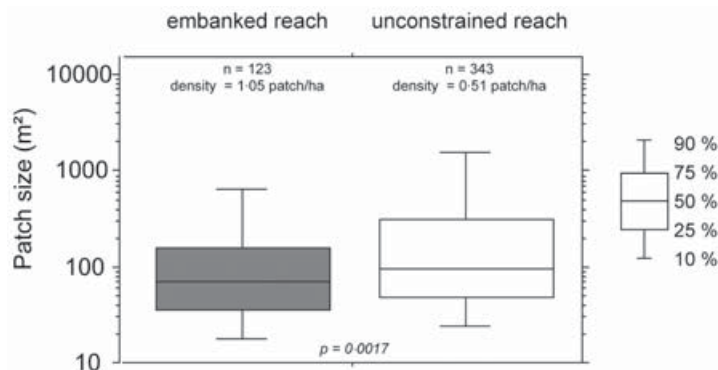
Differences in channel geometry between the embanked and unconstrained reaches can also be observed in terms of elevation along the channel profiles. Median relative elevations above the deepest point for each cross section were highest in the embanked study reach (1.3 m versus 1.1 m). Relative elevations reaching 2 m along each of the cross sections in the embanked reach were more frequent compared with the unconstrained reach (9.2–26.7% of constrained transect lengths in comparison with 5.7–18.2% of unconstrained transects). In both study reaches, pioneer units of woody vegetation occupied the highest points along cross sections. Because of the distributional differences in elevation between the two contrasting channel reaches, pioneer units of vegetation were invariably located at elevations that were twice as high in the embanked study reach (Table I).

During a discharge of 89 m<sup>3</sup> s<sup>-1</sup> (Saillans station, 18/19 April 2005), water levels were significantly higher in the embanked study reach compared with the unconstrained study reach with respective median elevations of 101 and 74 cm above the summer baseflow water level (Mann–Whitney test,  $p < 0.001$ ). This difference corresponds to a 35% difference in water heights between reaches for this same discharge.

The number and surface areas of pioneer islands were significantly greater in the unconstrained reach compared with the embanked reach (i.e. the area of islands in the unconstrained reach were on average 25 m<sup>2</sup> larger than in the constrained reach; Mann–Whitney test,  $p = 0.0017$ ) (Figure 3). Pioneer island density per unit area was, on the other hand, lower in the unconstrained reach compared with the embanked reach (0.5 vegetated patches ha<sup>-1</sup> versus 1.1 vegetated patches ha<sup>-1</sup>).



**Figure 2.** Examples of two cross-sections: (A) in embanked study reach; (B) in unconstrained study reach.



**Figure 3.** Size distribution of pioneer islands (in m² for islands greater than 10 m²).

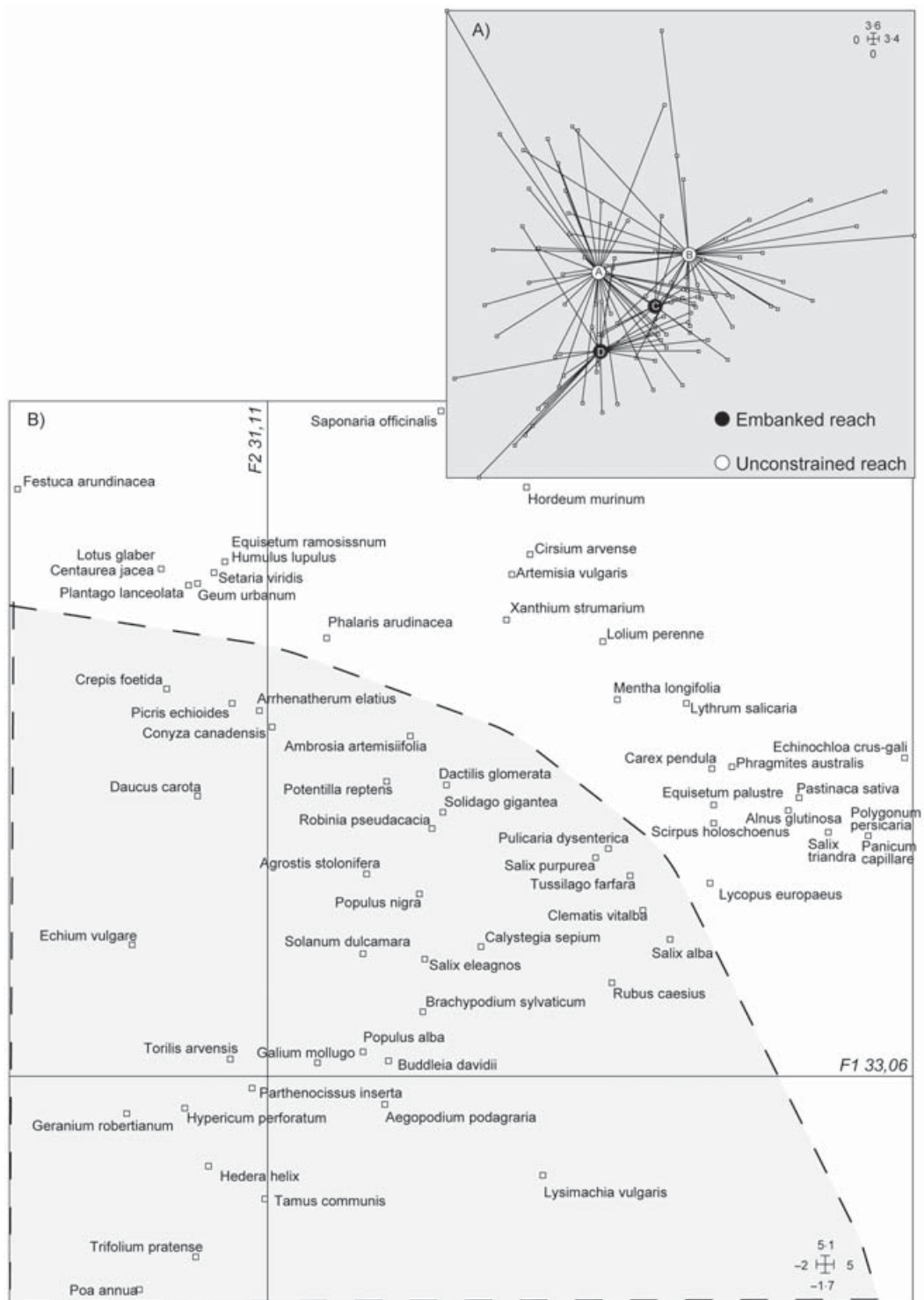
### Characteristics of pioneer woody vegetation units

