Morphological responses of seedlings of four species of Salicaceae to drought


Abstract: The riparian distribution patterns of floodplain species are affected by fluctuations in water level. Rapidly declining water levels in river banks during the growing period of plants can result in limited availability of water, particularly on coarse substrates. Differences in drought resistance among Salix alba, Salix triandra, Salix viminalis, and Populus nigra, four species dominating river banks along the River Rhine, could explain part of the riparian distribution patterns. Mortality and growth responses of seedlings grown under well-watered and dry conditions were studied in a greenhouse experiment. Drought-induced mortality was 0% in S. alba and P. nigra, 37.5% in S. triandra, and 62.5% in S. viminalis, which correlated with differences in water-loss characteristics of the species studied: S. triandra and S. viminalis had much higher transpiration rates under well-watered conditions than S. alba and P. nigra. Decreased shoot to root ratios were observed in all species after 3 weeks of drought. The increase after drought of the root length to leaf area ratio was greatest for P. nigra, indicating that this species has a relatively efficient water economy. Specific leaf areas of droughted plants decreased in S. alba and P. nigra, reflecting smaller transpiration areas. Drought also affected root distributions, resulting for all four species in deeper rooting and increased root length in deeper soil layers. Salix viminalis and S. triandra showed the greatest increase in root length in deep soil layers. We concluded that P. nigra is most resistant to drought followed by S. alba and then S. triandra and S. viminalis, and that these differences are reflected in the distribution patterns of these species observed on the banks of the River Rhine.

Key words: drought resistance, Salix, Populus, root distribution, transpiration, leaf conductance.

Résumé : Les patrons de distribution riparienne des espèces de plaines alluviales sont affectés par les fluctuations du niveau de l’eau. Une baisse rapide des niveaux de l’eau, sur les platières de rivières au cours de la période de croissance des plantes, peut conduire à une disponibilité limitée de l’eau, surtout sur les substrats grossiers. Les différences de résistance à la sécheresse parmi les Salix alba, Salix triandra, Salix viminalis et Populus nigra, quatre espèces dominant les platières riveraines du Rhin, pourraient expliquer leurs patrons de distribution riparienne. Les auteurs ont étudié en serres expérimentales la mortalité et les réactions de croissance de plantules cultivées sous des conditions bien humides et sous des conditions sèches. Sous l’influence de la sécheresse la mortalité a été de 0% pour le S. alba et le P. nigra et de 37,5 et 62,5% pour les S. triandra et S. viminalis, respectivement, ce qui correspond avec les différences des caractéristiques de perte en eau par les espèces étudiées : le S. triandra et le S. viminalis montrent des taux de transpiration beaucoup plus élevés, sous des conditions de bonne irrigation, que le S. alba et le P. nigra. On observe une diminution des rapports tige à racine chez toutes les espèces après 3 semaines de sécheresse. L’augmentation, après sécheresse, de la longueur racinaire par rapport à la surface foliaire est plus élevée chez le P. nigra, ce qui indique que cette espèce possède une économie de l’eau relativement efficace. La surface foliaire spécifique des plantes soumises à la sécheresse, diminue chez le S. alba et le P. nigra, ce qui reflète des surfaces de transpiration plus petites. La sécheresse affecte également la distribution des racines, ce qui se traduit chez les quatre espèces par un enracinement plus important, soient une augmentation des longueurs racinaires dans des couches plus profondes du sol. Les auteurs concluent que le P. nigra est plus résistant à la sécheresse, suivi par le S. alba et enfin les S. triandra – S. viminalis, et que ces différences se reflètent dans les patrons de distribution de ces espèces observés le long de rives du Rhin.

Mots clés : résistance à la sécheresse, Salix, Populus, distribution racinaire, transpiration, conductance foliaire.

Received January 30, 1996.

