Root anchorage of saplings and cuttings of woody pioneer species in a riparian environment

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Summary
1. The root anchorage ability of saplings and vegetative propagules may be decisive for persistence of woody pioneers in the highly disturbed habitat of floodplains.
2. Vertical uprooting resistance was investigated in saplings of three floodplain pioneers of central Europe, Alnus incana, Populus nigra and Salix elaeagnos, at the near-natural River Tagliamento, north-east Italy. Uprooting resistance of planted cuttings of P. nigra and S. elaeagnos was studied at this site and in an experimental garden.
3. Uprooting resistance was lowest in saplings of A. incana, intermediate in P. nigra, and highest in S. elaeagnos. For cuttings, differences in uprooting resistance between species were evident only under floodplain conditions, where resistance was higher in P. nigra than in S. elaeagnos. This difference was related to better growth in P. nigra.
4. The anchorage ability of saplings may be one factor influencing the longitudinal and transverse zonation of species in floodplains, as S. elaeagnos is restricted to highly disturbed sites close to the main channel, whereas A. incana and P. nigra occupy more stabilized habitats. For vegetative propagules, in contrast, regeneration ability may be more important than uprooting resistance.

Key-words: Alnus incana, floodplain, Populus nigra, resprouting, Salix elaeagnos, species zonation, uprooting resistance


Introduction
Woody pioneer species of the active floodplain of rivers readily colonize fresh sand and gravel bars created by flood disturbance (Hupp & Osterkamp 1996; Gurnell et al. 2001). In the Northern Hemisphere these pioneers are mainly species of the genera Alnus, Populus and Salix (Malanson 1993; Karrenberg, Edwards & Kollmann 2002). All three genera reproduce sexually by wind-dispersed seeds, but also have a high capacity for vegetative reproduction. Because of frequent disturbance by flooding, pioneer stands usually do not persist for more than 20 years (Bayard & Schweingruber 1991; Karrenberg et al. 2003). Thus rapid growth and anchorage ability of both saplings and vegetative resprouts may be decisive for plant survival.

In central Europe, Alnus incana, Populus nigra and Salix elaeagnos are frequent woody pioneers on near-natural floodplains. Regeneration sites in the middle sections of large rivers may support mixtures of seedlings and resprouts of all three species (van Splunder et al. 1995; Kollmann et al. 1999; Karrenberg et al. 2003). However, extensive stands of A. incana are found mainly in the upper reaches and those of P. nigra mainly in the lower reaches, whereas S. elaeagnos has a wide altitudinal range (Ellenberg 1996). Populus nigra may be climatically excluded from mountain areas (Schütt et al. 1999), but the reasons why A. incana does not occur in the lowlands remain elusive (Schwabe 1985; Ellenberg 1996). Across the active floodplain, the tall shrub S. elaeagnos is found in the most disturbed areas, whereas the trees P. nigra and A. incana are dominant in more stabilized parts (Ellenberg 1996). In this study, we ask if differences in root anchorage among these species are consistent with these distributions.

Root anchorage depends on properties of the root system such as topology and root tensile strength, as well as on soil conditions. Wet, heavy soils, for example, provide more resistance to uprooting than do dry, sandy soils (Ennos 1990; Goodman & Ennos 1999). As roots are usually more flexible than the soil, physical
stress causes the roots to bend or stretch and eventually to break proximally before the soil/root connection is disrupted distally. Anchorage is achieved by strengthening the proximal parts of the root system, while the distal parts are mainly for absorption (Ennos & Fitter 1992; Ennos 2000). Root anchorage is a plastic trait, and root growth reactions to soil characteristics (Oplatka & Sutherland 1995; Goodman & Ennos 1999) and mechanical forces such as wind or bending (Stokes & Guitard 1997) are common. For this reason, comparative measurements of root anchorage need to be made in natural habitats.