In both study reaches, all trees cored in 2001 suggested ages of between 6 and 7 years. Tree ages must, however, be interpreted with caution since significant burial by sediment may lead to an underestimate of true tree ages (i.e. where tree age is determined for a side-branch rather than the main tree trunk). Evidence to support the estimated timing of colonization of the trees that have been cored is provided by aerial photographs, which also indicate a likely initial colonization of the active channel in 1994 or 1995, possibly after a major flood during January 1994 (discharge of 387 m³ s⁻¹ at Saillans, equivalent to a  $Q_{50}$  event).

There were only three plant species that occurred uniquely in the pioneer woody vegetation units of the embanked reach (*Poa annua*, *Parthenocissus inserta* and *Trifolium pratense*). These had relative frequency values of 8.1, 2.7 and 2.7, respectively. This contrasts with 33 vegetation species encountered uniquely within the unconstrained reach. These results are confirmed by a within-reach analysis of floristic similarity. Vegetation sampled in quadrats within the embanked reach had a greater index of similarity than vegetation sampled in quadrats within the unconstrained reach (similarity index of 0.43 versus 0.37,  $p < 0.001$ ).

A factorial analysis (DCA) on the complete set of vegetation samples in both study reaches (108 quadrats with a total of 64 species; Figure 4) demonstrates that (i) pioneer vegetation units in the embanked and unconstrained reaches





**Figure 4.** Plots of (A) samples and (B) species with respect to the first two axes of a detrended correspondence analysis (DCA). Axis limits are indicated in the corner of each plot. In (B) the area shaded in grey denotes the common pool of species found in the two study reaches, whereas the unshaded area includes species that were only found in the unconfined reach.

**Table II.** Species richness, density and growth in pioneer woody vegetation units. The median and inter-quartile range of vegetation species is given for the quadrats in the embanked or unconstrained study reaches

		Embanked reach	Unconstrained reach	p
Specific richness (No. of species per quadrat, 4 m <sup>2</sup> )	Ligneous species	2 (1)	3 (2)	<0.001
	Herbaceous species	5 (3)	6 (3)	<0.01
	All species	6 (2)	9 (3.5)	<0.001
Density (No. of stems per quadrat, 4 m <sup>2</sup> )	<i>Populus nigra</i>	15 (20)	5 (9)	<0.001
	<i>Salix eleagnos</i>	0 (3)	3 (8)	<0.01
	<i>Salix purpurea</i>	0 (1)	1 (6.5)	<0.05
	All species	19 (15)	14 (18)	NS
Mean diameter (cm)	<i>Populus nigra</i>	1.9 (1.3)	1.1 (1.2)	<0.01
	<i>Salix eleagnos</i>	0 (2)	1.4 (2.6)	<0.01
	<i>Salix purpurea</i>	0 (1.2)	0.8 (1.5)	NS
	All species	2.2 (1.1)	1.7 (1.3)	NS

