Streamside trees: responses of male, female and hybrid cottonwoods to flooding

JULIE L. NIELSEN,1 STEWART B. ROOD,1,3 DAVID W. PEARCE,1 MATTHEW G. LETTS2 and HESTER JISKOOT2

1 Department of Biological Sciences, University of Lethbridge, Alberta, Canada T1K 3M4
2 Department of Geography, University of Lethbridge, Alberta, Canada T1K 3M4
3 Corresponding author (rood@uleth.ca)

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Summary  Cottonwoods, riparian poplars, are dioecious and prior studies have indicated that female poplars and willows can be more abundant than males in low-elevation zones, which are occasionally flooded. We investigated the response to flooding of clonal saplings of 12 male and 9 female narrowleaf cottonwoods (Populus angustifolia) grown for 15 weeks in a greenhouse, along with three females of a co-occurring native hybrid (Populus × jackii = Populus deltoides × Populus balsamifera). Three water-level treatments were provided, with substrate inundation as the flood treatment. In the non-flooded condition, the hybrids produced about four-fold more dry weight (DW) than the narrowleaf cottonwoods (P < 0.01). In both cottonwood taxa, flooding reduced stem height and DW, root and leaf area and weight, leaf chlorophyll and stomatal conductance (all P < 0.01). Inundation increased the foliar carbon-to-nitrogen ratio (+11%; P < 0.05) but did not significantly alter leaf water potential (mean ~1.5 MPa), or foliar δ13C, which was lower in P. angustifolia (~32.8‰) than P. × jackii (~31.5‰; P < 0.05). Water level influenced the root distribution as roots were sparse in the saturated substrate and abundant in the capillary fringe above. The male and female P. angustifolia genotypes grew similarly with the favorable water levels, but the males tended to be more inhibited by flooding. Sapling DW of males was reduced by 56% compared with a 44% reduction for females (P = 0.1), and there were similar lower reductions for leaf, stem and root DW in females. These results demonstrate the inundation response of floodplain trees and suggest relative flood tolerance as: P. angustifolia female > P. angustifolia male > P. × jackii female. This indicates that narrowleaf cottonwoods are relatively flood tolerant and suggests that females are more flood tolerant than males. We propose the concept of ‘strategic positioning’, whereby the seed-producing females could be better adapted to naturally flooded, low-elevation streamside zones where seedling recruitment generally occurs.

Keywords: dioecy, growth, inundation, Populus, riparian, sex differentiation, water relations.

Introduction

About 6% of flowering plant species are dioecious, with male and female reproductive structures on separate individuals (Renner and Ricklefs 1995). In contrast, ~30% of the individual riparian shrubs and trees of the North American semi-arid intermountain west are dioecious, including cottonwoods (riparian poplars; Populus spp.), willows (Salix spp.) and box elder (Acer negundo) (Freeman et al. 1980). Like some other dioecious plants, these riparian trees and shrubs may display ‘spatial segregation of the sexes’, with differing distributions of the males versus females (reviewed by Hultine et al. 2007, Hughes et al. 2010). Males of some species are more drought tolerant and consequently more abundant in drier zones (Dawson and Bliss 1989, Zhang et al. 2004, Xu et al. 2008a, 2008b), whereas females can be more abundant in lower elevation, wetter, resource-rich environments (Dawson and Ehleringer 1993, Dawson and Geber 1999, Hughes et al. 2000, Hultine et al. 2007). In the lower riparian zones, flooding is a common stress, but there has been limited investigation of possible sex differentiation in flood tolerance (Hultine et al. 2007), which could contribute to the spatial segregation. We thus undertook this study to compare the flood responses of male and female narrowleaf cottonwoods (Populus angustifolia), which commonly occur close to stream edges and may be more flood tolerant than other Populus species (Rood et al. 2003, 2010).

