



Relative contributions of sexual and asexual regeneration strategies in *Populus nigra* and *Salix alba* during the first years of establishment on a braided gravel bed river

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Abstract. *Populus nigra* L. var *betulifolia* and *Salix alba* L. var *alba* are early successional riparian tree species threatened throughout Continental Europe by significant changes to the natural physical processes governing their natural habitat – geomorphologically active floodplains. River management activities have dramatically altered natural patterns of river flow and rates of sediment delivery along rivers, with possible consequences for the balance between sexual and asexual regeneration strategies in these species. Conservation strategies will benefit from a greater understanding of the ways in which dynamic physical processes on the floodplain influence sexual and asexual recruitment. This paper describes a field survey investigating the relative abundance and spatial distributions of *P. nigra* and *S. alba* sexual and asexual recruits during the first years of establishment along a braided gravel bed river. Sexual and asexual recruits were identified by excavation along transects in a wet and a dry field season and distributional differences were described in terms of elevation on the floodplain, local sediment type and exposure to floodwaters. Regeneration was overwhelmingly from seed in the first 2–3 years following recruitment, but poor survival rates among sexual recruits saw a shift in the relative abundance of regeneration strategies over time. In relating hydrological data to recruitment, unseasonal flood disturbances had a negative effect on recruitment from seed and a positive effect on vegetative regeneration. Seedlings were associated with fine sediment deposits and were restricted primarily to low elevations on the flood plain, while asexual recruits had a wider spatial distribution. Certain microsite types were unique to either regeneration strategy.

Key words: clonal vs. sexual recruitment, flood disturbance, floodplain woodland, microsites, *Populus nigra*, regeneration, river, Salicaceae, *Salix alba*, spatial pattern

Introduction

An understanding of the relative abundance and distribution of sexually and asexually derived individuals in natural populations of clonal plant species provides valuable information for the conservationist and population biologist. It allows for (i) estimates of the genotypic diversity of a population, thereby

contributing to an understanding of effective population sizes (Parker and Hamrick, 1992; Lynch, 1996), (ii) assessment of the implications of variation in key life history parameters for population and community dynamics (Falińska, 1995; Gardner and Mangel, 1999) and (iii) the testing of hypotheses relating to evolutionary change through selective and demographic pressures (Jelinski and Cheliak, 1992; Harada *et al.*, 1997).

Among those studies seeking to understand the respective contributions and spatial distributions of sexual and asexual regeneration strategies in clonal plant species, surprisingly few have been devoted to woody species, despite the very significant role they play in communities as 'ecosystem engineers' (but see Held, 1983; Cheliak and Pitel, 1984a; Huenneke, 1985; De Steven, 1989; Hermandutz *et al.*, 1989; Escaravage *et al.*, 1998). Frequently there is also only limited attention given to the processes (biotic or abiotic) influencing sexual and asexual recruitment. Despite clear evidence of significant variation in the balance and distribution of sexual and asexual individuals within (Falińska, 1995; Prati and Schmid, 2000) and among populations of clonal plant species (Read and Hill, 1985; Maddox *et al.*, 1989; Mandujano *et al.*, 1998), few studies have attempted to address the source(s) of this variation. Harshness of environmental conditions (i.e. in terms of nutrient availability, levels of competition, climatic conditions) and natural disturbances, of differing frequencies and intensities, have been cited in several cases as determining factors in the balance of recruitment strategies in clonal populations (De Steven, 1989; Hunter, 1993; Kudoh *et al.*, 1999; Tardif and Bergeron, 1999; Prati and Schmid, 2000). This may be attributed to variable responses of sexually and asexually derived individuals of the same species along resource gradients, where variation in response can be related to fitness and physiological differences between regeneration strategies (Ellstrand and Antonovics, 1985; Michaels and Bazzaz, 1989; Mandujano *et al.*, 1998). Differential propagation and dispersal, or spread of sexual and asexual recruits, may further explain disparities in the distributions of sexually and asexually derived individuals.

Populus nigra L. var *betulifolia* and *Salix alba* L. var *alba* are early successional floodplain woodland species capable of both sexual and asexual regeneration. Occurring along rivers with relatively free-draining substrates throughout Continental Europe, both species often dominate the active zones of alluvial plains where they play important roles as the first woody species to colonise and stabilise sites recently disturbed by flooding. Flooding events, while momentarily highly destructive, act in favour of these species by releasing space and resources on the floodplain; i.e. competing vegetation is removed, water tables are replenished and there is a renewal of nutrient-enriched sediment deposits, providing ideal colonisable surfaces for regeneration. However, despite having breeding systems designed to maximise sexual recruitment (*P. nigra* and *S. alba* are both out-crossing species with high fecundity and very

high production of germinable, wind-dispersed seeds, timed for release from May to mid-July to coincide with the abatement of spring floods), frequent and unpredictable flood disturbances on the natural floodplain, followed by rapidly declining water table levels, provide a narrow window of opportunity for recruitment from short-lived seeds. Vegetative regeneration, as an alternative regeneration strategy, is promoted through extended periods of submergence and/or mechanical damage to parental plants which act to stimulate dormant primordia in roots and shoots (Barsoum, 1998). Asexual regeneration in these species can thus occur from translocated fragments of the parent plant, or through sprouting from roots and shoots of damaged plants (Legionnet *et al.*, 1997); sprouting is otherwise not spontaneous in these species.

Over the past century, an intensification in river management activities throughout Europe (e.g. impoundments, gravel extraction, channelisation, water abstraction) has resulted in significant alterations to natural patterns of sediment deposition, water table fluctuations and river flow, affecting in particular, the frequency, timing and magnitude of flooding events (Petts, 1989). These changes have implications not only for regeneration potential in *P. nigra* and *S. alba*, but potentially also for the balance and distribution of sexual and asexual recruits in these species. Slow early growth and limited re-sprouting abilities in seedlings (Van Splunder *et al.*, 1996; Barsoum and Hughes, 1998) leaves this regeneration strategy comparatively susceptible to the mechanical impact of floods, burial and drought stress; this is especially true during the first few months following seed dispersal when seedlings are most vulnerable. Vegetative recruits have the advantage of carbohydrate reserves, pre-formed root and shoot primordia (Schier and Campell, 1976) and possible pre-established links to water sources via the parent plant; these physiological differences would be expected to confer certain advantages in the face of flooding events of increasing irregularity, frequency and/or magnitude, as well as unpredictable fluctuations in ground water levels, by reducing the degree of reliance on the timing of disturbances and water table levels. There may also be greater survival rates among vegetative recruits where sediment delivery rates to floodplains are significantly altered; vegetative recruits are expected to show better survival following burial by sediments and are expected to be less dependent on specific microsite types for recruitment (e.g. areas with damp, fine sediment deposits).

The majority of studies investigating regeneration in members of the Salicaceae family (willows and poplars) have focused on seedling recruitment as the main regeneration strategy employed (Noble, 1979; Bradley and Smith, 1986; Johnson, 1994; Van Splunder *et al.*, 1995), with vegetative recruitment remaining primarily an observed phenomenon (Everitt, 1968; Zasada *et al.*, 1981; McBride and Strahan, 1984; Shafroth *et al.*, 1994). Only Rood *et al.* (1994) and Gom and Rood (1999) are known to offer detailed quantitative

investigations of the range and relative proportions of sexual and asexual regeneration strategies in a number of *Populus* species, both studies highlighting significant recruitment differences between related species. In light of the intense modification of dynamic physical processes along European river courses, there is a need for a better understanding of recruitment in the Salicaceae species occurring along these rivers and in particular, to understand how the balance in regeneration strategies might be affected by these changes.