Introduction

The establishment and development of floodplain forests along rivers is mainly determined by local hydrological conditions (Pantou and Décamps 1985; Walker et al. 1986; Dister et al. 1989; Schnitzler et al. 1992). Intermittent floods may hamper the establishment of floodplain forests, despite the relative high tolerance of floodplain species for waterlogging and submergence (Bell 1980; Walker et al. 1986; Krasy et al. 1988a, 1988b; Liu and Dickmann 1993). Additionally, drought

resulting from rapidly declining water levels can easily result in greatly reduced water availability for plants. Seed germination and seedling survival are especially susceptible to drought (Pickett and Bazzaz 1978; Krasny et al. 1988a; Burton and Bazzaz 1991; Sacchi and Price 1992).

The grain size of substrates influences soil-moisture availability and consequently the distribution of species (Roberts 1966). For instance, on gravel banks of the River Allier in France, floodplain forests are dominated by *Populus nigra* (Dister et al. 1989), whereas sandy banks along the River Rhine in the Netherlands are dominated by *Salix* spp. (Van Splunder et al. 1995). When water levels recede, water availability is greater in sandy soil than in gravelly soils because of capillarity in sandy soils (Mahoney and Rood 1992). A similar substrate-related distribution has been observed in poplars and willows along the lower Dry Creek in California (McBride and Strahan 1984).

Drought might influence the distribution of floodplain species at several life stages. Differences in drought resistance could result in a zonation of riparian plant species along the elevation gradient. Zonation may develop during the germination stage. Niiyama (1990) and Van Splunder et al. (1995) found differences among Salicaceae species in response to drought during seed germination. In years when water levels fall rapidly during the growing season, differences in drought resistance between species might result in a more distinct distribution pattern than in years with less pronounced decline (Mahoney and Rood 1992). The desiccation of susceptible species on higher and drier elevations, and the survival of these species closer to the water level, can result in a zonation of the vegetation. Species that are relatively more drought resistant may be found at higher elevations. For example, Salicaceae species, which root superficially, are potentially more vulnerable to rapidly declining groundwater levels than deep-rooting species. In extremely dry years, the susceptible species may die and the more drought-resistant species could become dominant. In older growth stages of floodplain species, drought remains a stress-inducing factor.

The objective of the study was to assess differences in drought-resistance properties among the floodplain species *Salix alba*, *Salix triandra*, *Salix viminalis*, and *Populus nigra* during their seedling stage. Therefore, growth under well-watered and dry conditions was compared to elucidate the mechanisms of drought avoidance. We also measured transpiration rates and leaf conductances. The results were related to the observed field distributions of the four species along the River Rhine in the Netherlands.

**Materials and methods**

**Water-level fluctuations of the River Rhine**

Daily water levels of the River Rhine were collected from a gauge station near the city of Nijmegen, the Netherlands (51°52'N, 5°67'E). Years with continuing declining water levels during the growing season (May–August) were selected between 1981 and 1995. The mean water level of each 7-day period was calculated. For each year, the rate of water level decline was calculated in cm day⁻¹, starting at the highest mean water level after 1 May until the end of August.

**Species, growth conditions, and drought treatment**

Fresh seeds of floodplain forest species *S. alba* L. (white willow), *S. triandra* L. (almond willow), *S. viminalis* L. (common osier) and *P. nigra* L. (black poplar) were collected from shrubs and trees growing along the River Rhine. Seedlings were raised in a greenhouse in PVC tubes 15 cm in diameter and 50 cm tall, containing a mixture of clay and sand (1:19, v/v) with 1 g L⁻¹ fertilizer (Osmocote slow release fertilizer). Three groups of 32 tubes each were placed in basins in which the water level was kept at 15 cm below the soil surface. The light intensity in the greenhouse on sunny days was reduced using white cloth. Sodium lights were installed to increase low light intensities during the dark early morning and evening or on cloudy days. The photoperiod was 16 h light: 8 h dark; during the light period, a minimum light intensity of 200 µmol m⁻² s⁻¹ was supplied.

After 4 weeks of growth (time, t = 0), the first group (eight replicates of each species) was harvested. At the same time, one of the basins (containing the second group) was emptied, so the substrate would start drying out slowly. The third group continued to grow under the original moisture conditions. Groups two and three were harvested after 3 weeks.