We have been studying a group of male and female narrowleaf cottonwoods within their natural floodplain grove (Willims et al. 2006, Letts et al. 2008), and for the present study we clonally propagated saplings from these parental trees, and grew the saplings in a controlled greenhouse environment. The investigation of juvenile saplings would avoid the possible influence of reproductive allocation, the physiological demand on females associated with seed production (Charlesworth and Morgan 1991). We also investigated two cottonwood taxa to provide a further comparison and predicted: (a) differentiation in growth and physiology between the cottonwood species and intersectional hybrids.
(Kalischuk et al. 2001, Rood et al. 2003, Pearce et al. 2006); (b) more modest ecophysiological differentiation between the male and female genotypes within a single cottonwood species (Hughes et al. 2000, Letts et al. 2008) and (c) greater flood tolerance of the narrowleaf cottonwoods versus the Jackii hybrids (Rood et al. 2010). There were three possible outcomes relative to the flood tolerance of male (♂) versus female (♀) narrowleaf cottonwoods. As the null hypothesis (H₀: ♂ = ♀), there could be a minimal difference and this might be consistent with the occurrence of both sexes in occasionally inundated floodplain zones where both would require reasonable flood tolerance. Alternatively, based on the reports of higher proportions of females in lower and wetter zones, our primary hypothesis was that females would be more flood tolerant than males (H₁: ♀ > ♂). The opposite hypothesis was that males could be more flood tolerant than females (H₂: ♂ > ♀) and this might follow from the observations that males are more drought tolerant and the prospect that males are more broadly water stress tolerant.

Methods

Our study design included two overlapping, paired comparisons: (i) male versus female narrowleaf cottonwoods (P. angustifolia James) and (ii) narrowleaf versus Jackii cottonwoods (Populus × jackii Sarg. = Populus balsamifera × Populus deltoides). The Jackii cottonwoods are natural intersectional hybrids that co-occur with the narrowleaf cottonwoods along some rivers in southwestern Alberta (Gom and Rood 1999, Willms et al. 2006). Populus angustifolia and P. balsamifera are related species of the section Tacamahaca, while the section Aigeiros P. deltoides generally occurs in warmer and drier downriver prairie regions (Kalischuk et al. 2001). With limited greenhouse space and anticipating subtle differences between males and females, we increased the numbers of genotypes of the narrowleaf sexes, rather than including a fourth category of male P. × jackii, or including more female P. × jackii genotypes. Numerous measurements of these plants were undertaken and we have previously compared photosynthesis and contrasted patterns of leaf development (Rood et al. 2010).

Plant materials and conditions

Similarly sized, apparently healthy and reproductively mature parental trees were selected within a riparian cottonwood grove at Pearce Corner (49°51'03"N, 113°15'18"W), along the Oldman River near Lethbridge, Alberta (Willms et al. 2006, Letts et al. 2008, Rood et al. 2010). Twelve male and nine female P. angustifolia trees, and three female Jackii cottonwoods, were sampled. Of these, four female and four male narrowleaf trees had been previously studied in relation to sap flux, water relations and foliar gas exchange in field conditions (Letts et al. 2008). To avoid sampling clonal trunks, parental trees were a minimum of 30 m apart or were of different sexes, and trees of the same sexes located within 70 m displayed distinctive bud flushing phenology (cf. Gom and Rood 1999). Branch cuttings were harvested from vegetative shoots in late April 2007, and clonal saplings were grown in 20 cm (diameter) × 14 cm pots with a 2:3 mixture of fine gravel:coarse sand, positioned in 1.2 m diameter × 30 cm deep pools (Figure 1). The study involved a randomized block design with six complete blocks, each consisting of a pool containing 18 pots with four saplings per pot, to include one sapling of each of the 24 genotypes in each of three water treatments. The study thus commenced with 432 saplings: 6 blocks × 3 treatments × 24 genotypes.

The plants were grown in the greenhouse at the University of Lethbridge (49°41'N, 112°52'W), with temperature generally maintained between 18 and 25 °C, although afternoon temperatures occasionally rose above 30°C. A 16-h photoperiod was maintained with supplemental illumination from 5:30 to 7:30 and 19:30 to 21:30 h, with Sylvania S50 250 W Lumalux bulbs that provided ~91 μmol s⁻¹ m⁻² at 1 m above the pool, as measured with an LI190 quantum sensor (LI-COR Biosciences, Lincoln, NE, USA).

