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Establishment of alluvial forest species in floodplains: the role of dispersal timing, germination characteristics and water level fluctuations

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SUMMARY

The establishment of seedlings of four floodplain forest species (*Salix alba, S. triandra, S. viminalis* and *Populus nigra*) on river banks along the River Waal, the Netherlands, was studied. Seed germination patterns and timing of seed dispersal were studied under field conditions. Effects of temperature and substrate moisture content on germination percentages and the viability of the seeds were investigated in a laboratory experiment. Along the River Waal, seed dispersal occurred in spring in the following sequence: *S. viminalis, S. triandra, S. alba* and *P. nigra*. Seeds germinated in narrow belts parallel to the river; seedlings of *S. viminalis* were found at a higher elevation than *S. alba* seedlings. The elevation of the seedlings on the river bank was related to the water level during the dissemination period for *Salix* spp., but not for *P. nigra*.

Temperature had no effect on germination percentage within the range of 5–25°C. *P. nigra* showed a significantly longer seed viability than the *Salix* species and germinated at a lower soil moisture content. The zonation of seedlings observed in the field could be explained by the germination responses of the species; timing of seed dispersal and water level fluctuation appeared to be the major determinants of initial floodplain forest zonation.

Key-words: dispersal timing, floodplain forest, germination, *Salix, Populus*, moisture content.

INTRODUCTION

Alluvial forests cover the banks along large rivers in western Europe (Karpati & Tóth 1962; Kop 1961; Farjon & Bogaers 1985; Schnitzler *et al.* 1992). Such forests are more or less extensive depending on the state of regulation of a river. The most frequently flooded parts of the forests are dominated by species of Salicaceae like willows (*Salix* spp.) and black poplar (*Populus nigra*) (Noble 1979). Low grazing intensity by cattle is required for the development of these forests (Fenner *et al.* 1985).

River floodplains are characterized by periodic massive germination of willow or poplar seeds resulting in the establishment of young riparian forests, and high floods

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carrying away the vegetation and eroding the river banks (Shull 1944; Bégin & Lavoie 1988). Consequently, the development of zonation of alluvial vegetation is determined by the hydrology and morphology of rivers (Dister *et al.* 1989; Blom *et al.* 1990).

The importance of water level fluctuations for the establishment of species starts with seed dispersal (Noble 1979; McBride & Strahan 1984; Bradley & Smith 1985). The plumed seeds of willows and poplars are dispersed by both wind and water (Lautenschlager 1984; Walker *et al.* 1986), and are trapped in large numbers to the moist surface of river banks (Noble 1979).

After seeds are stranded on the riverbank, germination may occur on moist, bare soil (Noble 1979; Lautenschlager 1984). If soil moisture content is too low it may result in the desiccation of the seed or seedlings. Moisture content is related to coarseness of the substrate. McBride & Strahan (1984) found *Populus fremontii* more on sandy or gravely parts of the banks, whereas *Salix* spp. preferred finer grained substrates. After germination, water level fluctuations (either flooding or rapid lowering of ground water levels) are still important for the survivorship of seedlings (McLeod & McPherson 1973; McBride & Strahan 1984; Bishop & Chapin III 1989; Sacchi & Price 1992). The roles of seed dispersal and germination characteristics in the establishment of alluvial forests species in relation to water level fluctuations along rivers are unclear.

The objectives of this paper were to determine (i) the timing of seed dispersal and seedling emergence along the banks of the River Waal in the Netherlands; (ii) the influence of soil moisture and temperature on germination of three species of *Salix* and one of *Populus* species.

MATERIALS AND METHODS

Species

Along the River Waal, present fragments of floodplain forests are dominated by white willow (*Salix alba* L.) and common osier (*S. viminalis* L.) and to a lesser extent by almond willow (*S. triandra* L.) and black poplar (*P. nigra* L.). These species are all dioecious tree species that occur in floodplains all over Europe. Plumed seeds are produced in massive amounts in spring.