One difficulty with measurements of root anchorage is the application of realistic forces. Studies on root anchorage have been conducted in relation to the leaning over (‘lodging’) of crops and forest trees (Kevern & Hallauer 1983; Crook & Ennos 1993; Crook & Ennos 1996; Goodman, Crook & Ennos 2001; Mickovski & Ennos 2002) as well as in relation to soil erosion control (Oplatka & Sutherland 1995; Nilaweera & Nutalaya 1999). These applied studies have employed vertical and lateral displacement (pulling plants over), whereas studies on the mechanism of root anchorage in artificial systems have focused on vertical uprooting (e.g. Ennos 1990; Stokes et al. 1996; Bailey, Currey & Fitter 2002).

Mechanical forces exerted by floods on tree saplings and vegetative resprouts may be impossible to mimic, as they act at varying angles with additional effects of surface erosion and waterlogging of the sediment. We therefore chose to measure vertical uprooting resistance of entire saplings and cuttings as a simple surrogate for root anchorage strength. Specifically, this study investigates root anchorage in naturally grown saplings of *A. incana*, *P. nigra* and *S. elaeagnos*, and in planted cuttings of *P. nigra* and *S. elaeagnos*. The effect of sediment properties and growth form on root anchorage in saplings was also studied.

### Materials and methods

#### STUDY SITE

The River Tagliamento is an unconstrained seventh-order river in north-east Italy with a catchment area of 2580 km². It arises in the limestone mountains near the border with Austria and flows 172 km to the Adriatic Sea, exhibiting a sequence of constrained, braided and meandering reaches. Peak flows occur in spring and autumn, but discharge is extremely variable throughout the year (Edwards et al. 1999). Compared with other European rivers, the Tagliamento has an exceptionally low human impact (Ward et al. 1999).

Experiments were conducted in spring and summer 2000 within a 2 km section of the river near the village of Pinzano, west of Udine (46°12′ N, 12°58′ E). In this region the river leaves the Alps and enters the north-eastern Italian plain. The climate is warm-temperate with a mean annual precipitation of 1900 mm and a mean annual temperature of 13 °C (Poldini 1991). The study area was confined to the active zone of the river corridor, which is about 800 m wide and consists of multiple channels, gravel bars and vegetated islands. The principal woody species that form these islands are five species of *Salix*, *Populus nigra* and *Alnus incana* (Kollmann et al. 1999; Karrenberg et al. 2003).

The sediments of the Tagliamento floodplain are mostly calcareous and very heterogeneous, due to size sorting by retracting floods and frequent morphological reorganization of the entire active zone (Petts et al. 2000). Most higher bars are a result of layering of fine (silt, sand) and coarse (pebble, cobble) sediments. Where pioneer vegetation grows, the vegetation itself retains fine sediments and organic material, and initial alluvial soils develop (Edwards et al. 1999). However, larger floods regularly remove these vegetated islands, so most islands do not persist for long. In the active zone of the Tagliamento, the mean age of vegetated islands is 8-4 years (Karrenberg et al. 2003).

Regeneration sites for the woody pioneers, which are the focus of this study, are exposed, nutrient-poor sediments of various grain sizes; the median grain size of exposed bars is 8 mm in the study area (Petts et al. 2000). The surface sediments consist mostly of gravel, but especially downstream and on the sides of obstacles such as gravel bars, vegetated islands or large wood deposits, plumes of finer sediments are formed (Edwards et al. 1999). We selected our study saplings on a representative sample of these surface sediments and planted cuttings in sandy deposits near vegetated islands (see below).

#### STUDY SPECIES

All three study species, the trees *Populus nigra* L. (Salicaceae) and *Alnus incana* (L.) Moench (Betulaceae), and the tall shrub *Salix elaeagnos* Scopoli (Salicaceae), are fast-growing, woody pioneers of active floodplains in Eurasia (Schütt et al. 1999). *Populus nigra* is endangered by introgression from commercially grown poplar hybrids (*P. × euramericana*), and morphological differentiation of introgressants and pure *P. nigra* is difficult (Böcker & Koltzenburg 1996). We cannot be certain that the plants investigated in the present study were pure *P. nigra* genotypes, although none of the traits described for hybrids was found (Böcker & Koltzenburg 1996). Thus, the name *P. nigra* is used throughout the manuscript.