During a 48-day establishment period, all pots were maintained in 3 cm of standing water with added fertilizer (50 ppm N; Peters Professional Peat-Lite-Special, 20-10-20 with micronutrients, TerraLink Horticulture, Abbotsford, Canada). Each week, the water and nutrient solution was changed and the pots and pools were rotated to control for environmental variation within the greenhouse. On Day 49, the water treatments commenced. The water depth in each pool was increased and the six pots in each treatment were positioned on combinations of bricks and ceramic tiles to provide water levels of 1 cm (Water 1), 7 cm (Water 2) or 11 cm (Flood) from the base of the 11-cm deep substrate (Figure 1). The fertilizer concentration was doubled at this time and the solutions continued to be renewed weekly when the pots and pools were rotated.

Growth measurements

The saplings were assessed weekly for survival and height. Saplings were harvested by pool, from 96 to 108 days after planting. At harvest, the potting substrate was poured out, each sapling was gently uprooted and the roots were washed to remove substrate. Leaves were cut off and stems were separated into the enlarged original cutting and the newly elongated stem section. Roots were excised separately from the upper 3 cm and lower 2 cm of the cuttings and major roots (>3 mm diameter) were counted. Measurements of the upper and lower root areas were determined using an LI3000 Portable Area Meter with an LI3050A Transparent Belt Conveyer (LI-COR Biosciences). This technique did not determine the full root areas, but provided measurements that would be comparable across the treatments.
The sapling organs were placed in paper bags, air-dried in the greenhouse for at least 8 weeks and weighed. Initial saplings were also oven-dried at 80 °C, but there was no further reduction in dry weight (DW) and consequently air drying was sufficient.

Physiological measurements

Stomatal conductance (gs) was measured from the abaxial leaf surfaces, with an LI-1600 Steady-State Porometer (LI-COR Biosciences) 3 days before the treatments (46–48 days after sticking, leaves positioned two nodes above the preformed leaves), and 6 days into the treatments (74–83 days after sticking, leaves positioned two nodes below a mark at the position of the uppermost expanded leaf made 1 week earlier). Measurements were taken between 12:30 and 17:30 h, and before each measurement the leaf was in full sunlight for a minimum of 5 min. After the gs measurement, the leaf was excised and the leaf water potential (Ψl) was determined with a Model 1000 Pressure Chamber (PMS Instruments, Albany, OR, USA) as described by Amlin and Rood (2003).

The relative abundance of leaf chlorophyll (Chl) was measured with a CCM-200 Chlorophyll Content Meter (Opti-Sciences, Hudson, NH, USA) 53, 69, 76, 81 and 87 days after sticking. At 53 days, a 'lower leaf', on the second node above the preformed leaves, was measured and marked. On subsequent days, all saplings from three pools were sampled with another measurement of the Day 53 lower leaf, as well as of the third leaf below the apex as a new 'upper leaf' that had developed during the experimental treatment.

Foliar C and N composition was determined for leaves which had developed during treatment, from the 15th node above the preformed leaves. As the Water 1 and Water 2 saplings appeared to grow similarly, foliar elemental analysis was only undertaken on leaves sampled from the Water 1 and Flood treatments. Leaves were cut and placed in paper envelopes in an oven at 80 °C for 24 h and placed in a desiccator. The dried leaves were cut to remove the mid-vein and petiole and the remaining leaf blades were frozen in liquid nitrogen, and finely ground with a mortar and pestle. Subsamples were analyzed for carbon and nitrogen content and carbon isotopic composition (δ13C) at the University of California, Davis, Stable Isotope Facility, with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd, Crewe, UK).