Moisture content of the substrate was measured in tubes without plants at 1, 3, 7, and 15 days after the start of the experiment (t = 0), by taking three replicate samples (minimum of 5 g) at depths of 5, 10, 15, 20, 30, and 40 cm below ground level. The samples were weighed immediately after sampling, dried 24 h at 100°C, and reweighed. The bulk density of the substrate (1.44 kg L⁻¹) was used to calculate the volumetric moisture content (cm³ cm⁻³) of the samples.

**Harvesting technique and parameters measured**

The plants were harvested by cutting the above-ground parts at the base of the stem and separating the material into leaves and stem. Total leaf area per plant was measured with a portable leaf-area meter (LI-COR 3000). The soil, including the roots, was carefully removed from the tube and cut into five slices 10 cm thick. Maximum rooting depth was recorded. The roots from each soil slice were rinsed and their total length was measured using a Root Length Scanner (Commonwealth Aircraft Corporation, Melbourne, Australia). Median root depth was calculated to analyse the change in root distribution after drought for species studied. Fifty percent of the total root length is found below or above this depth. The dry weights of leaves, stem, and roots (from each 10-cm slice) were obtained after drying the material at 70°C for 24 h. Internal ratios of the plants were analysed by calculating shoot to root ratio (shoot dry weight to root dry weight) and the ratio of water input to water loss (root length (m) to leaf area (m²)). Specific leaf area (leaf area (m²) to leaf dry weight (g)) was also calculated.

**Transpiration and leaf conductance**

Seedlings of *S. alba*, *S. triandra*, *S. viminalis*, and *P. nigra* (n = 5) were grown in pots (volume 1.7 L) containing a 1:19 mixture of clay and sand supplied with 1 g L⁻¹ Osmocote slow-release fertilizer in a greenhouse. The light conditions were similar to those described above. Throughout the experiment, the substrate of the plants was kept moist. After 3 months of growth, the ground was covered with plastic sheet so the only water loss could be via transpiration. Each plant plus substrate (including pot and plastic sheet) was weighed. After 1 day, the pots (totals) were reweighed and total leaf areas of all replicates per species were measured. Transpiration rates were calculated per hour and per leaf-area unit (cm²).

Differences in leaf conductance (being the sum of stomatal plus cuticular conductance) between the species studied was measured using a steady-state diffusion porometer (LI-COR 1600). The plants were grown as described earlier under *Species, growth conditions,* and drought treatment. After 2 months of growth, the leaf conductance (cm s⁻¹) was measured before and after 1 week without watering. Each plant was measured 6 times during 1 day at the fol-
Fig. 1. Water levels during the growing season (May–August) in 1983 (--), 1985 (---), 1990 (----), and 1994 (----). Data (m asl) were collected at Nijmegen gauge station in the Netherlands. Average rate of decline in each year (cm day\(^{-1}\)) is shown in the figure.

lowing times: 7:00 (when the light was switched on), 9:30, 12:00, 14:00, 16:30, and 19:00. Measurements were taken from the first fully grown leaf (from the top of the stem). The leaf conductance was only measured on the abaxial surface of the leaves.

Statistical analyses

Biomasses and leaf conductances were log-transformed before analysis to obtain normal distribution. The effect of drought on the species studied was tested using an F test. Differences in means of growth parameters, transpiration rates, leaf conductances, and depth of median root lengths as a result of drought treatment were analysed using the least significant difference test (LSD; \(p < 0.05\)).

Results

Water-level fluctuations of the River Rhine

Figure 1 shows the course of the water level from May to August in the selected years 1983, 1985, 1990, and 1994. The rates at which the water level declined ranged from 2.9 to 6.6 cm day\(^{-1}\). In the figure, the range between 7.0 and 8.5 m above sea level (standardized to gauge station Nijmegen) is of special interest. Seedlings of Salicaceae have been found at this elevation range along the River Rhine in the Netherlands in the past 5 years (data not published).