#### MEASURING UPROOTING RESISTANCE

Vertical uprooting resistance was measured using a device that was designed for the purpose and built in cooperation with the Technical Workshop of the Institute of Biology II/III, University of Freiburg (Fig. 1; further inquiries to T.S.). The uprooting device consists of a steel tripod and a crank and a gearing system...
constructed to pull plants slowly in an upward direction. Before uprooting, saplings were cut 20 cm above ground. The shoot was then fixed in a metal grip after removing the cortex at the point of attachment to prevent slippage. The use of various grips allows the device to be used on plants of various sizes up to 4 cm stem diameter. However, in woody saplings on floodplains, the maximum force applicable (2 kN) limits the use of the apparatus to saplings with less than 2 cm stem diameter. During the pulling process, the force (accuracy 0·1 N) and displacement (up to 50 cm, accuracy 0·1 mm) were measured simultaneously at 0·5 mm intervals by transducers attached to the pulling device (Burster Präzisionsmesstechnik, Gernsbach; Megatron Sensorsysteme, Putzbrunn/München, Germany) and logged to a portable computer. The resulting force–distance diagrams show a steep slope until the maximal force ($F_{\text{max}}$) is reached and root breakage occurs (Fig. 2, cf. Ennos 1990). Further steps in the curve can be correlated with the breaking of roots (cf. Bailey et al. 2002). However, in many study plants it was impossible to match individual broken roots reliably with drops in the force displacement curve, because simultaneous root breakage may occur and breaking order is not necessarily related to root size (Bailey et al. 2002). We concentrated on $F_{\text{max}}$ and critical stress ($\sigma_{\text{crit}}$) at the point of breaking.

**Fig. 1.** The uprooting device used for testing plant anchorage with forces up to 2 kN (construction in cooperation with the Technical Workshop, Institute of Biology II/III, Freiburg University, Germany); scale 50 cm.

**Fig. 2.** Force–displacement curve resulting from vertical uprooting of a sapling of *Populus nigra* (86 cm high) that had established naturally in gravel sediments of the River Tagliamento, north-east Italy. (a) Failure of the main root; (b) failure of a side root.

**MEASUREMENTS ON SAPLINGS**

Saplings of *S. elaeagnos* ($n = 36$), *P. nigra* ($n = 36$) and *A. incana* ($n = 17$) were uprooted on days with fair weather in May 2000. To obtain a representative sample of saplings, the total study area was divided into six parts. In each part, six plants of *P. nigra* and *S. elaeagnos*, were selected, growing on two different surface sediments: three plants of each species in gravel (cobbles, 4–100 mm diameter, often in a finer matrix) and the other three in sandy sediments (c. 0·1–2·0 mm grain size). Saplings of *A. incana* were less common in the study area, and were uprooted only when encountered near the other species. The saplings were between 2 and 6 years old; mean age did not differ significantly between species (Table 1).

The critical stress ($\sigma_{\text{crit}}$) for a sapling – the force per unit area that is necessary to induce root system failure – was calculated by dividing $F_{\text{max}}$ by the cross-sectional area of root wood cylinders at the point of failure. This gives a good first-order approximation for the critical stress in the main anchoring roots. The cortex, which was frequently stripped off during uprooting and remained in the sediment, was excluded. The cortex of the root system still contributed to uprooting resistance by increasing root–soil friction through bark roughness. However, the cortex is of minor importance as a load-bearing tissue under tension, which is why total root diameter is not a reliable indicator of root tensile strength (Hathaway & Penny 1975) and can be ignored for calculating the critical stress in the main roots. To calculate the cross-sectional area, the largest and smallest root cylinder diameters were measured (ellipse approximation). Usually not more than three roots with breaking points could be identified, so measurements were made on three roots with the greatest cross-sectional area; these are termed the main root and lateral roots.