Study area

Fieldwork was conducted at two locations situated on sandy river banks along the River Waal in the Netherlands. The River Waal is a regulated river, with groynes perpendicular to the stream bed on both sides. Two locations (length 100 m; width depended on the water level) were selected: 'Klompenwaard' (51°53'N 6°03'E) and 'Staartjeswaard' (51°52'N 5°39'E). A small alluvial forest was present at site Klompenwaard, whereas site Staartjeswaard contained only a few solitary willow trees. At both locations, seedlings of *Salix* and *Populus* were found on the bare soil below the present vegetation.

Germination patterns on locations along the River Waal in 1993

Seedlings that had emerged in spring 1993 in belts on the river bank over the elevational gradient were counted on 1 July 1993 at the Klompenwaard and Staartjeswaard sites in seven transects with a breadth of 1 m and across the width of the germination belt at the location. The transects were divided in plots of 20 cm × 1 m, in which numbers of

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seedlings per species were counted. The elevation gradient was divided into a number of elevation classes, increasing by 2·5 cm. For each species, the average number of seedlings in each elevation class was determined (per 200 cm^2). Subsequently, the elevation range over which germination of each species had taken place was calculated. To compare the actual elevation of the two sites, the water levels at the sites were standardized to the levels at the gauge station Nijmegen (51°52'N 5°67'E). This was done by using both the distance from sites to gauge station and the slope of the river between the sites and gauge station Nijmegen. All elevations are expressed in meters above sea level.

Germination trials

General germination procedures. Inflorescences with unripe seeds of *S. alba, S. triandra, S. viminalis* and *Populus nigra* were collected from trees in the river area near Nijmegen (51°52'N 5°67'E). The inflorescences were stored dry at room temperature until they burst and the plumed seeds were released. Seeds were used within 24 h after release. The following experiments were performed.

Longevity. The released seeds of all species were kept under room conditions (±20°C, 50% average relative humidity) after the inflorescences had burst open. After 0, 1, 2, 3, 4, 8, 11, 21, 28, 36, 41 and 48 days, seed viability was tested.

Temperature. Germination of seeds of each species was tested in rooms with a controlled constant temperature of 5, 10, 15, 20 and 25°C.

Water potential. Seeds of all four species were incubated in various concentrations of polyethyleneglycol (PEG). The osmotic potential (π), which equals the water potential (Salisbury & Ross 1985), was calculated using the equation:

$$\pi = -m.\mathrm{i}.\mathrm{R}.T$$

in which m is the molality of the solution (mol PEG l^{-1} H_2O); i is the ionization constant (1); R is the gas constant (0·00831 MPa mol^{-1} K^{-1}); T is the temperature (°K). After Bishop & Chapin (1989), a range of water potentials, −0·10, −0·13, −0·16, −0·20, −0·23, −0·26 and −0·30 MPa, was used.

In the experiments on longevity, temperature and water potential, 40 seeds were incubated on a layer of Whatman glass microfibre filter paper in plastic Petri dishes (five replicates per treatment). The filter papers were saturated with tap water (3 ml) or PEG-solution. The Petri dishes were placed in a temperature-controlled room at 20°C (unless another temperature is specified) with a photoperiod of 16 h (54 μE m^{-2} s^{-1}).

In the experiments, a seed was considered to have germinated when a ring of root hairs between hypocotyl and future root had emerged and the green cotyledons were visible. Germinated seeds were counted after 3 days of incubation.