Statistical analysis

For each measurement, analysis of variance (ANOVA) was performed with the univariate General Linear Model analysis with Type III sum of squares, in SPSS 16.0 (SPSS Inc., Chicago, IL, USA). Initial ANOVAs investigated the effects of genotype (24 genotypes), water treatment (3 treatments) and pool (or 'replicate', 6 pools). The pool effect was not significant for total sapling DW and we subsequently calculated the mean values for each dependent variable from the replicates across the six pools. These mean values for each genotype were then analyzed with two-way ANOVAs to investigate the effects of genotype groups such as P. angustifolia male (n = 12), P. angustifolia female (9) and P. × jackii female (3) and water treatment (three conditions). The ANOVAs were followed by Tukey's honestly significant difference (HSD) test and for all statistical analyses we noted statistically significant effects (P < 0.05, P < 0.01 and P < 0.001) and statistical trends (P ≤ 0.1).

The ANOVAs for foliar elemental composition (N and C) included only two treatment conditions of Water 1 and Flood, and for some measurements, root or leaf position (upper versus lower) were also included as fixed factors. To
specifically compare the growth responses of the male versus female narrowleaf cottonwoods. ANCOVAs were performed with the sapling or component DW for each genotype in the Flood versus Water 2 treatment. Similar results were observed in a comparison with Water 1 (not shown). These ANCOVAs thus compared relative growth responses, with sex as the fixed factor, Water 2 DW as the covariate and Flood DW as the dependent variable.

Results

Survival

Most of the cottonwood genotypes were readily propagated from the branch cuttings and 80% survived to the harvest (Table 1). A few cuttings initially failed to flush (leaf bud expansion), but more displayed some flushing and subsequently died during the early establishment phase, when the initial adventitious roots were being formed and before water-level treatments commenced. There was very little further mortality during the water-level treatments and no significant difference in final survival across the water treatments (Table 2). There were significant differences across the genotypic groups (Tables 1 and 2), with greater survival of female hybrid P. × jackii (91%) than female P. angustifolia (68%). Survival of male P. angustifolia was intermediate (81%).

Growth

Most of the growth parameters displayed a common pattern among the groups, with the hybrid P. × jackii female saplings growing considerably larger than the male or female P. angustifolia saplings (Figure 2). This produced highly significant (P > 0.01) effects of genotypic group in the ANOVAs for all DW components (Table 2). The increased hybrid growth was most prominent in the more favorable treatments, Water 1 and Water 2, as the hybrid saplings were taller and had substantially greater root, stem and leaf DW (Table 2, Figure 2). With these more favorable water treatments, the total sapling DW of the hybrids averaged ~3.9-fold more than that of the P. angustifolia saplings. In the more favorable conditions of Water 1 and Water 2, the male and female P. angustifolia saplings exhibited similar root, stem, leaf and, subsequently, whole sapling DW (Figure 2).

All three genotype groups (male and female P. angustifolia, and female P. × jackii) displayed reduced root, stem and leaf growth, with the Flood treatment (Figure 2). This produced highly significant (P < 0.01) ANOVA Treatment effects for each of the plant component DW (Table 2). The growth reductions were not uniform across the organs and roots were especially reduced, increasing the shoot:root ratio. In addition to the significant group (G) and Treatment (T) effects, the G × T interaction was statistically significant (P < 0.05) for stem, leaf, shoot and sapling DW, and a statistical trend (P < 0.1) was detected for the G × T interaction for root DW (Table 2). The interactions indicated that the three genotypic groups were not uniformly depressed by the Flood treatment. The proportional reduction was greatest for the P. × jackii saplings (Figure 2) and this is consistent with the greater flood response that we previously reported, based on leaf growth patterns across these same genotypes (Rood et al. 2010). Within P. angustifolia, proportional growth reduction was apparently greater for the male than female clones for the leaf, stem and root components (Figure 2). Consequently, proportional reductions in overall sapling DW were 56 and 44% for the males and females, respectively.