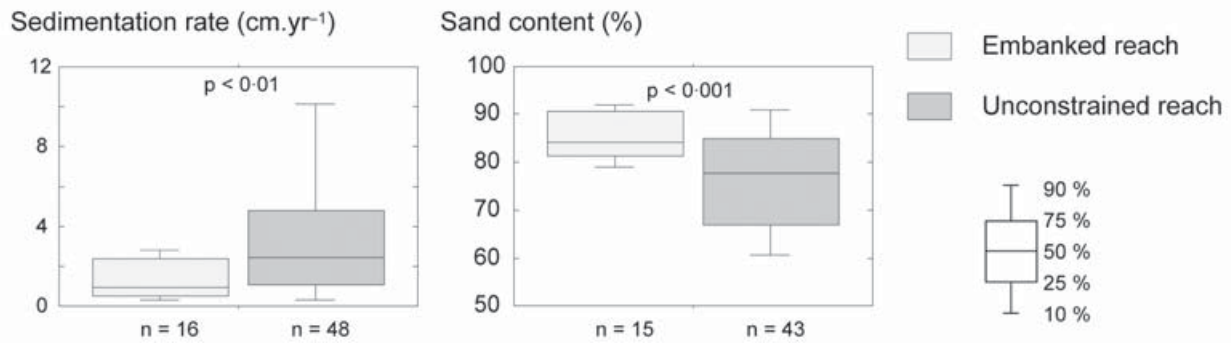
have similar, but non-identical, vegetation communities (ANOSIM,  $p < 0.001$  but  $R = 0.1628$ ) and (ii) some quadrats in the embanked reach are very different from those in the unconstrained reach (Figure 4(A)). Thus, we can distinguish a common pool of species present in the pioneer woody vegetation units present along the downstream sections of the Drôme River (the area shaded in grey in Figure 4(B)) and a relatively high number of vegetation species that are unique to the unconstrained reach (the unshaded area in Figure 4(B)), occurring in several (but not all) of the quadrats.

At the scale of each pioneer island, vegetation species richness was lower in the embanked reach compared with the unconstrained reach (24 and 23 versus 43 and 49 species). Even when we adjust for the positive association between species richness and sampling area by estimating a corrected value of species richness, TSR (the number of species divided by the logarithm of the sampling area) (Whittaker, 1975), species richness is still lower in the embanked reach compared with the unconstrained reach (14.0 and 11.6 versus 20.2 and 22.6). At the quadrat scale, richness is also significantly lower in the embanked reach for both ligneous and herbaceous species and for all species combined (Table II).

Three ligneous species made up 90% of stems present in quadrats along belt transects in both study reaches: *Populus nigra* (46.9%), *Salix eleagnos* (22.9%) and *Salix purpurea* (17.3%). Total stem density was highest in quadrats situated in the embanked reach (median value of 19 stems per m<sup>2</sup> compared with 14 stems per m<sup>2</sup> in the unconstrained reach), although this difference was not statistically significant (Table II). The relative densities of the three most common ligneous species were significantly different between the contrasting study reaches. There were significantly more *P. nigra* stems per unit area in the embanked reach, while stem densities of *S. eleagnos* and *S. purpurea* were significantly greater in the unconstrained reach. The higher local densities of *Populus nigra* and *Salix eleagnos* in the embanked and unconstrained reaches, respectively, were complemented by significantly ( $p < 0.01$ ) larger stem diameters, which is indicative of comparatively good conditions for growth in either reach. Thus, the structure and composition of woody pioneer vegetation species differs between the two study reaches. *P. nigra* dominates pioneer woody vegetation units in the embanked reach, while in the unconstrained reach there is a more heterogeneous composition of ligneous vegetation species (the dominance index for ligneous species is 0.36 and 0.39 in the unconstrained reach versus 0.79 and 0.94 in the embanked reach).

## Patterns of sedimentation

Fine sediment (sand and finer) thickness was significantly lower in the pioneer units of the embanked reach, where maximum sediment thickness was 24 cm compared with 96 cm in the pioneer vegetation units of the unconstrained reach. As islands of pioneer vegetation were thought to be age equivalent in both study reaches, sedimentation rates of sand and finer sediment in pioneer woody vegetation units in the embanked reach were estimated to be lower than in pioneer woody vegetation units of the unconstrained reach (median value of 0.93 versus 2.43 cm yr<sup>-1</sup>,  $p < 0.01$ ) (Figure 5). Median values of the percentage of sand in these sand and finer sediment samples indicate a further significant difference ( $p < 0.001$ ) between the contrasting study reaches, with a value of 90.1% sand in the embanked reach and 60.6% sand in the unconstrained reach. Heterogeneity values for sedimentation rates and for relative proportions of sand in sediment samples were lowest in the embanked reach (Figure 5). Estimates of annual sedimentation rates obtained from sampled sites in the embanked reach varied from 0.2 cm yr<sup>-1</sup> (10th percentile) to 2.8 cm yr<sup>-1</sup>



**Figure 5.** Box and whisker plots of (left) estimates of the annual rate of deposition of sand and finer sediments on pioneer vegetated patches in the two study reaches and (right) the percentage sand content of the sand and finer sediment.