Moisture content

The substrate in the tubes started drying out from the moment the basin was emptied. At \(t = 0\) days, the substrate was saturated except for the upper 10 cm, where the soil was moist. The largest amount of moisture was lost within a day. The soil mainly consisted of sand, so a large part of the water was lost because of gravity. A decrease in moisture content between days 1 and 15 was evident, but the rate was much slower than from day 0 to 1. Figure 2 shows the decline in moisture content from 0.081 cm\(^3\) cm\(^{-3}\) at the top sample to 0.30 cm\(^3\) cm\(^{-3}\) at the bottom of the tube. After 15 days, the moisture content was only slightly lower: 0.074 cm\(^3\) cm\(^{-3}\) at the top and 0.28 cm\(^3\) cm\(^{-3}\) at 40 cm depth.

Influence of drought on biomass allocation

Although all replicates of the species studied survived in conditions of plentiful water, only seedlings of \(S.\) alba and \(P.\) nigra were all alive 3 weeks after the basin had been emptied. \(S.\) viminalis and \(S.\) triandra numbers were reduced under dry conditions: three replicates of \(S.\) viminalis survived drought, five of \(S.\) triandra (Table 1).

Drought-induced growth reduction was greatest in the leaves and stem (Table 1): all species except \(S.\) viminalis showed statistically significantly lower leaf and stem weights as a result of drought. Similar to leaf weights, the leaf areas of all species except \(S.\) viminalis were significantly smaller under dry conditions than under well-watered conditions. Drought had no significant effect on root dry weight. Under well-watered conditions the root depth of \(S.\) alba species was greater than \(P.\) nigra. The root distribution of the well-watered \(P.\) nigra was concentrated in the upper 10 cm; 97% of the roots were in this top layer (Fig. 3), compared with 67% under dry conditions. Drought greatly affected root depth and root length distributions (Table 1; Fig. 3). In all species, the root depth increased under dry conditions. \(P.\) nigra showed the largest relative increment of root depth under dry conditions but also had the most shallow root depth under well-watered conditions. Drought had no significant effect on root dry weight. Under well-watered conditions the root depth of \(S.\) alba species was greater than \(P.\) nigra. The root distribution of the well-watered \(P.\) nigra was concentrated in the upper 10 cm; 97% of the roots were in this top layer (Fig. 3), compared with 67% under dry conditions. Drought greatly affected root depth and root length distributions (Table 1; Fig. 3). In all species, the root depth increased under dry conditions. \(P.\) nigra showed the largest relative increment of root depth under dry conditions but also had the most shallow root depth under well-watered conditions. Under dry conditions, the proportion of root length of \(S.\) alba species was greater in the deeper soil layers and the root distribution was more uniform than under well-watered conditions. A change in root distribution as a result of drought was demonstrated by testing the mean depth of median root length of the species studied. The mean depth was significantly lower after drought in all \(S.\) alba species, coinciding roughly with an increase from 8 to 25 cm depth (Fig. 3). However, we found no significant change in the mean depth of median root length after drought treatment.
### Table 1. Dry weight (DW) of leaves, stem, and roots, rooting depth, and leaf area of seedlings of *S. alba*, *S. triandra*, *S. viminalis*, and *P. nigra* under well-watered and drought conditions (mean ± SE).