The aims of this study, therefore, were: (i) to determine, by excavation techniques along transects on a semi-natural, braided gravel bed river floodplain, the primary regeneration strategies of *P. nigra* and *S. alba* (during the first year of their establishment) in a hydrographically quiet year and in a year of unseasonal flood disturbances; (ii) to investigate, in these contrasting field seasons, the spatial distributions of sexual and asexual recruits of *P. nigra* and *S. alba* (during their first year of establishment) along elevational gradients and in relation to different microsite types and (iii) to assess temporal variations (first 4 years following establishment) in the relative proportions of sexually and asexually derived recruits.

Materials and methods

Study area

Field work was undertaken in the Ramières Nature Reserve along a 2 km unembanked reach of the Drôme River floodplain in south-eastern France (44°44' N and 4°57' E; 155 m altitude). Along this reach the study was conducted uniquely in the active alluvial zone of the floodplain (up to 400 m wide) which is bordered by over 110 ha of riparian woodland. Significant proportions of this woodland comprise mature *P. nigra* and *S. alba* trees, producing prodigious quantities of seed on an annual basis (e.g. at least 74 *P. nigra* seeds caught in 37 × 24 cm² seed traps from May to July in both 1995 and 1996; Barsoum, 1998). The active alluvial plain is a highly heterogeneous environment comprising a wide variety of depositional features which are intersected by a network of large and smaller channels. The granulometry at low elevations, where there is high current velocity (i.e. adjacent to main channels), consists essentially of coarse material (sand, gravel, cobbles and stones). Along the edges of lesser channels and also downstream of debris dams and tufts of instream vegetation, reduced current velocity allows for the deposition of fines, leaving a poorly sorted profile of silt, coarse and fine sands and gravel. Scattered throughout the floodplain are also pockets of silty loam deposits where significant quantities of fine materials have accumulated in depressions in the floodplain relief. Occasionally, early successional woody riparian vegetation is

able to develop and form islands in the active zone promoting extensive zones of aggradation.

The regional climate can be described as warm temperate (mean summer temperature of 20 ± 0.4 °C) and is influenced by elements of both a Mediterranean and Continental climate. Rainfall is periodic with violent rainstorms in autumn and spring, but a dry period in the months of July and August. The Drôme River itself is a 6th order (by the Strahler 1957 system) free-flowing, piedmont river (daily mean discharge 18.4 ± 0.2 m³ sec⁻¹; at Saillans, CNR). The combination of a steep slope ($3\text{--}28$ m km⁻¹), abundant bedload and a hydrological regime characterised by high flood peaks defines the braided pattern of this gravel bed river. Flood peaks are typically in the early spring and autumn, while the summer months are generally periods of exceptionally low flow ($2\text{--}3$ m³ sec⁻¹).

The study was carried out during the summers of 1995 and 1996. Climatic and hydrological conditions differed considerably between these 2 years over the summer periods (May–August) (Fig. 1), while outside of these periods, flood peaks were of similar frequency and magnitude. 1995 was comparatively dry, with low flow throughout the summer; between May and August, total rainfall was 182 mm compared with an average of 280 mm (Divajeu, Météo, France). In the summer of 1996, sporadic heavy downpours in May, June and July resulted in a fluctuating hydrograph eventually culminating in a one in 50-year summer flooding event (168 m³ sec⁻¹; Loriol, CNR) on the 8th of July; rainfall was 426 mm from May to August in this year.

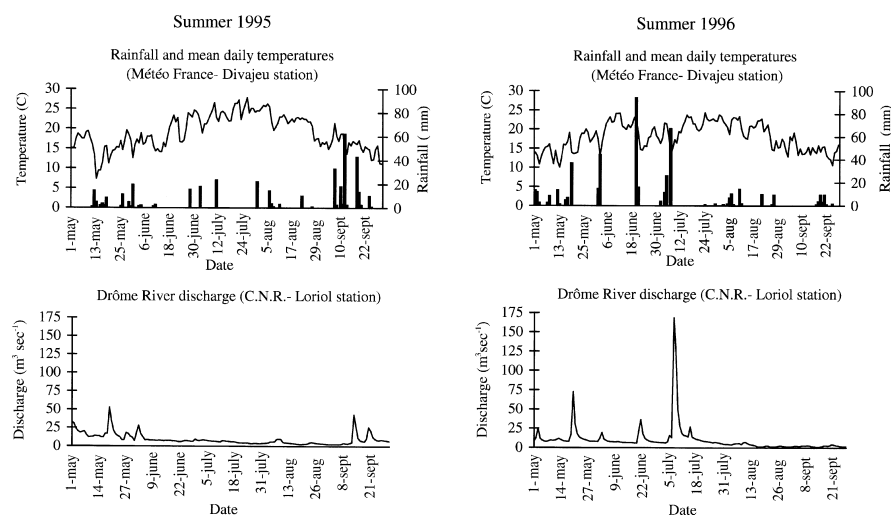


Figure 1. Climatic and hydrological conditions on the Drôme River over the summers of 1995 and 1996.

Sampling procedure

In August 1995 and 1996, detailed field surveys of *P. nigra* and *S. alba* recruitment were undertaken along 8–14 non-permanent, 20 cm wide belt transects forming a combined length of 1.5 km in both years; each transect was divided into 20 cm wide \times 100 cm long sampling units. Transects were positioned to cross the open floodplain generally in a north-south direction from a randomly chosen point along the right bank to a point directly opposite on the left bank (transect lengths varied from 107 to 280 m). The ends of the transects were defined by established floodplain woodland, or a major terrace (more than 3.0 m above river stage). Where dense stands of mature vegetation (an island) or large piles of woody debris were encountered, the transect was continued on the opposite side.

Within each 20 \times 100 cm² sampling unit along the belt transects, any sexual or asexual *P. nigra* and *S. alba* recruits of the year were excavated to determine the origin of regeneration and their positions along the transects were recorded. Seedlings were distinguished from vegetatively regenerating individuals by their smaller size and by their tap roots which tapered progressively downwards displaying limited lateral root extension (Rood *et al.*, 1994). Vegetative regeneration was often instantly recognisable as clumps of sizeable shoots rising vertically from the ground and occasionally occurring in rows. Four different categories of vegetative recruitment were recognised:

- (1) Flood training: sprouting of shoots from buried parental stems which were frequently deflected downstream, parallel to the main channel, by floodwaters (Everitt, 1968),
- (2) Translocated fragments: sprouting of shoots from completely detached fragments of the parental stem,
- (3) Coppice re-growth: resprouting from a parental shoot above the ground surface either in response to beaver foraging, or mechanical damage from floods,
- (4) Suckering: sprouting of shoots from roots exposed by floodwaters. Where exposed roots were re-buried, suckering was only identifiable by establishing a link with lateral root connections to a parental plant nearby.