The ANOVA results of Table 2 reflect the combined comparisons across the P. × jackii and the male versus female P. angustifolia. Restricting our analysis to P. angustifolia saplings, we also tested between-sex differences in flood-related relative growth reduction (Figure 3). The relationship between total sapling DW in the Flood treatment versus sapling DW in the Water 2 treatment for both male and female P. angustifolia displayed linear patterns with strong correspondences (R²). The regression line for the female P. angustifolia was apparently offset upwards, suggesting that the females displayed less growth inhibition with the Flood treatment than the males. An initial factorial ANCOVA indicated that the interaction between the covariate (Water 2 DW) and Group was not significant and the ANCOVA was subsequently rerun without the interaction term (adjusted R² = 0.83). This confirmed that sapling DW in the Flood treatment was strongly associated with sapling DW in Water 2 (F(1,18) = 91.1, P < 0.001) and suggested that there may be differences in relative performance between the sexes (F(1,18) = 2.90, P = 0.106). Similar analyses for the constituent organ DW also demonstrated upward offsets of the regressions and the associated ANCOVA also suggested increased flood tolerance of the females with respect to roots (F(1,18) = 3.31; P = 0.086), and stems and cuttings (F(1,18) = 2.72; P = 0.117).

Table 1. Characteristics of male (M) and female (F) cottonwood saplings grown in greenhouse conditions with different water levels.

<table>
<thead>
<tr>
<th>Group</th>
<th>Treatment</th>
<th>Survival* (%)</th>
<th>Height* (cm)</th>
<th>Relative chlorophyll abundance*</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. angustifolia</td>
<td>Water 1</td>
<td>84.4a</td>
<td>60.4b</td>
<td>38.1ab</td>
</tr>
<tr>
<td></td>
<td>Water 2</td>
<td>86.9a</td>
<td>58.0b</td>
<td>28.9b</td>
</tr>
<tr>
<td></td>
<td>Flood</td>
<td>71.7a</td>
<td>29.7c</td>
<td>16.9c</td>
</tr>
<tr>
<td>P. angustifolia</td>
<td>Water 1</td>
<td>65.2b</td>
<td>62.7b</td>
<td>36.3ab</td>
</tr>
<tr>
<td></td>
<td>Water 2</td>
<td>66.7b</td>
<td>57.2b</td>
<td>30.9ab</td>
</tr>
<tr>
<td></td>
<td>Flood</td>
<td>72.2ab</td>
<td>37.4c</td>
<td>18.2c</td>
</tr>
<tr>
<td>P. × jackii</td>
<td>Water 1</td>
<td>94.4a</td>
<td>110.1a</td>
<td>41.8a</td>
</tr>
<tr>
<td></td>
<td>Water 2</td>
<td>88.9a</td>
<td>108.2a</td>
<td>36.9a</td>
</tr>
<tr>
<td></td>
<td>Flood</td>
<td>88.9a</td>
<td>62.8b</td>
<td>34.1a</td>
</tr>
</tbody>
</table>

Values in columns followed by the same letter do not differ significantly at P = 0.05.

*Survival and height at harvest, chlorophyll in upper leaves on Day 87.
Although the results demonstrated the greatest differences between the Flood treatment and either Water 1 or Water 2, there were also some differences between the two more favorable water treatments. Growth of each of the three genotype groups was slightly greater in Water 1 than in Water 2 and root distribution was particularly influenced (Figure 4, Table 2). With the higher water level of Water 2, there was a reduction in the number and area of roots emerging from the lowest 2 cm of the branch cuttings (Figure 4). The Flood treatment produced a further change in root distribution as few roots were present at harvest on the lowest segment of the cuttings and some of the upper roots were near the top of the substrate or even above. These observations indicate that cottonwood roots do not grow well in a saturated substrate, but are instead abundant in the moist capillary fringe above the water table (Figure 1).

**Physiology**

Stomatal conductance was significantly reduced in the Flood treatment, especially in the *P. angustifolia* saplings (Figure 5, Table 2). The midday leaf water potentials were about −1.5 MPa (Figure 6) and these did not differ across the genotype groups or with the Flood treatment (Table 2). There was increasing leaf chlorosis in lower and even in upper leaves with the Flood treatment (Tables 1 and 2). Foliar carbon-to-nitrogen ratios were lower in *P. × jackii* than in *P. angustifolia* and were increased with the Flood treatment of all three cottonwood groups, but apparently less so for the female *P. angustifolia* (Figure 6). Foliar δ\(^{13}\)C composition differed between *P. × jackii* and *P. angustifolia*, but this ratio was not significantly altered by the Flood treatment (Figure 6, Table 2) and there was no apparent difference between the *P. angustifolia* males and females.