<table>
<thead>
<tr>
<th>Growth parameter</th>
<th>Well-watered 0 weeks</th>
<th>Well-watered 3 weeks</th>
<th>Drought 3 weeks</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>DW leaves (mg)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. alba</em></td>
<td>29.8±4.4 (8)</td>
<td>546.3±127.7 (8)***</td>
<td>157.3±44.0 (8)</td>
</tr>
<tr>
<td><em>S. triandra</em></td>
<td>32.7±7.3 (8)</td>
<td>695.1±111.3 (8)*</td>
<td>274.0±58.6 (5)</td>
</tr>
<tr>
<td><em>S. viminalis</em></td>
<td>43.0±9.8 (8)</td>
<td>763.6±166.7 (8)</td>
<td>404.1±303.6 (3)</td>
</tr>
<tr>
<td><em>P. nigra</em></td>
<td>19.7±3.8 (8)</td>
<td>338.4±91.6 (8)***</td>
<td>68.9±16.2 (8)</td>
</tr>
<tr>
<td><strong>DW stem (mg)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. alba</em></td>
<td>5.1±0.7 (8)</td>
<td>217.4±57.7 (8)*</td>
<td>45.5±17.4 (8)</td>
</tr>
<tr>
<td><em>S. triandra</em></td>
<td>9.1±2.0 (8)</td>
<td>404.5±74.0 (8)*</td>
<td>144.4±32.7 (5)</td>
</tr>
<tr>
<td><em>S. viminalis</em></td>
<td>13.1±3.8 (8)</td>
<td>503.8±127.3 (8)</td>
<td>232.1±165.3 (3)</td>
</tr>
<tr>
<td><em>P. nigra</em></td>
<td>3.8±0.7 (8)</td>
<td>100.0±30.6 (8)*</td>
<td>4.2±6.4 (8)</td>
</tr>
<tr>
<td><strong>DW roots (mg)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. alba</em></td>
<td>8.0±1.5 (8)</td>
<td>217.5±57.7 (8)</td>
<td>68.7±21.7 (8)</td>
</tr>
<tr>
<td><em>S. triandra</em></td>
<td>10.1±2.0 (8)</td>
<td>210.1±26.4 (8)</td>
<td>174.6±71.6 (5)</td>
</tr>
<tr>
<td><em>S. viminalis</em></td>
<td>10.2±2.0 (8)</td>
<td>215.1±45.6 (8)</td>
<td>186.2±142.9 (3)</td>
</tr>
<tr>
<td><em>P. nigra</em></td>
<td>3.8±0.7 (8)</td>
<td>63.1±19.0 (8)</td>
<td>25.7±5.8 (8)</td>
</tr>
<tr>
<td><strong>Rooting depth (cm)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. alba</em></td>
<td>17.5±1.7 (8)</td>
<td>33.2±2.6 (8)***</td>
<td>44.4±4.1 (8)</td>
</tr>
<tr>
<td><em>S. triandra</em></td>
<td>17.6±3.1 (8)</td>
<td>32.3±1.7 (8)*</td>
<td>48.4±0.4 (5)</td>
</tr>
<tr>
<td><em>S. viminalis</em></td>
<td>18.3±2.7 (8)</td>
<td>29.4±1.7 (8)*</td>
<td>41.3±7.7 (3)</td>
</tr>
<tr>
<td><em>P. nigra</em></td>
<td>8.8±0.9 (8)</td>
<td>13.9±1.3 (8)*</td>
<td>26.9±5.6 (8)</td>
</tr>
<tr>
<td><strong>Leaf area (cm²)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. alba</em></td>
<td>6.7±1.5 (8)</td>
<td>168.4±38.2 (8)***</td>
<td>40.6±11.8 (8)</td>
</tr>
<tr>
<td><em>S. triandra</em></td>
<td>8.7±1.9 (8)</td>
<td>251.5±36.7 (8)*</td>
<td>100.1±25.4 (5)</td>
</tr>
<tr>
<td><em>S. viminalis</em></td>
<td>11.9±4.0 (8)</td>
<td>257.4±52.2 (8)</td>
<td>108.0±78.2 (3)</td>
</tr>
<tr>
<td><em>P. nigra</em></td>
<td>4.4±1.1 (8)</td>
<td>104.0±28.2 (8)***</td>
<td>16.8±4.3 (8)</td>
</tr>
</tbody>
</table>

Note: Values in parentheses are numbers of replicates. Significant differences between the 3-week-old well-watered and drought groups are indicated by *, P < 0.05 and ***, P < 0.001; F test.

### Table 2. Internal ratios of different growth parameters in seedlings of *S. alba*, *S. triandra*, *S. viminalis*, and *P. nigra* under well-watered and dry conditions (mean ± SE).