As root anchorage of entire plants can be expected to be related to plant size, the following size parameters were recorded: basal shoot diameter, shoot height and total shoot dry mass (after drying at 70 °C until constancy). In addition, the age of saplings was determined by ring counting at the base of the stem. When comparing the three species, two specific contrasts were calculated to avoid confounding trait similarity with common descent (Silvertown & Dodd 1996): (i) *A. incana* (Betulaceae) vs. Salicaceae (*S. elaeagnos* and *P. nigra*); (ii) *S. elaeagnos* vs. *P. nigra*. 
EXPERIMENTS WITH CUTTINGS

The uprooting resistances of cuttings of *Salix elaeagnos* and *P. nigra* were investigated at the River Tagliamento. A similar experiment was set up in the experimental area of the Botanic Garden of Freiburg University (47°59′ N, 7°51′ E) as a backup for potential losses due to flooding or dry spells at the floodplain site. Eighteen individuals per species were selected as donors for cuttings. We took care to avoid sampling from the same clonal genotype by taking plants from the whole study area. We produced 20 cuttings per genotype. These were about 20 cm long and had a diameter of 1.5–2.5 cm, as previous work has shown that cuttings of this size establish well (Burgess, Hendrickson & Roy 1990). Cuttings were stored in moist plastic bags at 4°C until planting.

At the floodplain site, 480 cuttings were planted in five plots with sandy substrate and low vegetation cover (<10%) on 20 and 21 April 2000. The plots were spread over the study area and situated near vegetated islands distant from the major channels to reduce the risk of losses due to flooding. In each plot, 96 cuttings (four of each of 12 different genotypes per species) were assigned randomly within a triangular grid arrangement. The study plots were watered and covered with a transparent plastic foil for 2 weeks. After that period the plots were watered occasionally for another 25 days.

In the experimental garden of Freiburg University, 240 cuttings were planted in nutrient-rich, sandy-loamy soil on 11 April 2000, using 20 cuttings of each of six genotypes per species. These were not the same genotypes as those used in the floodplain experiment, because many of the shrubs were fully used with the production of 20 cuttings. The experimental area was partitioned into six adjacent plots to which genotypes were randomly assigned within a triangular grid. Good water availability was maintained by regular watering according to weather conditions.

In the floodplain experiment, respouting of the cuttings was recorded after 4 weeks. After 12 weeks the uprooting experiments were conducted on all cuttings that were still alive (46 *P. nigra*, 13 *S. elaeagnos*). In the experimental garden we selected cuttings at predefined planting grid points for uprooting 17 weeks after planting (20 *S. elaeagnos*, 13 *P. nigra*). At the same time, respouting frequency was recorded. After the destructive uprooting measurement, resprouts were collected for determination of dry mass (drying at 70°C until constancy). All data analyses were conducted with JMP 4·0·3 (SAS Institute Inc. 2000) based on Zar (1999).