Multiple shoots from the same plant were not each counted as separate vegetative recruits; one vegetative recruit comprised all inter-connected ramets. To provide comparative measurements of above-ground biomass, total shoot dry weights (10 days; 70 °C) of all sexual recruits, all asexual recruits linked to a parental plant (i.e. suckers, flood-trained shoots, and coppice shoots) and all asexual recruits not linked with the parental plant (translocated fragment shoots) were determined; i.e. within each 20 \times 100 cm² sampling unit along the transects, above-ground biomass of seedlings was combined, while each vege-

tative recruit was weighed individually. Where multiple adjacent shoots sprouting from the ground were identified as vegetative recruits originating from the same parental unit, only the largest vegetative shoot among these in any given $20 \times 100 \text{ cm}^2$ sampling unit was removed to substrate level for destructive measurements. A number of descriptive parameters were also measured along the transects at 1 m intervals. These included (1) elevation on the floodplain with respect to river stage and (2) predominant microsite type encountered (more than 50% cover in each $20 \times 100 \text{ cm}^2$ sampling unit).

Eight distinct microsite types were identified on the open floodplain as colonisable patches created by flood disturbances. These differed in terms of elevation on the floodplain and texture of surface sediments (either predominantly gravel, sand or fine sand and silt), the latter revealing the extent of erosional or depositional processes at work in a localised area. Four of the microsites always occurred no more than 0.7 m above river stage (low elevation microsites), while three other microsite types occurred always at least 0.7 m above river stage (high elevation microsites). Low elevation microsites included (1) gravel bars, (2) sand bars, (3) sediment-filled depressions along the river bed and (4) along the bottom and edges of side-channels cut-off from the main river in the summer months. High elevation microsites included (5) zones of aggradation downstream of established vegetation or woody debris, where frequently there were substantial sandy deposits, (6) raised pockets of sediment-filled depressions, similar to those at low elevation and (7) areas of erosion (over-bank scouring and scouring along bank edges). The final microsite type (8) included a fringe around piles of woody debris; this microsite type occurred mostly at high elevations (at least 0.7 m above river stage), but was also present at low elevations. Overall the eight microsite types offered variety in terms of exposure to flood disturbances and water availability (a key resource), the latter dictated by elevation above river stage and the differing water retention capacities of local sediment types (refer to Barsoum, 1998 for details of quantitative measurements of soil-moisture using tensiometers at the different microsite types) (Table 1); the relative proportions of the various microsite types and range of elevations where sampling took place, remained surprisingly consistent between years.

In the 1996 field season, there were a number of additions to the sampling procedure. In order to investigate temporal variations in the relative proportions of sexual and asexual regeneration strategies, excavation of seedlings and vegetative recruits was extended to all recruits from the current and three previous field seasons. Seedlings, or vegetative shoots regenerating in the 1996 growing season were classified as (at most) 4-month old recruits, 1 year if they survived from the 1995 growing season, 2 years if they survived from 1994 and 3 years if they had survived from 1993. The difficulty of ageing *P. nigra* and *S. alba* beyond 3 years and their size by that point, limited the study to recruits

Table 1. Relative abundance of microsites (1995 and 1996 data combined) and characteristics of each in terms of elevation above river stage at low flow on a given day^a

Microsites	Relative abundance of microsites (%)	Elevation above river stage (m)	Sediment texture ^b in surface layers showing typical ratios of different sediment categories	Range of soil suction readings (kPa)
Gravel bar	39	≤0.65	Gravel:sand (9:1)	-11 to 5
Sand bar	9	≤0.65	Coarse sand:fine sand:clay-silt (6:3:1)	-11 to 5
Low depression	5	≤0.65	Coarse sand:fine sand:clay-silt (1:4:5)	-9 to 5
Side-channel	9	≤0.55	Gravel:sand (9:1)	-12 to 5
Zone of aggradation	20	≥0.75	Gravel:coarse sand: fine sand (3:6:1)	-45 to -15
High depression	4	≥0.80	Coarse sand:fine sand:clay-silt (1:4:5)	-15 to -5
Bank scouring	11	≥0.70	Gravel:coarse sand:fine sand (4:5:1)	-60 to -15
Woody debris	3	≥0.55	Coarse sand:fine sand:clay-silt (6:3:1)	-40 to -5

^a Also, predominant sediment types in surface layers and the expected range of soil-suction readings at a depth of 50 cm where readings were collected from May to September in both years.

^b Clay-silt <63 µm; fine sand = 63–200 µm; coarse sand = 200 µm–2 mm; gravel >2 mm.

of no more than 3 years. Indicators of age included the number of annular bud scale scars on the main stem, stem thickness, the size and number of ramets (Sacchi and Price, 1992) and the colour and texture of the main stem. *Populus nigra* stems of the year were shiny and distinctively ochre-brown in color to begin with, while *S. alba* stems tended at first to be light green. The stems of both species turned dark, almost olive-green towards the end of the first growing season and in the case of *S. alba* gradually more glabrous, while shoots of the preceding years became increasingly grey-brown and weathered.

All transects were completed within the space of 1 month to avoid excessive temporal variation in ambient conditions. A fixed local datum allowed for calibration of all transect elevational data with respect to river stage on a given date (13 September 1995).

Results

Primary regeneration strategies of P. nigra and S. alba in the first year of establishment

Along total combined transect lengths of 1.5 km in both 1995 and 1996, *P. nigra* and *S. alba* seedling numbers greatly exceeded numbers of vegetative

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Table 2. Total combined and mean shoot dry weights (\pm 1SE) of first year *P. nigra* and *S. alba* seedlings and vegetative recruits excavated along 1995 and 1996 transects

Species	Vegetative recruits		Seedlings	
	1995	1996	1995	1996
<i>P. nigra</i>				
<i>n</i>	31	116	21909	3657
Total combined (kg)	0.375	1.927	24.100	5.023
Mean per recruit (g)	12.1 (5.2)	16.6 (6.1)	1.1 (0.3) ^a	1.4 (0.3) ^a
Mean per sampling unit (g)	13.9 (3.7)	17.8 (5.1)	19.5 (4.9)	13.5 (2.1)
<i>S. alba</i>				
<i>n</i>	17	62	1967	948
Total combined (kg)	0.047	0.291	1.043	0.436
Mean per recruit (g)	2.8 (1.6)	4.7 (2.2)	0.54 (0.21) ^a	0.46 (0.13) ^a
Mean per sampling unit (g)	2.9 (1.3)	4.8 (1.4)	4.1 (0.9)	2.7 (0.7)

^a As seedlings tended to be of similar size in each $20 \times 100 \text{ cm}^2$ sampling unit, mean shoot dry weights among individual recruits was estimated by dividing the total shoot dry weight of seedlings per sampling unit by the total number of seedlings found in each sampling unit. An overall mean dry weight of individual recruits was then derived by taking the mean of these estimates.