<table>
<thead>
<tr>
<th>Ratio</th>
<th>Well-watered 0 weeks</th>
<th>Well-watered 3 weeks</th>
<th>Drought 3 weeks</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Shoot:root</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. alba</em></td>
<td>4.89±0.60 (8)</td>
<td>4.86±0.60 (8)</td>
<td>3.02±0.15 (8)</td>
</tr>
<tr>
<td><em>S. triandra</em></td>
<td>4.25±0.40 (8)</td>
<td>5.10±0.33 (8)*</td>
<td>2.96±0.48 (5)</td>
</tr>
<tr>
<td><em>S. viminalis</em></td>
<td>5.51±0.77 (8)</td>
<td>5.74±0.32 (8)*</td>
<td>3.37±0.40 (3)</td>
</tr>
<tr>
<td><em>P. nigra</em></td>
<td>6.33±0.51 (8)</td>
<td>7.58±0.44 (8)*</td>
<td>3.51±0.26 (8)</td>
</tr>
<tr>
<td><strong>RL:LA (m m⁻²)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. alba</em></td>
<td>0.24±0.03 (4)</td>
<td>0.13±0.00 (6)*</td>
<td>0.18±0.01 (8)</td>
</tr>
<tr>
<td><em>S. triandra</em></td>
<td>0.21±0.04 (5)</td>
<td>0.14±0.00 (6)*</td>
<td>0.18±0.01 (5)</td>
</tr>
<tr>
<td><em>S. viminalis</em></td>
<td>0.20±0.03 (6)</td>
<td>0.16±0.02 (6)</td>
<td>0.17±0.03 (3)</td>
</tr>
<tr>
<td><em>P. nigra</em></td>
<td>0.18±0.03 (7)</td>
<td>0.12±0.01 (8)*</td>
<td>0.27±0.05 (8)</td>
</tr>
<tr>
<td><strong>SLA (m² g⁻¹)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S. alba</em></td>
<td>0.21±0.02 (8)</td>
<td>0.32±0.02 (8)***</td>
<td>0.25±0.01 (8)</td>
</tr>
<tr>
<td><em>S. triandra</em></td>
<td>0.27±0.02 (8)</td>
<td>0.37±0.01 (8)</td>
<td>0.35±0.02 (5)</td>
</tr>
<tr>
<td><em>S. viminalis</em></td>
<td>0.25±0.03 (8)</td>
<td>0.35±0.02 (8)</td>
<td>0.30±0.02 (3)</td>
</tr>
<tr>
<td><em>P. nigra</em></td>
<td>0.21±0.02 (8)</td>
<td>0.29±0.01 (8)*</td>
<td>0.23±0.02 (8)</td>
</tr>
</tbody>
</table>

Note: Values in parentheses are numbers of replicates. Deviation in the number of replicates of root length was caused by malfunction of the root length scanner. RL:LA, root length to leaf area; SLA, specific leaf area. Significant differences between the 3-week-old well-watered and drought groups are indicated by *, P < 0.05 and ***, P < 0.001; F test.
in *P. nigra*, although this species did increase its rooting depth (Table 1).

Biomass ratios of plants were computed to compare growth responses to drought among the species (Table 2). All species, except *S. alba*, had a significantly lower shoot to root ratio when growing under dry conditions compared with well-watered conditions. The decrease in the specific leaf areas of *S. alba* and *P. nigra* after 3 weeks drought was much greater than that of *S. triandra* and *S. viminalis*. Root length to leaf area ratio after drought treatment showed that *P. nigra* had both the highest absolute value and the largest increment of this ratio compared to the *Salix* species.