**Discussion and conclusions**

The reductions in stomatal conductance and shoot growth of the flooded cottonwood saplings are consistent with prior reports of the responses of cottonwoods and other poplars to flooding (Liu and Dickmann 1993, Cao and Conner 1999, Amlin and Rood 2001, Rood et al. 2010). The observed redistribution of root growth is more novel and is instructive relative to the water source for native riparian cottonwoods. With our different water-level treatments,
Figure 2. Constituent and total (sapling) DW for *P. angustifolia* males (M) and females (F), and *P. × jackii* females (mean ± SE; *n* = 12, 9, 3, respectively) grown in a greenhouse with three water-level treatments. The % change from Water 2 to Flood is shown.

Figure 3. Total sapling DW (mean ± SE, both axes) for 21 genotypes of female (closed circles, solid line) and male (open squares, dashed line) *P. angustifolia* grown in a greenhouse with pots inundated (Flood) versus the Water 2 treatment. Each plotted point represents a particular genotype with values based on up to six individual saplings grown in each of the two water treatments. The best-fit linear regressions are plotted and comparative analysis of covariance (ANCOVA) is described in the Results.
sapling roots were sparse in the saturated zone, which was probably anaerobic. The roots were favored in the moist capillary fringe that was above the water table and would have had greater oxygen exchange. While cottonwoods are phreatophytic, the observed root distribution indicates that the moisture source is not the saturated water table but is instead the capillary fringe. In a natural riparian zone, the water table would rise and fall along with the adjacent stream (Rood et al. 1995), and the capillary fringe would also rise and fall. From the sapling observations, we would predict that roots within the natural floodplain zone would be most extensive in the typical elevation of the capillary fringe. We would further anticipate that during a flood interval, this primary root zone would be inundated and this would inhibit transpirational water flux and plant growth as observed in this study and with prior investigations (Liu and Dickmann 1993, Amlin and Rood 2001). While riparian cottonwoods would benefit from the moisture recharge of flood events, we predict that growth would be depressed during the actual inundation. Thus, riparian cottonwoods are flood tolerant but not truly hydrophytic (Amlin and Rood 2001).

Accompanying the diminished root growth and reduced transpiration, there was also an apparent reduction in nitrogen content as evidenced by the increased foliar C:N ratios, and this would also be consistent with the observed leaf chlorosis. The altered C:N ratio could result from alterations to carbon and/or nitrogen patterns and with poplar root anoxia, N uptake and metabolism are altered (Kreuzwieser et al. 2009). This could provide another challenge in floodplain zones, which are typically N limited (Walker and Chapin 1986). It had been expected that stomatal closure would also have altered the foliar $^{13}$C ratio but this was not observed, although there were differences between the two cottonwood taxa, supporting the differences in water use efficiency in these trees (Rood et al. 2010).

As anticipated, there was differentiation in the growth of the narrowleaf versus Jackii cottonwoods (Figure 2). The natural intersectional hybrid, $P. \times$ jackii, grew much more rapidly than the $P. \text{angustifolia}$ genotypes, with the greatest difference in the favorable conditions of Water 1 and Water 2. Without observation of both parents, and particularly $P. \text{deltoides}$, which is in the section Aigeiros rather than the section Tacamahaca that contains $P. \text{balsamifera}$ and the closely related $P. \text{angustifolia}$, we are unable to determine whether the more vigorous growth of the hybrid is due to dominance for vigorous growth from $P. \text{deltoides}$, or if it reflects hybrid vigor. Heterosis or hybrid vigor is common in artificial intersectional poplar hybrids but may be less common for native intersectional hybrids (Campbell et al. 1993, Lojewski et al. 2009).