(90th percentile) in comparison with 0.2 (10th percentile) to 10.1 cm yr<sup>-1</sup> (90th percentile) in the unconstrained reach, whereas the 10th and 90th percentile estimates of percent sand in the samples varied from 78 to 91% in the embanked reach and from 60 to 90% in the unconstrained reach.

## Discussion

Previous studies have demonstrated that river embankments limit the re-working of alluvial sediments and favour the establishment of hardwood species outside the embanked area (Bravard *et al.*, 1986; Mendonça-Santos *et al.*, 1997). This field study along the River Drôme has shown how river embankments also generate significant topographical and hydrological changes within the embanked reach. The important changes in hydrogeomorphic conditions have a significant knock-on effect on pioneer units of woody vegetation colonizing the river-bed. The structure, composition and diversity of vegetation are altered in response to shifts in the elevation of colonizable landforms and patterns of sedimentation on these landforms.

### Channel geometry as a factor influencing pioneer woody vegetation structure and composition

Differences in hydraulic conditions between the embanked and unconstrained river reaches contribute to a narrower active zone and greater contrasts in the elevations of colonizable landforms in the embanked reach compared with the unconstrained reach. For an equivalent discharge, water levels in the embanked reach are also higher relative to the lowest level of the river-bed and there is evidence that this affects the relative abundance and growth of woody species.

First, pioneer vegetation units in the embanked reach occurred at higher relative elevations in the active channel with respect to the baseflow water surface level than pioneer vegetation units in the unconstrained reach. This suggests that there are likely to be more hydrological constraints on vegetation in the embanked reach, with comparatively rapid water level drawdown rates following the abatement of flood flows. A faster drawdown may, however, be compensated for by higher water levels during floods. Second, higher water levels for the same flow may produce greater shear stress in the active zone between dikes. This could make the riverbed less stable and lead to a relative coarsening of sediment in the embanked reach. Within pioneer vegetation units, fine sediments (sand and finer) are significantly coarser and thinner, most likely resulting in poorer moisture retention and thus drier conditions. Hydrology seems to be the key factor controlling sediment deposition since there is no evidence of a relationship between woody vegetation density (equivalent in both contexts, Table II) and sedimentation rates (higher rates in the unconstrained reach, Figure 5).

The higher frequency of *P. nigra* in the embanked reach is explained by its greater tolerance of rapid water table drawdown rates compared with the willow species commonly found along the River Drôme (Foussadier, 1998). The distribution of *P. nigra* is also more frequently linked to higher elevations within the active channel than, for example, *Salix eleagnos* (Francis *et al.*, 2006). Moreover, *P. nigra* also has the advantage of good anchorage and, consequently, significant resistance to uprooting (Karrenberg *et al.*, 2003). Where all the evidence is combined, *P. nigra* appears to have a clear competitive advantage over other woody species in the embanked context in comparison with the unconstrained reach, which may further explain its better growth.

In the recruitment stages of its lifecycle, *P. nigra* would be expected to occur in greater densities in the embanked reach, where *P. nigra* seedlings seem to have a greater chance of surviving flood disturbances at their higher elevations in the active channel than seedling recruits in the unconstrained reach. There was some evidence of this, where established pioneer stands in the embanked reach were frequently very densely and widely populated by *P. nigra* saplings of even height. Established pioneer stands in the unconstrained reach were also densely populated in some areas, but evidence of occasional stand dissection by ephemeral channels contributed to what appeared to be a greater overall mix in the age structure of these young stands.

Along the Drôme River, previous phyto-ecological characterization of pioneer islands recognized pioneer vegetation units simply as 'shrubby units' dominated by *Salix eleagnos*, *Salix purpurea* and *Populus nigra* (Franchon, 1996; Bonnefon-Craponne, 1996; Foussadier, 1998). Our results provide evidence of a 'dry island variant' dominated by *P. nigra* in the embanked reach and a comparatively 'mesic island variant' in the unconstrained reach with a more diverse species composition, including numerous *Salix sp.* and *Alnus glutinosa*. Each of these 'variants' appears to have evolved in direct response to the contrasting hydrogeomorphic conditions in the two study reaches.