**Transpiration rate and leaf conductance**

Transpiration rates of seedlings grown under well-watered conditions differed considerably between the species studied. The rates were highest in *S. viminalis*, followed by *S. triandra* and then by *S. alba* and *P. nigra*, which were significantly lower than *S. viminalis* (Table 3). The leaf conductance measurements showed similar results: *S. alba* and *P. nigra* had a rather constant and lower conductance during the day than *S. triandra* and *S. viminalis*. Leaf conductance of *S. triandra* and *S. viminalis* increased after the first measurement and decreased again after a few hours (Fig. 4). During the first few hours of light, leaf conductance of *S. triandra* and
S. viminalis was significantly higher than that of S. alba and P. nigra. After 1 week without watering, leaf conductance could not be detected in any of the plants, although the leaves still looked fresh.

**Discussion**

Several studies have shown that the early life stages of floodplain forest species are susceptible to the fluctuating hydrological conditions on river banks (Douglas 1995; Fenner et al. 1984; Sacchi and Price 1992; Segelquist et al. 1993; Shafroth et al. 1994). Rapidly declining water levels can cause severe drought at locations where germination occurs and this may be disastrous for the further development of seedlings on river banks. The rate of groundwater decline along the river often exceeds the rate of rooting-depth increment and probably causes the death of seedlings on river banks in unfavourable years (Mahoney and Rood 1991; Rood et al. 1995).

We compared the rate of water-level decline of the River Rhine in the Netherlands with the rate of increase of rooting depth under experimental conditions to see if drought occurs along the River Rhine and could affect the establishment of floodplain forest species. The rate of decline of the river water-level varied from 2.9 to 6.6 cm day$^{-1}$ during the four selected growing seasons (Fig. 1). Groundwater levels adjacent to the river closely follow the river water levels (Rood et al. 1995). Therefore, groundwater levels drop at a rate correlated with the rate of decline in the river. The rates of root-depth increment varied between 0.86 cm day$^{-1}$ for P. nigra and 1.28 cm day$^{-1}$ for S. alba. These figures suggest that riparian vegetation along the River Rhine does experience drought. The actual field situation is more complex: substrate type and heterogeneity, amount of precipitation, and vegetation present are important factors determining the success of seedlings under dry conditions.

Along the River Rhine, it has been observed that during dry years seedlings of P. nigra are abundant (I. Van Splunder, personal observation), while in years with larger discharges seedlings of S. viminalis and S. alba also occur (Van Splunder et al. 1995). This implies that in years with low water availability, P. nigra seedlings establish and survive better than Salix seedlings.

The flux of water in river banks can be divided into an input (precipitation, groundwater rise, and capillarity) and an output component (groundwater fall, evaporation of the soil, and transpiration by the vegetation). Drought resistance depends on the ability of a plant to regulate its water economy through drought avoidance and (or) tolerance mechanisms. Plants might avoid drought stress by limiting water loss and enhancing their capacity to take up water (Chapman and Augé 1994). These avoidance responses to drought were found in varying extent in the species investigated and were interpreted as morphological adaptations to drought stress.

During the experiment, transpiration rate and leaf conductance were high in S. viminalis and S. triandra under well-watered conditions. These water-loss characteristics were correlated with the mortality of these species when exposed to drought (62.5% of S. viminalis and 37.5% of S. triandra died). Since the number of replicates was relatively low, mortality cannot be used to explain the differences in drought resistance among the species studied. Generally, mortality owing to drought is correlated with the inability of plants to close their stomata (Dickmann et al. 1992). Salix alba and P. nigra had a transpiration rate approximately 40% lower than the other two species (Table 3) and they had a rather stable, low leaf conductance during the day (Fig. 4). All plants of S. alba and P. nigra survived drought. Given that water loss in plants is mainly regulated by stomatal aperture (Davies and Flore 1986; Harrison et al. 1989; Liu and Dickmann 1993), the low leaf conductance of P. nigra and S. alba during the day could be interpreted as a small water output component. Stomatal closure results in a slow transpiration stream and less water uptake by the roots (Granier and Loustan 1994; Hinckley et al. 1994). Consequently, a high transpiration rate reduces moisture availability near the roots (Huck and Hillel 1983). During the experiment, only the reduction of moisture content in the soil as a result of water level lowering and evaporation was measured. The actual moisture availability in pots of S. triandra and S. viminalis...
might be relatively lower than in pots of *S. alba* and *P. nigra* owing to their relatively high transpiration rate. Along the river, the situation is similar to the moisture conditions in the tubes: moisture availability and drought stress are caused by groundwater lowering, evaporation, and water uptake by plants.