Soil moisture content. Sand collected on a riverbank of the River Waal was homogenized and dried at 100°C for 24 h (modal grain size 250 μm). To obtain a water content range of 2, 4, 6, 8 and 12% (w/w), aluminium cylinders (5 cm diameter; 3·5 cm high) were filled with 100 g dried sand. Subsequently, all cylinders were saturated with tap water, and dried at 40°C until the desired water content was reached. All cylinders were covered with plastic for 24 h to obtain a homogeneous distribution of moisture throughout the

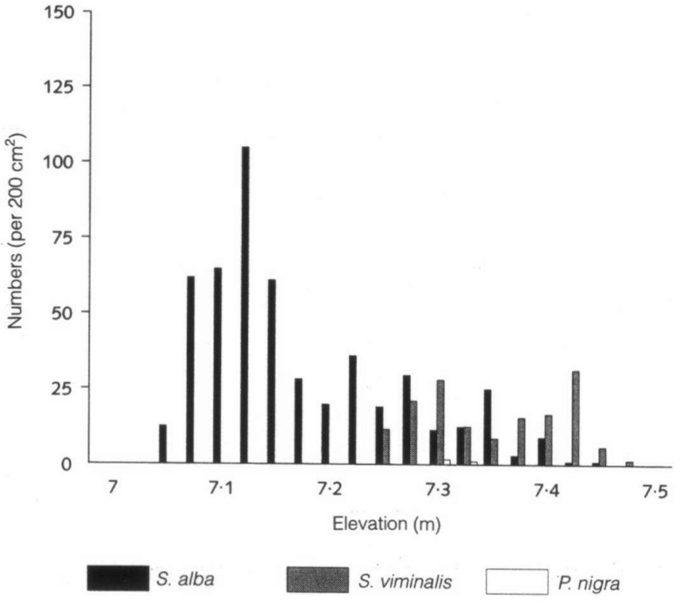

Fig. 1. Mean density of seedlings in 1993 of *Salix alba, S. viminalis* and *Populus nigra* (number per 200 cm^2) along transects over the elevation gradient at the Klompenwaard and Staartjeswaard sites. Elevation of the locations is standardized to elevation at gauge station Nijmegen in meters above sea level.

cylinders. In each of the cylinders 30 seeds were placed on the surface of the sand and carefully pressed upon to ensure good soil contact of the seeds. Seven cylinders per moisture treatment were used for each species. The cylinders were weighed just before the experiment started, to assess the starting moisture content. Cylinders with seeds were placed in a temperature-controlled room at 20°C and a photoperiod of 16 h (54 E m^{-2} s^{-1}). To avoid decreasing moisture content during incubation due to evaporation, the number of seedlings in each cylinder was counted after 24 h. In order to detect the first signs of germination (root hairs) a stereoscope (10 × magnification) was used.

Statistical analyses

Due to a lack of normal distribution (tested with Wilk–Shapiro at $P<0{\cdot}05$), germination percentages were compared between treatments and species with the non-parametric Kruskal–Wallis test ($P<0{\cdot}05$). Logistic regression (e.g. Ter Braak & Looman 1987) was used for the analyses of the experiment with different soil moisture contents, because it was impossible to produce identical replicates. The 95% confidence interval of the b_1 is calculated from 2·45 ± SE. Differences in frequency distributions of the seedlings on the river bank, were analysed using the Wilcoxon rank test ($P<0{\cdot}05$).

RESULTS

Seedlings occurred in narrow belts at the two investigated locations along the River Waal in 1993. Significant differences in seedling density distribution among species were observed between positions at the elevation gradient (Fig. 1). The seedlings of *S. viminalis* were found at a higher elevation than those of *S. alba* and *P. nigra*. No seedlings of *S. triandra* were detected at the two locations in 1993.

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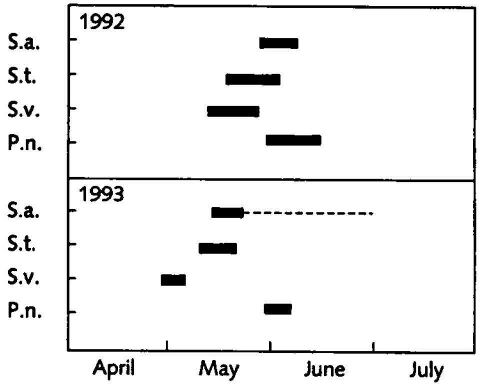

Fig. 2. Period of seed dispersal in 1992 and 1993 for *Salix alba* (S.a.), *S. triandra* (S.t.), *S. viminalis* (S.v.) and *Populus nigra* (P.n.). In 1993 the dispersal peak for *S. alba* had ended round 20 May but incidental seed fall was found until the beginning of July.