Results

UPROOTING RESISTANCE AND GROWTH PROPERTIES OF SAPLINGS

Uprooting resistance (*F*<sub>max</sub>) differed among the three species as follows: *A. incana* < *P. nigra* < *S. elaeagnos* (Fig. 3). In all species, *F*<sub>max</sub> on sand exceeded that on gravel; this difference was more pronounced in *A. incana* and *P. nigra* than in *S. elaeagnos*. When comparing species, both contrasts were significant: *A. incana* required a significantly smaller *F*<sub>max</sub> than the Salicaceae; among the latter, significantly less force was needed to uproot *P. nigra* in comparison to *S. elaeagnos* (Table 1). For calculation of multiple regression models of *F*<sub>max</sub> (least-squares method), the response variate *F*<sub>max</sub>, biomass and total root area at the breaking point were log-transformed. Biomass, sediment type and species identity together explained 43% of the variance and each had a significant effect on *F*<sub>max</sub> (Table 2). Interactions of species identity with biomass and sediment type were not significant and were therefore removed from the model. Biomass explained about 18% of the variance in *F*<sub>max</sub>, and species identity accounted for an
The critical stress ($\sigma_{\text{crit}}$) differed between the species in the same way as did $F_{\text{max}}$: it was lowest in *A. incana*, intermediate in *P. nigra*, and highest in *S. elaeagnos* (Table 1). Variation in $\sigma_{\text{crit}}$ was high (CV = 119%). No significant differences were found between *A. incana* and the Salicaceae, but within the two Salicaceae $\sigma_{\text{crit}}$ was significantly higher in *S. elaeagnos* than in *P. nigra*. *Alnus incana* did not differ significantly from the Salicaceae in terms of height, basal diameter, total root area and main root area (Table 1). However, between *S. elaeagnos* and *P. nigra* differences in growth form were evident. Above-ground biomass and basal diameter were significantly larger in *S. elaeagnos*, while *P. nigra* grew taller than *S. elaeagnos*.

**REGENERATION AND UPROOTING RESISTANCE OF CUTTINGS**

In the floodplain experiment nearly 30% of the *S. elaeagnos* cuttings and 24% of the *P. nigra* cuttings resprouted after 4 weeks; however, this difference was not significant (Table 3a). At least one cutting of each genotype resprouted. In July, after 12 weeks, less than a quarter of the resprouts of *S. elaeagnos* were alive (of seven genotypes), whereas the resprouting frequency of *P. nigra* was still about 20% (11 genotypes). In the garden experiment the percentage of resprouts 17 weeks after planting was about double the maximum in the floodplain (around 60%) and did not differ significantly among species (Table 3a). In this experiment, resprouts were also recorded from all genotypes.

Biomass production in the floodplain was <10% of the biomass produced in the experimental garden (Table 3b). In the floodplain experiment regrowth height rarely exceeded 0.4 m, whereas some garden-grown resprouts reached 2.0 m. In the floodplain experiment *P. nigra* produced significantly more biomass than *S. elaeagnos*, whereas in the experimental garden biomass was indistinguishable among species.
Root anchorage in woody pioneers

Fig. 4. Uprooting resistance ($F_{max}$, means ± SE) of plants regenerated from cuttings of two woody pioneer species grown in the floodplain of the River Tagliamento, north-east Italy (12 weeks) and in the experimental garden of Freiburg University, Germany (17 weeks). Dotted reference lines mark the uprooting resistance of cuttings without regrowth.

Table 4. ANOVA of maximal uprooting resistance ($F_{max}$) in cuttings of *Salix elaeagnos* and *Populus nigra* (a) after 12 weeks’ growth in a floodplain experiment (sandy sediments, floodplain of the River Tagliamento, north-east Italy); (b) after 17 weeks’ growth in an experimental garden in Freiburg, Germany (sandy-loamy soil)

<table>
<thead>
<tr>
<th>Source</th>
<th>d.f.</th>
<th>SS</th>
<th>$F$ ratio</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Floodplain</td>
<td></td>
<td></td>
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<td>Biomass</td>
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<td>19.27</td>
<td>&lt;0.001</td>
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<tr>
<td>Species</td>
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<td>0.74</td>
<td>0.81</td>
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<tr>
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<td>15.47</td>
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</tr>
<tr>
<td>Error</td>
<td>55</td>
<td>5.273</td>
<td>0.10</td>
<td></td>
</tr>
<tr>
<td>(b) Garden</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Biomass</td>
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<td>27.98</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Species</td>
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<td>0.14</td>
<td>0.70</td>
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<td>Plot</td>
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<td>1.48</td>
<td>0.23</td>
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<tr>
<td>Error</td>
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<td>2.924</td>
<td>0.12</td>
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Residuals conformed to the normal distribution (Shapiro–Wilk test, $P < 0.05$).