### Size and heterogeneity of pioneer woody vegetation units as factors influencing vegetation composition and structure

Several differences observed among pioneer woody vegetation units (e.g. species richness) were linked to differences in active channel planform and notably island size. Islands in the embanked reach were always smaller than those in the unconstrained reach, probably due to flow concentration between channel embankments. Higher water levels (for the same discharge) are likely to reduce the amount of sediment deposited within the embanked reach compared with the unconstrained reach, where the area occupied by the river channel itself is comparatively small relative to the surface area of the active channel. The positive effect of patch size on species richness has been extensively discussed and debated by previous authors (MacArthur & Wilson, 1967; Connor & McCoy, 1979; Wu & Vankat, 1995; Holt *et al.*, 1999; Kollmann *et al.*, 1999; Lomolino, 2001). Along the Drôme River, isolation of islands as a factor affecting vegetation species richness does not appear to be relevant in either study reach. This may be explained by the surrounding landscape matrix, which is likely to provide ample supplies of seed and vegetative propagules from both upstream sources and the surrounding forests in close proximity to islands. On the other hand, our results clearly indicate reduced environmental heterogeneity in the embanked reach compared with the unconstrained reach, which may explain lower vegetation species diversity (Williams, 1964; Huston, 1994; Bose, 2001). Kollmann *et al.* (1999) observed the same relationship between pioneer riparian vegetation patch size and species richness and attributed this to the larger sampling areas and related, higher habitat variability within vegetation units of larger surface areas. Microtopography is often cited as an important source of variability (Bratton, 1976; Tweedy *et al.*, 2001). Patterns of sedimentation along the River Drôme contribute to subtle yet seemingly important variations in the colonization potential of landforms. In the embanked reach of the River Drôme there was lower local variability of fine sediments (grain size and abundance) and pioneer islands were smaller and narrower than in the unconstrained reach. Other evidence of greater heterogeneity in the pioneer vegetation units located in the unconstrained reach is given by the vegetation species that occur uniquely in this context. Species occurring here collectively require a broader range of ecohydrological conditions compared with vegetation in the embanked reach. For example, species typical of wetter conditions (e.g. *Alnus glutinosa*, *Carex pendula*, *Phragmites australis* etc.) occurred alongside vegetation species that are associated with drier conditions (e.g. *Cirsium arvense*, *Echium vulgare* etc.). Furthermore, in the unconstrained reach we encountered vegetation species that are associated with (i) coarse, gravelly substrates (e.g. *Xanthium strumarium*, *Setaria viridis* and *Polygonum persicaria*), (ii) grasslands and fallow fields (e.g. *Lolium perenne*, *Pastinaca sativa*, *Torilis arvensis* etc.) and (iii) mature woodlands (e.g. *Geum urbanum*, *Humulus lupulus*, *Clematis vitalba* etc.).

Heterogeneity of pioneer vegetation units appears, furthermore, to be directly linked to island type. Islands in the unconstrained study reach were dissected by small ephemeral channels (probably generated at different points in time) to create a mixture of bars and dense vegetation patches. Considering the three pioneer vegetation unit types described by Gurnell *et al.* (2001), the two islands in the embanked reach might be classified as 'building islands'. In the unconstrained reach, they are 'complex islands' generated from components of 'building islands'. In our case, island dissection by shifting river channels creates a similar level of complexity to 'island coalescence' as described by Gurnell *et al.* (2001).

### Perspectives for the conservation and rehabilitation of pioneer woody riparian vegetation units

Along many western European rivers, pioneer woody vegetation units have strongly regressed over the past two centuries, notably in response to civil engineering works. As a result, the question of the long-term conservation of

these fleeting vegetation units and of their associated genetic resource is of increasing relevance (Lefèvre *et al.*, 2001; Douhovnikoff *et al.*, 2005).

At the scale of pioneer woody vegetation units in active river channels, further scientific work is needed especially regarding (i) the effects, not integrated into the present study, of living and dead vegetation on patterns of sedimentation and habitat variability (i.e. the relative influence of high concentrations of large wood deposited in an unconstrained reach compared with an embanked reach) (Tabacchi *et al.*, 2000; Gurnell *et al.*, 2001), (ii) our understanding of the physical conditions defining vegetation community and species divergences, such as spatial segregation of genders due to differences in water and/or nutrient availability (Hughes *et al.*, 2000), and (iii) the accurate quantification of riparian vegetation species thresholds (i.e. hydrological, disturbance and other thresholds), inclusive of the implications these thresholds have for wood production (i.e. dead/live wood biomass ratios) and different modes of reproduction (sexual/vegetative) etc. (Francis *et al.*, 2006).

The preservation of functional sites for pioneer species conservation must be managed at the river basin scale. Our results highlight the need for flow management (Cordes *et al.*, 1997; Johnson, 2000; Hughes & Rood, 2003) to be coupled with the management of channel dynamics (lateral erosion and sediment deposition processes). This can be achieved through the combined management of bedload transport and river corridors: i.e. encouraging the construction of an 'erodible corridor' (Dufour, 2005; Piégay *et al.*, 2005), rehabilitation practices involving the setting back of levees or local dike removal (Rohde, 2004). We can expect that channel widening would offer a positive restoration strategy in terms of an increase in riparian species richness, where a range of physical conditions (i.e. variable hydraulic patterns and water availability across the active channel) are created.