The second genotypic comparison was between female and male $P. \text{angustifolia}$. From prior investigations, we
expected differences in growth and physiology to be slight (Hughes et al. 2000, Letts et al. 2008). Consistent with this expectation, the male and female groups performed very similarly in the favorable Water 1 and Water 2 conditions. There were apparent differences between the males and females in their responses to the Flood treatment and this provided an upward shift for females in the relationship between leaf, root, stem and cutting, and sapling DW in the Flood versus Water 2 (or Water 1) conditions (Figure 3). However, there was substantial variation across the particular genotypes within the male and female groups and statistical analyses revealed trends \( P \leq 0.1 \) rather than major differences. This apparent differentiation would be consistent with the differentiation in leaf growth patterns of these saplings (Rood et al. 2010) and is consistent with our initial Hypothesis 1 \( (H_1: \varphi > \sigma') \), whereby female cottonwoods could display increased flood tolerance. This conclusion is strengthened by consideration of prior reports, including increased occurrence of female cottonwoods in low elevation, streamside zones (Gom and Rood 1999, Hughes et al. 2000). The favored occurrence of females closer to stream channels or in other wetter sites is also apparent in some willows (Dawson and Bliss 1989, Ueno and Seiwa 2003) and it has also been observed that in wetter environments, female poplars and willows can grow more vigorously than males (Winfield and Hughes 2002, Tozawa et al. 2009, Hughes et al. 2010). A similar pattern is also observed in another riparian tree, A. negundo (box elder), as females are more prevalent in low-elevation streamside zones (Freeman et al. 1976, Ward et al. 2002) and also grow better than males with wetter, more nutrient-rich conditions (Dawson and Ehringer 1993). However, the differential growth of males versus females relative to elevational streamside position and the associated physiological differentiation may be subtle and even absent in some situations (Kaul and Kaul 1984, Ueno et al. 2007, Letts et al. 2008). There are also other ecological factors, such as differential herbivory, that can also influence the spatial distribution of the sexes (Boecklen et al. 1990).

While female shrubs and trees are apparently favored in the wetter, low-elevation riparian zones, the opposite differentiation is also displayed, with males sometimes prevailing in higher elevation and drier locations (Dawson and Bliss 1989, Rowland and Johnson 2001). Consistent with that spatial distribution, females are apparently more vulnerable to drought stress (Ueno and Seiwa 2003) and this is probably reflected in the loss of female cottonwoods in riparian zones along dammed rivers in regions with substantial water withdrawal for irrigation and other uses (Braatne et al. 2007). There is thus probably a trade-off between adaptations favoring drought tolerance, which is more characteristic of males, versus flood tolerance, which is more typical of females of the riparian woody plants, cottonwoods, willows and box elder (Hultine et al. 2007).
The differences in drought versus flood tolerance would contribute to the spatial segregation of the sexes that is apparent in some riparian environments (reviewed in Hultine et al. 2007, Hughes et al. 2010). As an evolutionary basis, some researchers have emphasized the physiological cost of reproductive allocation, or other aspects related to the adaptation of male versus female trees (Hultine et al. 2007). We propose an alternative explanation for differentiation between the sexes, and this would relate to reproduction and the prospect for seedling recruitment success (Figure 7).

Cottonwoods are prolific seed producers, but the seeds have a short period of viability and have narrow seedling recruitment requirements (Amlin and Rood 2001, Karrenberg et al. 2002). The tiny seeds are dispersed by wind and also float on water. For seedling success, the seeds are deposited along stream bank zones that are moistened by the receding stream level. The positioning of the seed-producing female trees in low-elevation zones close to the barren stream banks would be advantageous as this would result in the abundant dispersal of seeds into the recruitment bands. For the females to survive in these naturally flooded, low-elevation zones, a reasonable degree of flood tolerance would be beneficial. Following from the collective conclusion that female cottonwoods are probably more flood tolerant than males, we thus propose the concept of ‘strategic positioning’, whereby females are adapted to the naturally flood-prone, low-elevation riparian zones near the barren, paraluvial surfaces where seedling recruitment is most successful. We propose that increased flood tolerance of female cottonwoods, willows and box elder would be strategi
c for reproduction and would thus provide a population benefit rather than an advantage to the particular individual.

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