recruits during their first year of establishment; i.e. *P. nigra* and *S. alba* seedlings made up at least 97 and 94% of all recruits, respectively (Table 2). This was despite a significant reduction in seedling numbers following a mid-summer flooding event in 1996 and an almost fourfold increase in the number of vegetative recruits in response to this disturbance. The large differences in the relative proportions of sexual and asexual recruits are reflected in the much greater total combined shoot dry weights of seedlings (e.g. in 1995, 24.1 kg for *P. nigra* seedlings compared with 0.4 kg for vegetative recruits), especially when considering much lower estimated mean shoot dry weights of individual *P. nigra* and *S. alba* seedlings and similar mean dry weights of sexual and asexual recruits among $20 \times 100 \text{ cm}^2$ sampling units (Table 2). A comparison of 1995 and 1996 shoot dry weights of sexual and asexual *P. nigra* and *S. alba* recruits in $20 \times 100 \text{ cm}^2$ sampling units using the General Linear Model (GLM), in fact revealed no significant difference in the biomass of sexual and asexual recruits, although a highly significant interaction was detected between year of recruitment and the shoot biomass of either regeneration strategy (GLM: *P. nigra*: $F = 13.6$, $p = 0.001$, $d.f. = 1739$; *S. alba*: $F = 23.2$, $p = 0.001$, $d.f. = 486$), highlighting the contrasting effect of hydrological conditions in 1995 and 1996 on sexual and asexual regeneration (i.e. shoot dry weights of seedlings and vegetative recruits were highest in 1995 and 1996, respectively). Among *P. nigra* and *S. alba* asexual recruits, significantly greater biomasses were observed for individuals continuously linked with a parental plant (shoots originating from coppice re-growth, flood-training, or root suckers) compared

Table 3. Average shoot dry weights (g) (\pm 1SE) among individual *P. nigra* and *S. alba* asexual recruits in the first year of establishment where links are either severed or still maintained with the parent plants

Species	<i>P. nigra</i>		<i>S. alba</i>	
	1995	1996	1995	1996
<i>n</i>	16	53	7	26
Links severed with parent plant (translocated fragments)	8.7 (0.5)	13.4 (0.3)	2.9 (0.2)	4.5 (0.4)
<i>n</i>	15	63	10	36
Links maintained with parent plant (coppice, flood-trained and sucked shoots combined)	15.6 (0.5)	19.9 (0.3)	4.5 (0.4)	5.2 (0.2)

with those individuals with severed links (translocated fragments) (GLM: *P. nigra*: $F = 45.9$, $p = 0.001$, $d.f.$ 143; *S. alba*: $F = 6.7$, $p = 0.01$, $d.f. = 75$) (Table 3). A highly significant increase in the biomass of all types of asexual recruits was also confirmed between 1995 and 1996 (GLM: *P. nigra*: $F = 127.9$, $p = 0.001$; *S. alba*: $F = 59.6$, $p = 0.001$).

All categories of vegetative regeneration were observed in *P. nigra* and *S. alba*, although there was a significant difference ($p < 0.001$) in the relative proportions of each category both in 1995 and 1996, this difference in relative proportions remaining consistent between years (Table 4). Translocated fragments were the most common type of asexual recruitment in *P. nigra* and

Table 4. χ^2 analysis for departure from equal proportions of different asexual regeneration strategies along transects in 1995 and in 1996

	Percentage of each asexual regeneration strategy				Differences in proportions			
	Flood training	Translocated fragments	Coppice re-growth	Suckering	χ^2	$d.f.$	p	n
<i>P. nigra</i>								
1995	39 (12)	52 (16)	3 (1)	6 (2)	10.13	3	0.001	31
1996	35 (41)	46 (53)	5 (6)	14 (6)	27.95	3	0.001	116
Between years					4.28	3	NS	147
<i>S. alba</i>								
1995	24 (4)	41 (7)	35 (6)	0 (0)	0.44	2	0.001	17
1996	31 (19)	43 (26)	26 (16)	1 (1)	15.76	3	0.001	62
Between years					2.27	2	NS	79
Between species (1995 and 1996 data combined)					26.37	3	0.001	226

χ^2 Analysis for significant changes in proportions of each asexual regeneration strategy between years and species. Data sets analysed include only first year *P. nigra* and *S. alba* asexual recruits found along 1995 or 1996 transects. Sample sizes are given in parentheses.

S. alba, while suckering was relatively rare in both species. Despite these general similarities, proportions of each type of vegetative regeneration differed significantly between species ($p < 0.001$), notably in terms of a greater frequency of coppice re-growth in *S. alba* and fewer suckering shoots than *P. nigra*. In *S. alba* approximately 12% of all translocated fragments and 50% of all coppice re-growth was promoted by beaver foraging, while in *P. nigra* beaver foraging was observed much less frequently.

Spatial distribution of sexual and asexual recruits

Distribution along elevational gradients

Populus nigra and *S. alba* seedlings were restricted to low elevations on the floodplain, within specific elevational ranges above river stage (Fig. 2(a) and (c)). Upper and lower limits of these elevational ranges shifted between years, in response to prevailing climatic and hydrological conditions. For example, in 1995 a peak in *P. nigra* seedling numbers occurred between 0.4 and 0.6 m. A shift in peak seedling numbers to between 0.6 and 0.8 m in 1996 is likely to have been the result of both milder climatic conditions in this year, contributing towards an increase in the upper limit of the elevational band, and a summer flood which significantly reduced seedling numbers at the lower end of the elevational range. Similar distributional trends were observed among *S. alba* seedlings, although overall, seedlings of this species tended to occur at lower elevations than *P. nigra* seedlings and in fewer numbers.

Populus nigra and *S. alba* first year vegetative recruits were present across a wider elevational range than seedlings and displayed very scattered distributions (Fig. 2(b) and (d)). No overall patterns in distribution could be observed with respect to elevation, in either 1995 or 1996, although *S. alba* vegetative recruits clearly occurred at lower elevations on the floodplain than *P. nigra* vegetative recruits and were also present in fewer numbers.

Distribution in relation to microsite type

Over a combined transect length of 3 km (1995 and 1996 transect data combined) and some 3000 stratified random sampling units ($20 \times 100 \text{ cm}^2$), or microsites considered, seedlings and vegetative recruits of *P. nigra* and *S. alba* were observed to have differing associations with specific microsite types. Interspecies differences in terms of microsite association were also detected between *P. nigra* and *S. alba*, with the proportions of vegetative or non-vegetative recruits in these two species (average number of recruits per microsite type, inclusive of 0's, over sum of averages for all microsite types) varying significantly at specific microsite types from one field season to the next (Table 5(a)–(c)). *Populus nigra* seedlings were present at all microsite types in significantly different proportions (χ^2 : 1995: $F = 3685$, $p = 0.000$, $d.f. = 7$; 1996: $F = 1606$,