In Fig. 2 the timing of seed fall in 1992 and 1993 for the species under study along the River Waal is presented. In both years *S. viminalis* ripened first, followed by *S. triandra, S. alba* and *P. nigra*. All species disseminated over a short period of time, except *S. alba* from which seeds were found until the end of July.

Seed longevity is short for *S. alba, S. triandra* and *S. viminalis*. Almost 100% of the seeds of these three species lost their viability within 9 days after being released from the inflorescences (Fig. 3a). In contrast, seeds of *P. nigra* showed a much greater longevity: 10% of the seeds still germinated after 30 days of storage.

Seed germination did not differ significantly between the species in the temperature range between 5 and 25°C (Fig. 3b). Germination percentages at all temperatures varied between 80 and 100%.

In a series of PEG concentrations, germination of all species decreased from approximately 100% at $-0{\cdot}1$ MPa to 0% at $-0{\cdot}26$ MPa (Fig. 3c). *S. triandra* germinated at the highest PEG concentration ($-0{\cdot}23$ MPa). At $-0{\cdot}2$ MPa *S. triandra* and *P. nigra* showed a significantly higher germination percentage than *S. alba* and *S. viminalis*.

A different pattern was observed in the experiment concerning germination on sand with different moisture contents. In Fig. 4, each dot represents the number of germinated or non-germinated seeds of each cylinder, respectively. Differences in germination between the species due to soil moisture content were analysed using logistic regression (Table 1). Using the 95% confidence interval of the slope b_1 it can be concluded that *P. nigra* and *S. viminalis* showed a significantly stronger increase of germination percentage with increasing moisture than *S. alba* and *S. triandra*: *S. triandra* showed a significantly higher germination percentage than *S. alba* ($P<0{\cdot}05$).

DISCUSSION

Ripe seeds of Salicaceae species are transported by wind and water. When water levels recede during the seedfall period, moist, bare sand appears on the riverbank. These are optimal conditions for germination of willow and poplar seeds that are stranded on the