While there is no single solution for managing embanked reaches along gravel bed rivers (Piégay *et al.*, 2006), our results indicate how pioneer communities can be used as relevant indicators (*sensus* Water Framework Directive) of the hydrogeomorphic functional status of a river and thus of restoration practices that can be considered successful in terms of habitat diversification and increases in riparian species richness following embankment removal.

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## References

- Baron C, Vang E. 1996. *StatView User Guidebook*. Abacus-concepts: Berkeley, CA.
- Barsoum N. 2001. Regeneration requirements and promotion measures. In *EUFROGEN Technical Bulletin: In Situ Conservation of Populus nigra*, Lefèvre F, Barsoum N, Heinze B, Kajba D, Rotach P, de Vries SMG, Turok J (eds). International Plant Genetic Resources Institute: Rome; 16–35.
- Barsoum N, Hughes FMR. 1998. Regeneration response of black poplar to changing river levels. In: Wheaton H, Kirby C (eds). *Hydrology in a Changing Environment*, Volume I, Wiley: New York; 397–412.
- Bonnefon Craponne E. 1996. *La Réserve Naturelle des Ramières: Document de Cartographie Ecologique*, unpublished master's thesis, Université Joseph Fourier, Grenoble.
- Bose U. 2001. Relative importance of isolation, area and habitat heterogeneity for vascular plant species richness of temporary wetlands in east-German farmland. *Ecography* **24**: 722–730.
- Bradley CE, Smith DG. 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. *Canadian Journal of Botany* **64**: 1433–1442.
- Bratton SP. 1976. Resources division in an understory herb community: responses to temporal and microtopographic gradients. *The American Naturalist* **110**: 679–693.
- Bravard JP, Amoros C, Pautou G. 1986. Impacts of civil engineering works on the successions of communities in a fluvial system. A methodological and predictive approach applied to a section of the Upper Rhône River, France. *Oikos* **47**: 92–111.
- Brooks A. 1988. *Channelized Rivers: Perspectives for Environmental Management*. Wiley: New York.
- Clarke KR. 1993. Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology* **18**: 117–143.
- Connor EF, McCoy ED. 1979. The statistics and biology of the species–area relationship. *The American Naturalist* **113**: 789–796.
- Cordes LD, Hughes FMR, Getty M. 1997. Factors affecting the regeneration and distribution of riparian woodlands along a northern prairie river: the Red Deer River, Alberta, Canada. *Journal of Biogeography* **24**: 675–695.
- Décamps H. 1996. The renewal of floodplain forests along rivers: a landscape perspective. *Verhandlungen der Internationalen Vereinigung Fuer Theoretische und Angewandte Limnologie* **26**: 35–59.