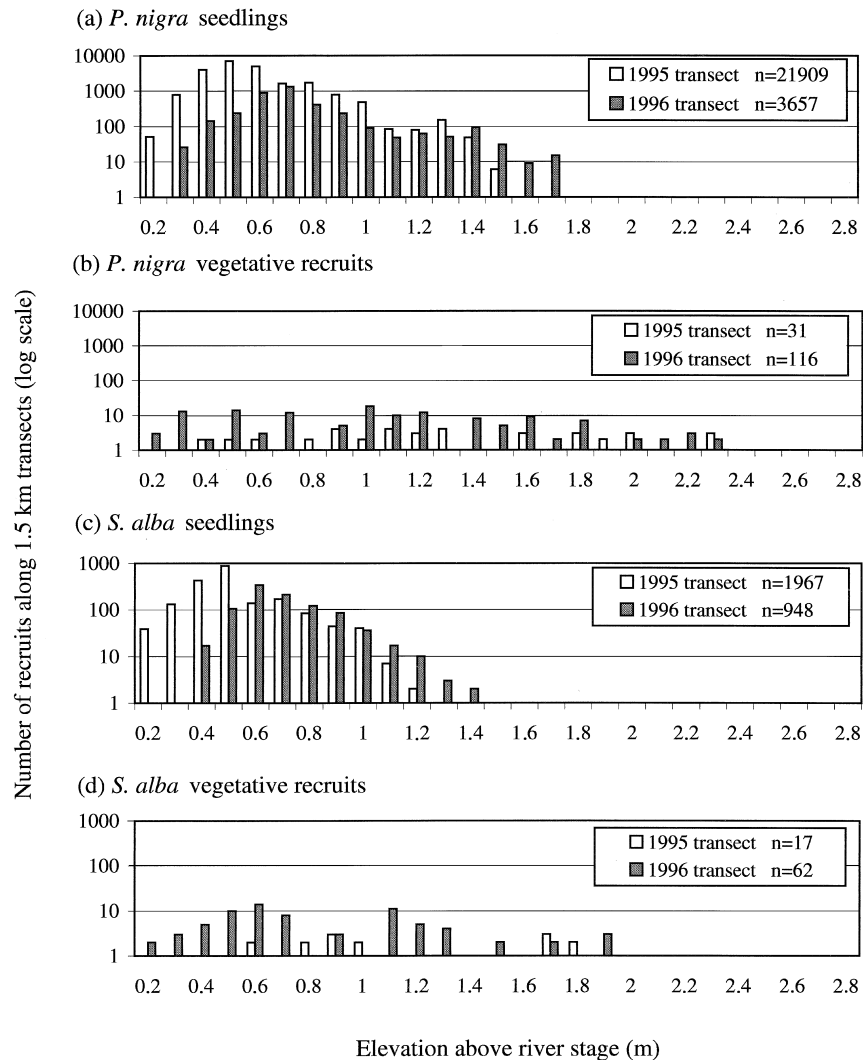


Figure 2. Total number of *P. nigra* and *S. alba* seedlings and vegetative recruits of the year found along 1.5 km transects in 1995 and 1996 against elevation above river stage.

$p = 0.000$, $d.f. = 7$). Seedlings were associated primarily with low elevation microsites (71%), although a substantial proportion (15%) were also present at higher elevations on the floodplain in sediment-filled depressions and at woody debris microsites where a positive association was detected in 1996 (Fig. 3(a)). At low elevations, *P. nigra* seedling recruitment demonstrated strong positive association in 1995 with gravel bars, sand bars and sediment-filled depressions; these relationships were less evident in 1996, however, as seedlings in sediment-

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Table 5. Proportions (%) of *P. nigra* and *S. alba* sexual and asexual recruits at various microsite types (average number of recruits per microsite type, inclusive of 0's, over sum of averages for all microsite types)

Microsites	Percentage <i>P. nigra</i> at each microsite type			Percentage <i>S. alba</i> at each microsite type		
	1995			1996		
	Vegetative shoots	Seedlings	Vegetative shoots	Vegetative shoots	Seedlings	Vegetative shoots
Side-channel	13	13	29	12	22	2
Gravel bar	7	21	4	12	6	13
Sand bar	3	15	2	–	15	10
Low depression	–	22	2	–	41	–
Zone of aggradation	16	8	16	17	–	16
Bank scouring	35	6	16	35	–	19
High depression	–	13	1	–	16	–
Woody debris	26	2	30	24	–	40
(a) Difference in proportions between regeneration strategies	1995		1996	1995		1996
χ^2	53.7		114.5	4.7		21
d.f.	5		7	1		2
p	0.001		0.001	0.05		0.001
(b) Differences in proportions among years						
	Vegetative shoots		Seedlings	Vegetative shoots		Seedlings
χ^2	14.4		25.2	15.5		12.6
d.f.	5		7	4		4
p	0.01		0.001	0.01		0.01
(c) Differences in proportions between species						
χ^2	1.4		35.3	15.4		61
d.f.	4		5	4		4
p	NS		0.001	0.01		0.001

χ^2 Analyses for departure from equal proportions of (a) sexual and asexual recruits at range of microsite types, (b) recruits (sexual or asexual) between 1995 and 1996 at the different microsite types and (c) *S. alba* and *P. nigra* recruits (sexual or asexual) at the range of microsite types.

filled depressions in particular, were either buried or washed away during the summer flooding event in this year. Milder climatic conditions in 1996 probably contributed towards improved survival rates at high depression microsites and may account for the increase in seedling abundance at this microsite type between 1995 and 1996 (Table 5).

Populus nigra vegetative recruits did not occur in similar proportions at the range of microsite types (χ^2 : 1995: $F = 6.3$, $p = 0.000$, $d.f. = 5$; 1996: $F = 5.3$, $p = 0.000$, $d.f. = 7$). Unlike *P. nigra* seedlings, *P. nigra* vegetative recruits were more often positively associated with high than low elevation microsites and were almost never encountered where fine sediments had accumulated in depressions on the floodplain. Positive associations were principally with four different microsite types (Fig. 3(a)); these included, at high elevations, areas of over-bank or bank edge scouring (20%), zones of aggradation (17%), directly adjacent to piles of woody debris (28%) and, at low elevation, along the bottom and edges of side channels (26%). Between 1995 and 1996, abundance of vegetative recruits at specific microsites showed a significant change ($p < 0.01$) with a particular increase along side-channels, a likely response to the incidence of flooding in this year (Table 5). At woody debris microsites and in zones of aggradation vegetative recruitment originated either through flood-training, or more often, from partially or completely buried translocated fragments stranded high on the floodplain with other depositional material left behind by floodwaters. In areas of over-bank and bank-edge scouring and along the bottom and edges of side-channels, vegetative regeneration occurred through coppice re-growth, through re-sprouting following flood-training and through suckering from exposed roots. Vegetative regeneration was similarly stimulated on gravel bars, but in much reduced proportions. Some coppice re-growth resulting from beaver foraging was observed along bank edges and along the edges of side-channels (8% of all coppice re-growth). These patterns relate to the foraging habits of beavers which tend to avoid travelling far from the safety of the river to feed (Erôme, 1982). Beaver also contributed towards vegetative regeneration by transporting stem fragments to their preferred feeding areas on gravel and sand bars at river level.