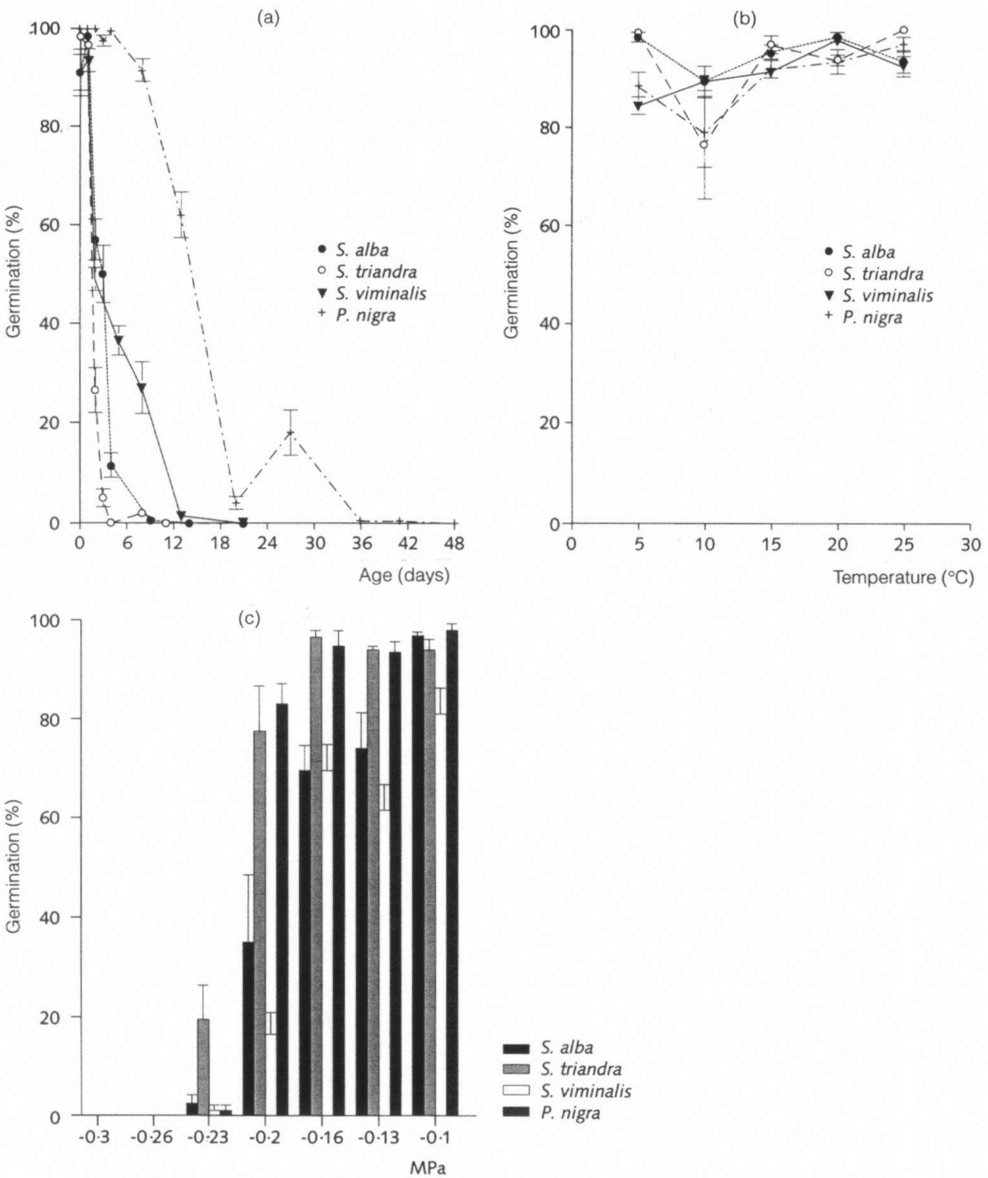

Fig. 3. Percentage germination (± SE) of seeds of *Salix alba, S. triandra, S. viminalis* and *Populus nigra* (a) after different periods of preservation; (b) at different temperatures; and (c) at a PEG-solution concentration gradient.

banks. Seeds blown towards the river banks by wind stick to the moist surface parallel to the river. Precipitation during germination will clearly decrease the probability of desiccation of the seedlings.

Seeds of the four alluvial forest tree species have in our study been observed to ripen in the following sequence: *S. viminalis, S. alba/S. triandra* and *P. nigra*. The highest density of *S. viminalis* seedlings was found at higher elevations (7·3/7·4 m) than that of *S. alba* seedlings (7·1 m). *P. nigra* seedlings were found only within a very narrow