Uprooting resistance of the cuttings was low in the floodplain experiment: $F_{max}$ of cuttings without regrowth was 15.0 N, which was more than half that of living cuttings (Fig. 4). *Populus nigra* cuttings required significantly larger uprooting forces than *S. elaeagnos* (signed rank test, $P = 0.04$). In a regression model of $F_{max}$ the effect of species was, however, not significant when the biomass effect, which explained about 14% of the variance in $F_{max}$, was included (Table 4a). Furthermore, plot identity significantly affected $F_{max}$ and explained the largest amount of variance of $F_{max}$ (45%).

In the garden experiment, the forces required to induce root failure (161–190 N) were nearly 10 times greater than in the floodplain; 102 N was needed to uproot a cutting without regrowth (Fig. 4). In a multiple regression model of $F_{max}$ biomass was the best predictor and explained more than 45% of its variance in $F_{max}$. Species and plot identity did not significantly affect $F_{max}$ (Table 4b).

**Discussion**

Uprooting resistance was lower in the saplings of *A. incana* than in saplings of the two Salicaceae. However, care must be taken in interpreting this result because *A. incana* saplings were not paired directly with the Salicaceae saplings. Nonetheless, *A. incana* saplings had inferior root anchorage, and it is reasonable to suppose that they are more easily removed during floods than are the Salicaceae saplings. In the upper course of the River Tagliamento, where *A. incana* dominates the pioneer vegetation, the vegetation is older (>15 years) than in the middle and lower reaches (<10 years; Karrenberg et al. 2003). This suggests a lower incidence of devastating disturbance in the upper than in the middle and lower reaches, possibly because the catchment area increases strongly in the middle reaches due to many confluences (Petts et al. 2000). The comparatively low uprooting resistance of *A. incana* saplings may have reduced the occurrence of this species in the lower parts of the river. However, other factors, such as a lack of seed input from stands outside the floodplain, are probably also important. Of the two Salicaceae, *S. elaeagnos* had a significantly higher uprooting resistance than *P. nigra*. This may partly explain the observed transverse zonation in floodplains, in which *S. elaeagnos* tends to occupy sites that are closer to the main channel and thus more frequently disturbed, whereas *P. nigra* dominates in more stable habitats (Ellenberg 1996). In highly disturbed conditions, *S. elaeagnos* may be favoured partly because of its greater uprooting resistance. In mixed stands, especially under favourable conditions, *P. nigra* would be expected to outcompete *S. elaeagnos* because of its taller growth.

**Influence of growth form, size and sediment properties on uprooting resistance of saplings**

Despite the difference in $F_{max}$ the root systems of *A. incana* and the Salicaceae were able to withstand a similar force per root diameter, that is, there was no significant difference in the critical stress ($\sigma_{cr}$). This suggests that factors other than root material properties, such as root topology, might be responsible for the greater $F_{max}$ observed in the Salicaceae. The root surface at the breaking point was smaller in *A. incana* than in the Salicaceae, although not significantly ($P = 0.09$; Table 1). However, the stem diameter was similar in all species (Table 1). This suggests that *A. incana* invested fewer resources than the other two...
species in root thickening. In contrast to the Salicaceae, *A. incana* produces nitrogen-fixing root nodules containing the bacterial symbiont *Frankia alni* (Schütt et al. 1999). This may be one reason for a smaller investment in root system structure. Within the Salicaceae, uprooting resistance and critical stress ($\sigma_{\text{crit}}$) were significantly higher in *S. elaeagnos* than in *P. nigra*. This suggests that, among other factors, superior material properties of the root tissues of *S. elaeagnos* account for greater root anchorage of this species.