Salix alba seedlings were present at only five of the eight microsite types and at these, seedlings were observed in significantly different proportions (χ^2 : 1995: $F = 248$, $p = 0.000$, $d.f. = 4$; 1996: $F = 252$, $p = 0.000$, $d.f. = 4$) (Fig. 3(b)). Similarly to *P. nigra* seedlings, the majority of *S. alba* seedlings were encountered at low elevation microsites (primarily in sediment-filled depressions, 42%, and along side-channel edges, 21%) and at higher elevations on the floodplain in sediment-filled depressions (20%). There was significant variation, however, in the proportions of *P. nigra* and *S. alba* seedlings at the range of microsites, particularly on gravel bars where *S. alba* seedlings were observed in far fewer numbers compared with *P. nigra*. Large differences in the level of

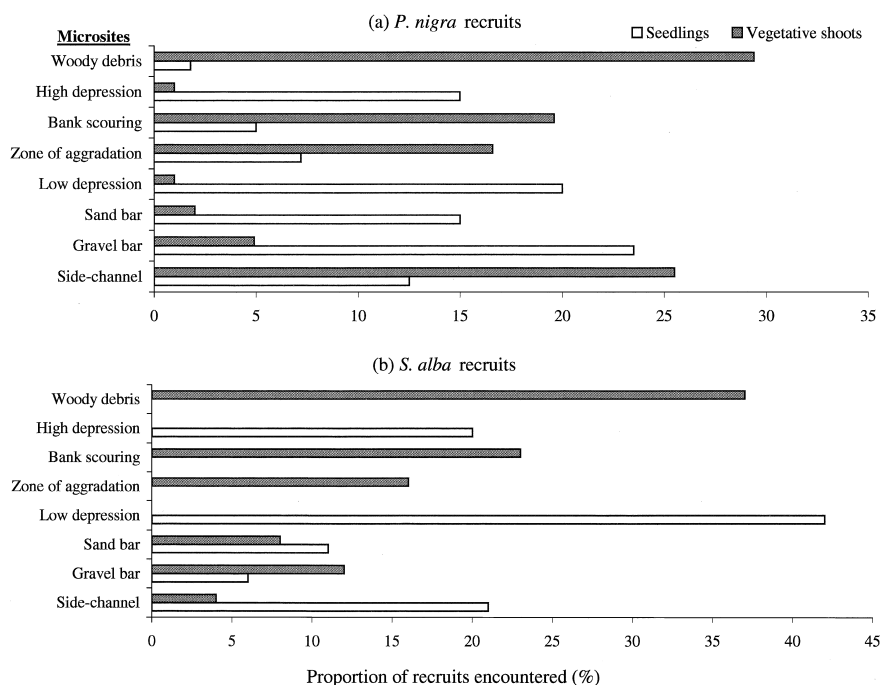


Figure 3. Proportions of *P. nigra* and *S. alba* seedlings and vegetative recruits encountered in different microsite types (average number of recruits per microsite type, inclusive of 0's, over sum of averages for all microsite types) 1995 and 1996 data combined.

association of *S. alba* seedlings among low elevation microsites were probably a function of the contrasting textural properties of surface sediments at the different microsite types and the relative sensitivity of this species to drought stress (Van Splunder *et al.*, 1996) (Tables 1 and 5); similarly, the high water retention capacities of fine sands and silt in high elevation depressions are likely to have contributed to the relatively high numbers of *S. alba* seedlings found at these microsites, especially where rainfall contributed moisture in 1996.

Microsite types associated with *S. alba* vegetative recruits differed significantly from those associated with seedlings both in 1995 and 1996 ($p < 0.05$ and $p < 0.001$, respectively) and distributions of vegetative recruits among these were disproportionate in both years (χ^2 : 1995: $F = 1.2$, $p = 0.000$, $d.f. = 4$; 1996: $F = 1.4$, $p = 0.000$, $d.f. = 5$) (Fig. 3(b); Table 5(a)). Like *P. nigra* vegetative recruits, *S. alba* vegetative recruits were most frequently encountered as part of or directly adjacent to woody debris (37%). Floodwaters also promoted substantial vegetative recruitment at high elevations (23%) through flood-training, coppice re-growth and suckering in areas of over-bank and bank-edge scour and from translocated fragments, or flood-trained individuals in zones of aggradation. *Salix alba* vegetative recruits were found in even lower proportions

than *P. nigra* vegetative recruits at low elevation microsites, on gravel and sand bars and along the edges of side-channels. Vegetative recruitment here was stimulated mainly through flood-training and coppice re-growth, although some coppice re-growth was due to beaver foraging. All vegetative recruitment encountered on sand bars was from translocated fragments, purposely transported to this microsite, in most cases, by beaver.

Temporal variation in numbers of sexual and asexual recruits

Excavation of *P. nigra* and *S. alba* seedlings and vegetative fragments in four different age categories (recruitment from 1993 to 1996) along the 1996 transects, revealed divergent trends in total numbers of seedlings and total numbers of vegetative recruits through time (Fig. 4(a) and (b)). Among vegetative recruits, there was a decrease in total numbers through the age categories. This decrease in numbers over time was not very great and numbers of 3 and 4-year old recruits were even very similar; i.e. 31 and 28 *P. nigra* vegetative recruits, and 13 and 14 *S. alba* vegetative recruits (established in 1994 and 1993, respectively) were encountered along the transects. Total seedling numbers also decreased through the age categories, although the drops in seedling numbers

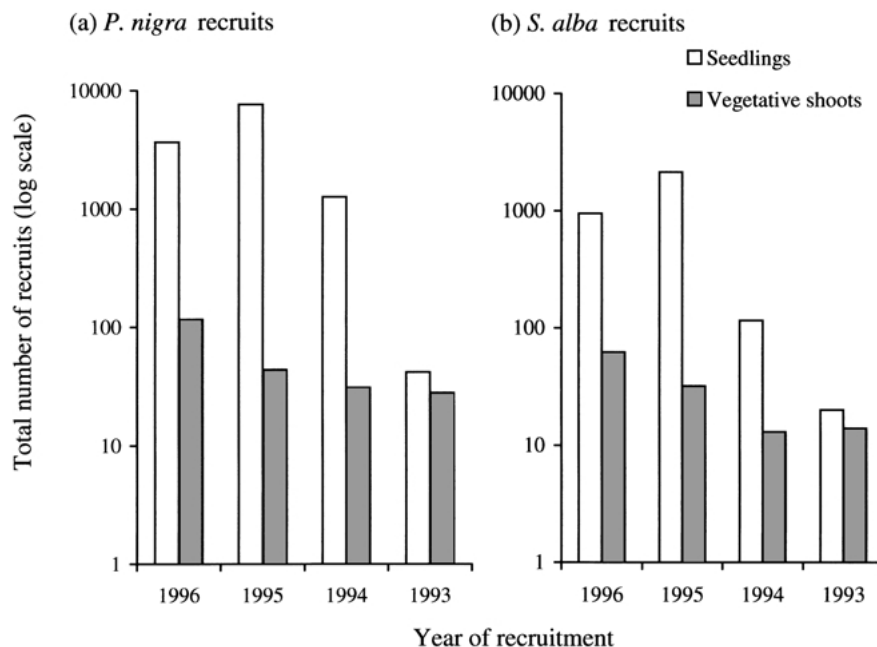


Figure 4. Number of *P. nigra* and *S. alba* sexual and asexual recruits encountered along 1996 transect from different years of establishment (1993–1996).

from one age category to the next were much sharper than for vegetative recruits. Poor *P. nigra* and *S. alba* seedling recruitment in 1996 due to a mid-summer flooding event in this year, gives the impression of better recruitment in 1995. However, a substantial drop in numbers from the total number of 1995-established seedlings to the total number of 1994-established seedlings (e.g. 7611 *P. nigra* 1995-established seedlings to 1263 1994-established seedlings), suggests that rates of seedling survival are very poor through time. This is confirmed by a further significant drop in numbers from the total number of 1994-established seedlings to the total number of 1993-established seedlings found along the transects (e.g. 1263 *P. nigra* 1994-established seedlings dropped to 42 1993-established seedlings); the numbers of 1993-established *P. nigra* and *S. alba* seedlings were in fact almost equal to the numbers of vegetative recruits in the same age category (e.g. among 1993-established recruits, 20 *S. alba* seedlings and 14 *S. alba* vegetative recruits were encountered along the transects).