- Douhovnikoff V, McBride JR, Dodd RS. 2005. *Salix exigua* clonal growth and population dynamics in relation to disturbance regime variation. *Ecology* **86**(2): 446–452.
- Dufour S. 2005. *Contrôles Naturels et Anthropiques de la Structure et de la Dynamique des Forêts Riveraines des Cours d'Eau du Bassin Rhodanien (Ain, Arve, Drôme et Rhône)*, unpublished PhD thesis, University of Lyon.
- Edwards PJ, Kollmann J, Gurnell AM, Petts GE, Tockner K, Ward JV. 1999. A conceptual model of vegetation dynamics on gravel bars of a large Alpine river. *Wetlands Ecology and Management* **7**: 141–153.
- Foussadier R. 1998. *Initiation des Successions Végétales dans les Lits Endigués des Cours d'Eau Alpines, Influence des Paramètres Abiotiques sur la Régénération des Salicacées*, unpublished PhD thesis, Université Joseph Fourier, Grenoble.
- Franchon C. 1996. *Cartographie Phytoécologique de la Réserve Naturelle des Ramières du Val de Drôme dans une Optique de Dynamique*, unpublished master's thesis, Université Joseph Fourier, Grenoble.
- Francis RA, Gurnell AM, Petts GE, Edwards PJ. 2006. Riparian tree establishment on gravel bars: interactions between plant growth strategy and the physical environment. In: Sambrook-Smith G, Best J, Bristow C, Petts GE (eds). *Braided Rivers: Process, Deposits, Ecology and Management*, Special Publication 36, International Association of Sedimentologists: Oxford; 396.
- Girel J, Garguet-Duport B, Pautou G. 1997. Present structure and construction processes of landscapes along diked European valleys. *Environmental Management* **21**(6): 891–907.
- Girel J, Manneville O. 1998. Present species richness of plant communities in Alpine stream corridors in relation to historical river management. *Biological Conservation* **85**(1/2): 21–33.
- Guilloy-Froget H, Muller E, Barsoum N, Hughes FMR. 2002. Regeneration of *Populus nigra* L. (Salicaceae): dispersal, germination and survival in changing hydrological conditions. *Wetlands* **22**: 478–488.
- Gurnell AM, Petts GE, Hannah DM, Smith BPG, Edwards PJ, Kollmann J, Ward JV, Tockner K. 2001. Riparian vegetation and island formation along the gravel-bed Fiume Tagliamento, Italy. *Earth Surface Processes and Landforms* **26**: 31–62.
- Hammer Ø, Harper DAT, Ryan PD. 2004. *PAST – PAleontological Statistics*, Version 1.32. <http://folk.uio.no/ohammer/past> [15 August 2005].
- Holt RD, Lawton JH, Polis GA, Martinez ND. 1999. The trophic rank and the species–area relationship. *Ecology* **80**: 1495–1504.
- Hughes FMR, Barsoum N, Richards KS, Winfield M, Hayes A. 2000. The response of male and female black poplar (*Populus nigra* L. subspecies *betulifolia* (Pursh) W. Wettst.) cuttings to different water table depths and sediment types: implications for flow management and river corridor biodiversity. *Hydrological Processes* **14**: 3075–3098.
- Hughes F, Harris T, Richards K, Pautou G, El Hames A, Girel J, Peiry JL, Barsoum N. 1997. Woody riparian species response to different soil moisture conditions: laboratory experiments on *Alnus incana* (L.) Moench. *Global Ecology and Biogeography Letters* **6**: 247–256.
- Hughes FMR, Rood SB. 2003. Allocation of river flows for restoration of floodplain forest ecosystems: a review of approaches and their applicability in Europe. *Environmental Management* **32**(1): 12–33.
- Huston M. 1994. *Biological Diversity*. Cambridge University Press: Cambridge.
- Johnson WC. 2000. Tree recruitment and survival in rivers: influence of hydrological processes. *Hydrological Processes* **14**: 3051–3074.
- Kalischuk AR, Rood SB, Mahoney JM. 2001. Environmental influences on seedling growth of cottonwood species following a major flood. *Forest Ecology and Management* **144**: 75–89.
- Karrenberg S, Edwards PJ, Kollmann J. 2002. The life history of Salicaceae living in the active zone of floodplains. *Freshwater Biology* **47**: 733–748.
- Karrenberg S, Blaser S, Kollmann J, Speck T, Edwards PJ. 2003. Root anchorage of saplings and cuttings of woody pioneer species in a riparian environment. *Functional Ecology* **17**: 170–177.
- Kollmann J, Vieli M, Edwards PJ, Tockner K, Ward JV. 1999. Interactions between vegetation development and island formation in the Alpine river Tagliamento. *Applied Vegetation Science* **2**: 25–36.
- Landon N. 1999. *L'évolution Contemporaine du Profil en Long des Affluents du Rhône Moyen, Constat Régional et Analyse d'un Hydrosystème Complexe, la Drôme*, unpublished PhD thesis, Université Sorbonne Paris IV.
- Landon N, Piégay H. 1994. L'incision de deux affluents submediterranéens du Rhône: la Drôme et l'Ardèche. *Revue de Géographie de Lyon* **69**: 63–72.
- Lefèvre F, Barsoum N, Heinze B, Kajba D, Rotach P, de Vries SMG, Turok J. 2001. *EUROGEN Technical Bulletin: In Situ Conservation of Populus nigra*. International Plant Genetic Resources Institute: Rome.
- Lomolino MV. 2001. The species–area relationship: new challenges for an old pattern. *Progress in Physical Geography* **25**(1): 1–21.
- MacArthur RH, Wilson EO. 1967. *The Theory of Island Biogeography*. Princeton University Press: Princeton.
- McBride JR, Strahan J. 1984. Establishment and survival of woody riparian species on gravel bars of an intermittent stream. *The American Midland Naturalist* **112**: 235–245.
- Mendonça-Santos ML, Guenat C, Thevoz C, Bureau F, Vedy JC. 1997. Impacts of embanking on the soil–vegetation relationships in a floodplain ecosystem of a pre-alpine river. *Global Ecology and Biogeography Letters* **6**: 339–348.
- Merigliano MF. 1998. Cottonwood and willow demography on a young island, Salmon River, Idaho. *Wetlands* **18**: 571–576.
- Naiman RJ, Décamps H, McClain ME. 2005. *Riparia: Ecology, Conservation and Management of Streamside Communities*. Elsevier–Academic: San Diego.
- Osterkamp WR. 1998. Processes of fluvial-island formation, with examples from Plum Creek, Colorado, and Snake River, Idaho. *Wetlands* **18**(4): 530–545.
- Pautou G, Girel J. 1994. Interventions humaines et changements de la végétation alluviale dans la vallée de l'Isère (de Montmélian au Port de St Grevais). *Revue de Géographie Alpine* **2**: 127–146.
- Peeters ETHM, Tachet H. 1989. Comparison of macrobenthos in braided and channelized sectors of the Drôme river, France. *Regulated Rivers: Research and Management* **4**: 317–325.