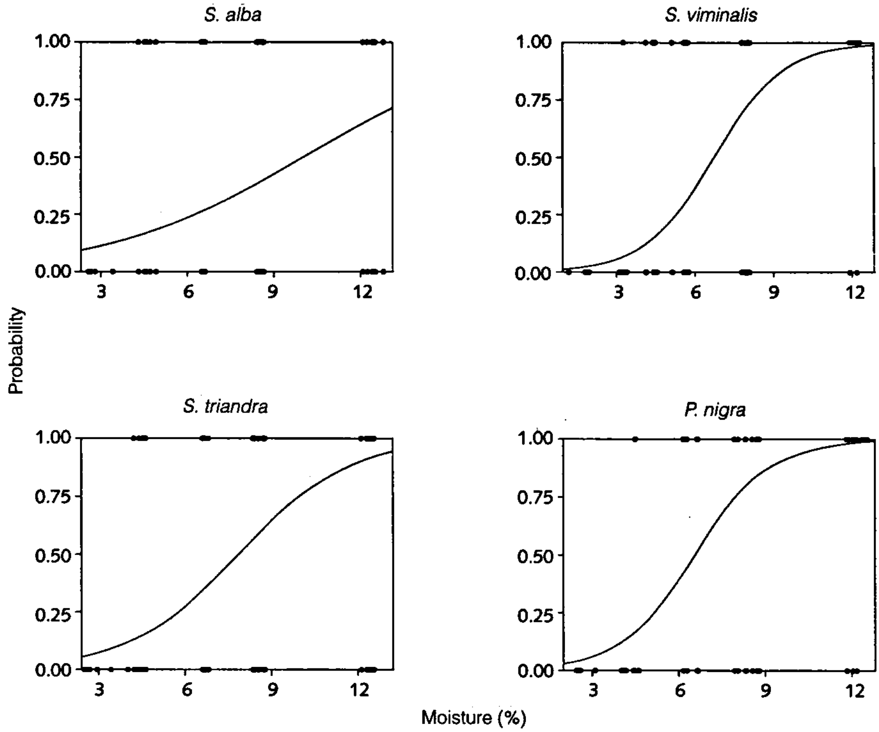

Fig. 4. Regression lines of germination of seeds of *Salix alba, S. triandra, S. viminalis* and *Populus nigra* on sandy substrate with different moisture content (w/w). The success of the seeds in each replicate is represented by a dot: 0=seeds not germinated; 1=seeds germinated.

Table 1. Using logistic regression the following models for *Salix alba, S. triandra, S. viminalis* and *Populus nigra* were produced to give the probability of seeds germinating as a function of moisture content. Probability is given as the equation: $P=[\exp(b_0+b_1x)]/[1+\exp(b_0+b_1x)]$. The 95% confidence interval (2·45 ± SE) of the b_1 is given between parentheses. P is the probability of germination; x is moisture content (w/w)

Species	Function
S. alba	$P=[\exp(-2{\cdot}72+0{\cdot}27x)]/[1+\exp(-2{\cdot}72+0{\cdot}27x)]$ (±0·054)
S. triandra	$P=[\exp(-3{\cdot}70+0{\cdot}48x)]/[1+\exp(-3{\cdot}70+0{\cdot}48x)]$ (±0·072)
S. viminalis	$P=[\exp(-5{\cdot}06+0{\cdot}75x)]/[1+\exp(-5{\cdot}06+0{\cdot}75x)]$ (±0·103)
P. nigra	$P=[\exp(-4{\cdot}68+0{\cdot}71x)]/[1+\exp(-4{\cdot}68+0{\cdot}71x)]$ (±0·103)

elevation range (7·3/7·35 m). In 1993, no seedlings of *S. triandra* were found. In Fig. 5 the seedling distribution is plotted along with the water levels of the River Waal at station Nijmegen from April till August. It is suggested that the elevation of the belts of *S. viminalis* and *S. alba* corresponds with the highest water level during dissemination.

The results of the experiments suggest that temperature is not a factor limiting germination. Therefore, the investigated species all have a comparable germination potential, independent of temperature.