Discussion

The results of this study demonstrate that the relative abundance of sexual and asexual recruits in *P. nigra* and *S. alba* during the first years of establishment, are initially primarily dictated by a single stochastic process, flood disturbance, which itself is a function of climate. Floods promote regeneration in these species by freeing space and resources on the floodplain for recruitment from seed and actively initiating vegetative regeneration. At the same time, floods act both as dispersal agents for seed and asexual fragments and as a selective force, removing the most vulnerable recruits – these tend to be recruits established at low elevation on the floodplain and are most likely to be those with limited re-sprouting potential and/or superficial root systems. It follows that the timing of flooding events can have an important influence on regeneration strategy response, particularly in relation to the timing of *P. nigra* and *S. alba* seed dispersal and developmental stage of sexual and asexual recruits.

During intervals between floods, the relative abundance and distributions of sexual and asexual recruits are influenced by other processes. In the free-draining sediments and semi-arid conditions along the Drôme River, *P. nigra* and *S. alba* sexual and asexual recruits were influenced by water availability associated with patterns of fine sediment deposition. The sensitivity of seedlings to soil-moisture conditions was reflected by clear association with low-lying microsites, or with microsites at higher elevation where substantial fine sediment deposits were present; this trend was especially evident during the dry summer of 1995. The distribution of vegetative recruits was less obvious in relation to water levels, displaying a very scattered distribution over a wide

elevational band. However, in many cases, the presence of vegetative recruits at high elevations on the floodplain could often be explained by pre-formed connections, via the parent plant, to well-established root systems. Otherwise, many thriving vegetative fragments were observed in fine sediment deposits (e.g. around woody debris, or sand bars) transported to these sites either by the river, or beaver; the greater water retention capacity of fine sediments probably enhanced survival rates of asexual recruits at these locations.

Process and relative abundance of sexual and asexual recruits

An unseasonal flooding event along the Drôme River in early July 1996 highlighted the importance of the timing of flooding events on *P. nigra* and *S. alba* recruitment and the contrasting effects floods can have on the relative abundance of sexual and asexual recruits. The 1996 summer flood actively reduced the number of first year *P. nigra* and *S. alba* sexual recruits by approximately 17 and 48%, respectively, compared with the 1995 field season which was flood-free during the summer months; this was despite greater seedling recruitment in 1996 due to milder climatic conditions (Barsoum, 1998). Seedlings of both species are vulnerable to sedimentation and to the mechanical impact of flood waters during the first few months after germination because of slow early growth and limited re-sprouting potential, the former a function of very limited starting resources compared with vegetative recruits (Van Splunder *et al.*, 1996; Barsoum, 1998; Barsoum and Hughes, 1998). *Salix alba* seedlings are likely to be particularly vulnerable to burial and removal by floodwaters as they occur across a narrower elevational band, at lower elevations on the floodplain, than *P. nigra* seedlings, and display a prostrate growth form compared with the more upright growth of *P. nigra* seedlings during the early stages of development. Vegetative regeneration, in contrast, appeared to be enhanced by floods and the milder climatic conditions in early July 1996 with a 27% increase in numbers of first year *P. nigra* and *S. alba* vegetative recruits compared with the previous year. The mid-summer flood waters in 1996 (and warm ambient temperatures at this time of the year), will have not only initiated vegetative regeneration, but also encouraged rapid growth of shoot and root sprouts from damaged plants; i.e. shooting and rooting potential is especially high during the summer months since root primordia start to form in spring and then develop progressively in stems until they reach their maximum development by autumn (Carlson, 1938, 1950; Houle and Babeux, 1993).

Similar shifts in the relative abundance of sexual and asexual recruits in response to spatial or temporal variability in environmental processes have been observed in other plant species capable of asexual regeneration. Tardif and Bergeron (1999), for example, documented poor sexual recruitment in

populations of *Fraxinus nigra* growing along exposed lake shore edges in north-western Quebec compared with inland stands; lake shore trees were observed to maintain populations predominantly through sprouting, promoted by regular flooding and physical damage from floating ice and debris. In the eastern deciduous forests of North America, Held (1983) recorded a similar shift from seedling established populations towards a dependence on vegetative reproduction in *Fagus grandifolia* which was related to elevation and slope exposure. Mandujano *et al.* (1998) proposed that for the clonal cactus *Opuntia rastrera*, a combination of physiological differences between sexual and asexual regeneration strategies and greater resistance by asexual recruits to predation, explained the predominance of either clonal or sexual regeneration in contrasting habitats of the Chihuahuan Desert, Mexico. These shifts in regeneration response in relation to specific environmental stimuli, has implications for the structure and successional development of plant communities should growth forms of sexual and asexual recruits differ substantially. As dominant early successional woody species in many European floodplain environments, this possibility could easily apply to *P. nigra* and *S. alba* and warrents further investigation.

In this study, because the balance in regeneration strategies was examined only in the early recruitment stage of the life cycles of *P. nigra* and *S. alba*, the results are clearly not representative of the structure and composition of an adult stand. In such long-lived species, the relative abundance of individuals of sexual and asexual origin may diverge through time as, for example, each successive flood removes genets from the population, and/or competitive elements take over, improving the status of one regeneration strategy over another where competitive advantages exist in one regeneration strategy. In *P. nigra* and *S. alba* there was some evidence of a gradual loss in genet numbers through time during the first few years following establishment. While prodigious quantities of seed ensured that vegetative propagules were out-numbered for at least 3 years following seedling establishment, mortality rates among seedlings were very high on an annual basis through flood and drought-induced stresses (Barsoum, 1998) such that by their fourth field season, numbers of sexual and asexual recruits became very similar; i.e. vegetative offspring contributing 40% in *P. nigra* and 41% in *S. alba* to overall recruitment. It is likely that a comparatively gradual decline in numbers of asexual recruits reflects greater survival rates in this regeneration strategy, or an ever-increasing population of vegetative offspring as saplings of seed origin underwent vegetative expansion themselves. Nevertheless, while these findings suggest that the number of clones among adult stands of *P. nigra* and *S. alba* could be expected to be quite high, a number of studies applying molecular genetic techniques to sample adult *Populus* stands have yielded contrasting results; that is, even though clones were detected in all populations studied, in certain cases these

represented more than 50% of trees sampled, while in others only a few trees were recognised to have identical banding patterns within the sample populations (McKay, 1996; Legionnet *et al.*, 1997; Arens *et al.*, 1998; Gom and Rood, 1999).