The reduction of the water-loss component by means of morphological response was especially noticeable in *P. nigra* and *S. alba*, which reduced their shoot growth (both leaves and stem) significantly during drought. The smaller specific leaf areas (Table 2) of these species showed that the morphology of the leaves had changed in response to drought. Small specific leaf areas indicate that thicker leaves are produced with less transpiring area per leaf. The influence of drought on leaf morphology was studied by Abrams et al. (1990), who found that *Fraxinus pennsylvanica* Marsh. trees decreased leaf area and increased leaf thickness. Leaf area reduction and increased epicuticular wax content in leaves as a result of drought were found in *Alnus glutinosa* (Seiler 1985). Wax content was not measured in the present study, but it seems likely that a high wax content (thick, leathery *Populus* leaves) might be related to a small, but significant, amount of water loss (cuticular conductance), whereas a low wax content (in the thinner *Salix* leaves) is related to a larger amount of water loss.

Analysing the input of water into plants, we studied both root depth and total root length in relation to drought. Root length is known to correlate well with water-uptake area (Newman 1965). *Salix viminalis* and *S. triandra* responded to drought by increasing the proportion of roots in deeper soil layers (Fig. 3). Similarly, *P. nigra* roots were found in deeper soil layers after drought treatment, although root length in these deeper areas was only slightly increased. Mahoney and Rood (1991, 1992) and Reader et al. (1992) also found root depth increment to moister soil layers and (or) enlargement of water-uptake area as a response to drought treatment. Under well-watered conditions, *Salix* species showed a different root distribution than *P. nigra*. During our experiment, *Salix* roots slowly continued to grow deeper into the saturated soil, whereas *P. nigra* roots remained in the top layer. A diminished root growth of *P. nigra* under saturated conditions has already been described by Segelquist et al. (1993). Increased root depth of *P. nigra* in deeper soil layers after drought treatment might be triggered either by shortage of moisture, or by the removal of the inhibiting saturation. Immediately after the water level fell, most *P. nigra* roots were in the top soil. In contrast, roots of the *Salix* species were present at greater depths. Despite this relatively unfavourable root distribution at the start of the drought period, all *P. nigra* plants survived. Small leaf area of *P. nigra* at the start of the drought treatment could also account for the low water loss and high survival of these plants. *Salix triandra* and *S. viminalis* showed the highest transpiration rate and greatest mortality, although they considerably increased their root length at greater depths. From this, we conclude that root-length increment is a response to drought, but this strategy was not sufficient for *S. triandra* and *S. viminalis* in this experiment to survive drought. These two species were considered to be the most stressed during the given drought treatment.

*Populus nigra* had the greatest response to drought. This species showed the largest increase of water input to water loss ratio (root length to leaf area) after drought. It showed also the highest ratio compared with the other species, reflecting an efficient water economy. Because of this favourable ratio, we conclude that *P. nigra* adapted best to the decreased moisture availability.

The observed field distribution of Salicaceae species along the River Rhine reflects the differences among these species in drought resistance as demonstrated in our experiments. *Populus nigra* has been found on the river banks even in relatively dry years and adapted best to dry conditions during the experiment. *Salix triandra* and *S. viminalis* were least drought resistant and were not present along the River Rhine in dry years. The differences in drought resistance can be expected to result in a zonation of the species: *S. triandra* and *S. viminalis* cover the banks at relatively low elevations near the river, while *P. nigra* might be found up to higher elevations; *S. alba* covers intermediate sites.

**Acknowledgements**

We thank P. van de Sanden (AB-DLO) for use of the porometer and useful suggestions; N. Geilen for comments on the manuscript and for discussion; and the RIZA Department of Documentation and Presentation for preparing the figures.

**References**


Van Splunder et al. 1995