Published values of tensile strength for individual roots of the study species are in accordance with the $\sigma_{\text{crit}}$ values measured. Riedl (1937) recorded 22 MPa tensile strength for root segments of *A. incana* (10 mm diameter); Hiller (1966) found that small roots of *S. elaeagnos* (<2 mm diameter) have a tensile strength of 15 MPa; whereas Schiechtl (1980) reported a tensile strength of only 5–12 MPa for slightly larger roots of *P. nigra* (c. 3 mm diameter). Unfortunately these values are not comparable between species because of the different sizes of roots used. Generally, tensile strength decreases with increasing root diameter (Stokes 2002) due to differences in the lignin-to-cellulose ratio. This concept is difficult to apply to our study because we measured the failure of complex systems composed of many roots of different sizes. Therefore, we suggest that detailed studies of root system topology and root tensile strength should be made to explore the reasons for the differences in the root anchorage of whole plants.

Uprooting resistance was higher in sand than in gravel in all species, and sediment type had a significant but small effect on $F_{\text{max}}$. Differences in uprooting resistance between sediments are likely to be due to differences in root system development (cf. Ennos 2000). Roots that developed in sand had a regular round form, whereas those that forced their way through gravel generally had a contorted appearance with an irregular cross-section (Oplatka & Sutherland 1995). Therefore the uprooting force in sand may be more equally distributed over the root, while in gravel roots may break earlier by a different mechanism (cf. Oplatka & Sutherland 1995). We could not make more detailed descriptions of either sediments or root topology because it was nearly impossible to dig any deeper than 20–30 cm. However, small-scale differences in sediment properties, for example due to layering or the presence of single big stones, are likely to have added to the variability in $F_{\text{max}}$.

**REGENERATION AND ANCHORAGE OF CUTTINGS**

While *S. elaeagnos* and *P. nigra* cuttings produced a similar amount of biomass and had similar uprooting resistances under garden conditions, *P. nigra* clearly performed better than *S. elaeagnos* in the floodplain experiment. The greater uprooting resistance of *P. nigra* in the floodplain could be attributed to its greater biomass production. Water and nutrient availability were much better in the garden than in the floodplain, where the site located closest to a channel exhibited the highest survival and biomass production of cuttings. Therefore, drought is likely to have been the decisive factor for the regeneration of cuttings, as found by Hughes et al. (2000). When living plant fragments are dispersed by floods they are deposited as the water recedes (Gurnell et al. 2001). Depending on the height of the flood and speed of water level decrease, fragments may be deposited in different conditions. The sites in which we planted cuttings did not represent the full range of conditions in the active floodplain, and there are probably sites in which regrowth is more vigorous.

**Conclusions**

The anchorage ability of saplings may be a significant factor influencing the distribution of woody pioneer species in floodplains. *Salix elaeagnos*, the species with the greatest uprooting resistance as a sapling, grows in the most disturbed sites close to the main channel, whereas *A. incana* and *P. nigra* occupy more stabilized habitats. The tree *P. nigra* exhibited inferior anchorage as a sapling, but its cuttings had superior growth and anchorage ability under severe floodplain conditions. This may lead to greater success in vegetative reproduction in this species.

Cuttings of all three study species are recommended for use in bioengineering works along rivers (Schiechtl 1980), and our results underline their suitability for this purpose. Care has to be taken that the plantations are not affected by drought, which can arise from extended periods of low water flow. For restoration projects in riparian zones, where the development of near-natural floodplain vegetation is the aim, we suggest that seed propagation during favourable conditions, such as receding water levels, should be considered. The seeds of Salicaceae are short-lived but can be kept viable by freezing (Karrenberg et al. 2002). Seeding would lead to a near-natural zonation of the species over time as the trees *Populus* and *Alnus* are likely to outcompete the shrubby *Salix* species in the less disturbed parts. High genetic variability, which may be a quality wanted in near-natural stands, will be much easier to achieve with seeds than with cuttings.

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