Process and spatial distribution of sexual and asexual recruits

Seed dispersal in *P. nigra* and *S. alba* was not homogeneous across the floodplain, but was sufficiently widespread and locally dense to ensure that there was at least the potential for recruitment at most available microsites (Barsoum, 1998). Distributional patterns on the floodplain were therefore very much a function initially of microsite availability (as supplied by a recent flood disturbance event) and subsequently of water availability as dictated by rates of water table decline, local substrate type and climatic conditions. These variables contributed to an overall patchy distribution of seedlings within a specific elevational range at low elevations on the floodplain, with highest seedling densities on microsites with fine sediment deposits (i.e. sand bars, sediment-filled depressions); *S. alba* seedlings, as the more susceptible species to drought-induced mortality (Van Splunder *et al.*, 1996), demonstrated a strong association with these latter microsites types despite their comparative rarity on the floodplain (combined = 14% cover). High elevation, sediment-filled depressions provided a unique refuge for *P. nigra* and *S. alba* seedlings, but were also rare features of the active alluvial plain (4% cover). Large expected numbers of water-dispersed *P. nigra* and *S. alba* seed becoming trapped along the edges of side-channels in strand lines, probably explains the comparatively high numbers of seedlings at these microsites compared with gravel bars despite only 9% coverage and similar coarse grained sediments. Where seedlings survived drought stress during their first growing season, continued survival and development became primarily a function of river flow, depending on the changing direction and force of river flow in any one sector of the floodplain and the frequency and magnitude of flooding events to follow. Sexual recruits can be said, therefore, to be heavily reliant on the shape of the hydrograph, during and beyond initial colonisation, requiring a period without extremes of either high, or low water to ensure survival at certain points within their elevational range. In the face of flooding events of increased frequency, magnitude and/or irregularity, this could place this regeneration strategy at a distinct disadvantage compared with asexual recruits.

Vegetative regeneration in *P. nigra* and *S. alba* was observed to occur by multiple regeneration strategies; i.e. notably, from translocated fragments of the parent plant and through flood-training in *P. nigra*, but also often via coppice re-growth in *S. alba*; sprouting from root suckers were less common in both species. Each of these asexual regeneration strategies was primarily

dependent, in different ways, on velocity and patterns of river flow for initiation (and dispersal, in the case of translocated fragments), although beaver foraging also had a small role to play, particularly in *S. alba*. The result was a fairly predictable distribution of the various types of vegetative recruits, often in close association with specific microsite types throughout the floodplain; that is, coppice re-growth, suckering and flood-training were typically associated with (as has been observed in other *Populus* species) eroding surfaces such as areas of over-bank scouring, or scouring along bank edges and along the edges and bottom of side-channels at low elevations (Rood *et al.*, 1994; Gom and Rood, 1999). In areas of deposition such as zones of aggradation and adjacent to woody debris, sandy sediment deposits promoted vegetative recruitment from partially buried and trapped translocated fragments by providing a damp rooting medium. Beaver also contributed translocated fragments on sand and gravel bars, arguably promoting the vegetative spread of single genets through the active transportation of viable fragments to favourable sites along the river edge where fragments could be carried still further by floodwaters. Beaver foraging along bank edges yielded bushy re-growth from coppiced plants, possibly improving the competitive edge of these individuals by encouraging dense growth.

The overall scattered distribution of asexual recruits, is likely to be highly advantageous in that there is the potential for continued survival at high elevations on the floodplain, out of reach of flood waters, but also at low elevations, should water tables decline rapidly. In addition, asexual recruits represent a type of 'advanced regeneration', especially where physiological integration is still maintained with the parent plant. Integration may confer certain distinct advantages such as the ready translocation of resources (sugars, nutrients, water and/or hormones) in an acropetal direction, favouring accelerated maturity and rapid growth of the asexual recruit compared with seedlings, or those asexual recruits with no links to the parental plant (Cook, 1979; Philips and Shure, 1990; Caraco and Kelly, 1991); e.g. individual shoot dry weights of *P. nigra* and *S. alba* asexual recruits with links maintained to parental plants were significantly greater compared with seedlings or shoots originating from translocated fragments; these benefits could provide the new physiologically integrated recruit with a competitive edge and/or improve chances of survival in a resource-poor environment, thereby contributing to less restrictive spatial distributions (Lovett-Doust, 1981; Bloom *et al.*, 1985).

Numerous costs of physiological integration should, however, also be anticipated. These include metabolic costs of maintaining links between the parent plant and new asexual recruit and thus, a possible significant reduction in the growth rate of the mother plant as resources are diverted (Pitelka and Ashmun, 1985). There is also a greater risk of the spread of disease between connecting tissues, avoided to some extent among independent asexual units

(e.g. translocated fragments) (Cook, 1985). Furthermore, physiological integration with the parental unit implies limited spatial dissemination of genetic information, an especially risky strategy where sexual recruitment is poor. Among *P. nigra* and *S. alba*, the generation and dispersal of translocated fragments by the river could provide a means of spreading the risk of mortality of a particular genotype and act as a complementary or even alternative means of long-distance dispersal to vulnerable, short-lived seeds, albeit in a single direction. Indeed, there is some evidence of successful, long-distance dispersal and establishment (>10 km) of translocated fragments by the river in *S. fragilis* which have resulted in clones with large, but discontinuous distributions (Beismann *et al.*, 1997). In other species also, there is evidence of a significant role played by flowing water on the widespread dispersal of vegetative fragments and thus, the promotion of out-crossing and maintenance of genetic diversity through inter-mingling of genets (Parker and Hamrick, 1992; Johansson and Nilsson, 1993); this contradicts the notion that seed production is typically the primary means of long distance dispersal, with vegetative regeneration contributing mainly to local population growth (Piquot *et al.*, 1998).

Conclusions

The distributional differences between sexual and asexual recruits in *P. nigra* and *S. alba* clearly serve to increase the regeneration capacity of these species across a range of climatic and hydrological gradients and this plasticity provides a measure of security in an otherwise very unpredictable environment (Bond and Midgley, 2001); these species are therefore likely to be relatively insensitive to significant variations in seedling recruitment rates where (1) sufficient sexual recruitment is favoured at the metapopulation level (Piquot *et al.*, 1998) and/or (2) regular disturbances allow for at least some compensatory vegetative recruitment and repeated seedling recruitment, as described by Eriksson (1989; 1992) in discrete patches along the fringes of the adult population. There may be the danger, however, that the differences highlighted in this study between sexual and asexual recruits, may be sufficiently great to lead to a serious imbalance in regeneration strategies along managed river courses where natural processes are disrupted in such a way as to enhance these differences on a large scale; e.g. Shafroth *et al.* (1994) reported primarily asexual reproduction in *Salix × rubens* along channelised river reaches in Colorado where flood disturbances are frequent. A genetics-based study of how genotypic diversity of *P. nigra* or *S. alba* populations might be affected by different levels of flood disturbance and/or sediment delivery rates along different river reaches, could be a useful corollary to these findings; comparisons in this respect, might be made between fragmented populations growing along

rivers where river discharge favours asexual regeneration (e.g. frequent, high magnitude flooding disturbances occurring during periods of seedling establishment) and populations along rivers such as the Drôme River, which have hydrographs promoting both sexual and asexual recruitment.

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