- Peiry JL. 1988. *Approche Géographique de la Dynamique Spatio-Temporelle des Sédiments sur un Cours d'Eau Intramontagnard; l'Exemple de la Plaine Alluviale de l'Arve (Haute-Savoie)*, unpublished PhD Thesis, Université Jean Moulin Lyon 3.
- Piégay H, Darby SE, Mosselman E, Surian N. 2005. A review of technique available for delimiting the erodible river corridor: a sustainable approach for managing bank erosion. *River Research and Applications* **21**: 773–789.
- Piégay H, Grant G, Nakamura F, Trustrum N. 2006. Braided river management: from assessment of river behaviour to improved sustainable development. In: Sambrook-Smith G, Best J, Bristow C, Petts GE (eds) *Braided Rivers: Process, Deposits, Ecology and Management*, Special Publication 36, International Association of Sedimentologists: Oxford; 396.
- Poinsart D. 1994. Gestion des systèmes fluviaux aménagés: structure des dépôts et mobilité des alluvions du lit dans les vieux Rhône de Miribel et Donzère-Mondragon. *La Houille Blanche* **5/6**: 13–22.
- Rameau JC, Manson D, Dumé G, Timbal J, Lecointe A, Dupont P, Keller R. 1989. *Flore Forestière Française, Guide Ecologique Illustré*. Institut pour le Développement Forestier: Paris.
- Richards KS. 1976. The morphology of the riffle–pool sequence. *Earth Surface Processes and Landforms* **1**: 78–88.
- Ricks C. 1995. Effects of channelization on sediment distribution and aquatic habitat at the mouth of Redwood Creek, northwestern California. In: Nolan KM, Kelsey HM, Marron DC (eds). *Geomorphic Processes and Aquatic Habitat in the Redwood Creek Basin, Northwestern California*, Professional Paper 1454, US Geological Survey: Washington, DC; Q1–Q17.
- Rohde S. 2004. *River Restoration: Potential and Limitations to Re-Establish Riparian Landscapes. Assessment and Planning*, PhD thesis, Swiss Federal Institute of Technology, Zurich.
- Rood SB, Mahoney JM. 2000. Revised instream flow regulation enables cottonwood recruitment along the St. Mary River, Alberta, Canada. *Rivers* **7**: 109–125.
- Shafroth PB, Auble GT, Stromberg JC, Patten DT. (1998). Establishment of woody riparian vegetation in relation to annual patterns of streamflow, Bill Williams River, Arizona. *Wetlands* **18**: 577–590.
- Strahler AN. 1957. Quantitative analysis of watershed geomorphology. *American Geophysical Union Transactions* **38**: 913–920.
- Tabacchi E, Lambs L, Guilloy H, Planty-Tabacchi AM, Muller E, Décamps H. 2000. Impact of riparian vegetation on hydrological processes. *Hydrological Processes* **14**: 2959–2976.
- Thompson A. 1986. Secondary flow and the pool–riffle unit: a case study of the processes of meander development. *Earth Surface Processes and Landforms* **11**: 631–641.
- Tweedy KL, Scherrer E, Evans RO, Shear TH. 2001. Influence of microtopography on restored hydrology and other wetland functions. *ASAE Annual International Meeting*, Sacramento, CA, 2001, Paper 01-2061.
- Van Looy K, Honnay O, Bossuyt B, Hermy M. 2003. The effects of river embankment and forest fragmentation on the plant species richness and composition of floodplain forests in the Meuse valley, Belgium. *Belgian Journal of Botany* **136**(2): 97–108.
- Van Splunder I, Coops H, Voesenek LACJ, Blom CWPM. 1995. Establishment of alluvial forest species in floodplains: the role of dispersal timing, germination characteristics and water level fluctuation. *Acta Botanica Neerlandica* **44**: 269–278.
- Ward JV, Tockner K, Edwards PJ, Kollmann J, Gurnell AM, Petts GE, Brestschko G, Rossaro B. 2000. Potential role of island dynamics in river ecosystems. *Verhandlungen der Internationalen Vereinigung Fuer Theoretische und Angewandte Limnologie* **27**: 2582–2585.
- Whittaker RH. 1975. *Communities and Ecosystems*. MacMillan: New York.
- Williams CB. 1964. *Patterns in the Balance of Nature*. Academic: London.
- Wu J, Vankat JL. 1995. Island biogeography: theory and applications. In: Nierenberg WA (ed.), *Encyclopedia of Environmental Biology*, Vol. 2, Academic: San Diego; 371–379.