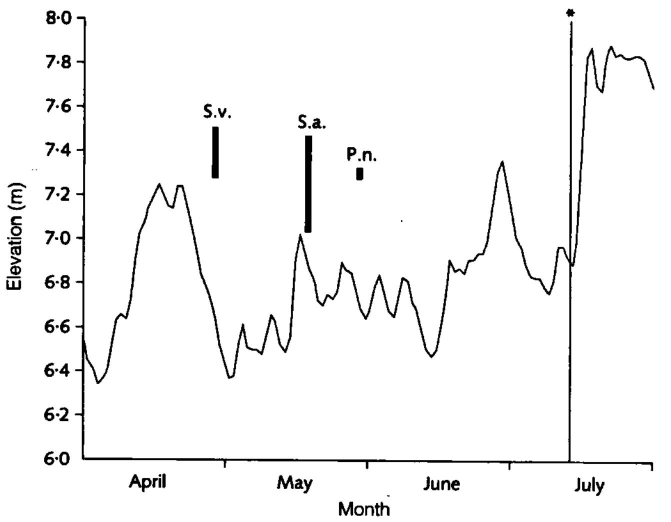

Fig. 5. Water level fluctuations (in m above sea level) at gauge station Nijmegen from 1 April to 31 April 1993 combined with distribution of seedlings of *Salix alba* (S.a.), *S. viminalis* (S.v.) and *Populus nigra* (P.n.). (* = date of investigation.)

Soil moisture content appeared to be an important factor for germination. *P. nigra* and *S. viminalis* were the most drought-tolerant species. Consequently, seedlings of these species were expected to be found in broader zones on the river bank than seedlings of *S. triandra* and *S. alba*. However, this was not observed at the field locations in 1993, probably due to environmental heterogeneity and complexity of factors regulating germination and seedling survival. Germination is not inhibited by a high soil water content. Additional experiments have shown that seeds germinate well under soaked conditions (results not presented). Hosner (1957) found that drowned seeds of *P. deltoides* and *S. nigra* behave in a similar way.

The differences between the results of the PEG and the soil-moisture experiment might be explained by the different contact with substrate of seeds and soil and of seed surrounded by PEG solution. Clearly, the soil moisture experiment reflects best the field situation. Due to the greater longevity of the seeds, the germination level of *P. nigra* may not only be determined by the water level in the period of seedfall, but also by the water level fluctuations after that period. Differences in length of seedfall periods might also confuse the link between water level and seedfall timing. Even though *P. nigra* seeds have greater longevity, *S. alba* seeds have a longer dispersal period. A short seed viability of *Salix* species was already reported by Moss (1938), Ware & Penfound (1949) and McLeod & McPherson (1973).

In 1993, seeds of *S. viminalis* were dispersed first at the beginning of May during receding water levels. Only 3 weeks later the water reached the level of early May again: during that period the seedlings could grow and anchor. Seeds of *S. alba* were dispersed from 15 May on. At the time the field observations were made (July), the seedlings of *S. viminalis* were significantly larger in size than *S. alba* (results not shown). Moss (1938) and Fenner *et al.* (1984) also stressed the general importance of a stable environment for germination and young seedlings. They found that after germination the soil had to remain moist for at least 1 week: if the soil dries out or is disturbed by flooding, the hairs that are essential for the uptake of water and nutrients might be damaged and the seedling dies.

During the dissemination period of *S. alba* and *P. nigra*, the water levels fluctuated. It is likely that seeds of *P. nigra* were washed ashore during the short period of seedfall, and germinated. A greater longevity is only profitable if the seeds stay dry. Part of the seedlings were probably washed out during flooding at the end of June. Seeds of *S. alba*, which were dispersed over a longer period, may have had more opportunities to germinate and covered a larger elevation range on the banks. Fenner *et al.* (1985) also showed that a sinking water level during germination and seedling establishment was necessary for the successful establishment of willows and poplars.

The poor success of *P. nigra* seedlings in the field may also be due to the extremely wet conditions during this stage, caused by both high water levels and large amounts of precipitation. This is confirmed by field observations in the summer of 1994, when large numbers of *P. nigra* seedlings were found. In 1994 the water levels remained high until July. After July the water level dropped followed by a period of high temperatures and drought. No seedlings of *S. viminalis* or *S. triandra* were detected at all, and only few *S. alba* seedlings.

It may be concluded that the interaction between water levels and timing of seed dispersal of Salicaceae species is the dominating process determining success of establishment and zonation of Salicaceae species on river banks. The zonation is strongly influenced by length of dissemination period and longevity of seed, and to a lesser extent by differences in drought tolerance between species concerning seed germination.

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