Elevated CO_2 does not offset greater water stress predicted under climate change for native and exotic riparian plants

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Summary

- In semiarid western North American riparian ecosystems, increased drought and lower streamflows under climate change may reduce plant growth and recruitment, and favor drought-tolerant exotic species over mesic native species. We tested whether elevated atmospheric CO_2 might ameliorate these effects by improving plant water-use efficiency.
- We examined the effects of CO_2 and water availability on seedlings of two native (*Populus deltoides* spp. *monilifera*, *Salix exigua*) and three exotic (*Elaeagnus angustifolia*, *Tamarix* spp., *Ulmus pumila*) western North American riparian species in a CO_2-controlled glasshouse, using 1-m-deep pots with different water-table decline rates.
- Low water availability reduced seedling biomass by 70–97%, and hindered the native species more than the exotics. Elevated CO_2 increased biomass by 15%, with similar effects on natives and exotics. Elevated CO_2 increased intrinsic water-use efficiency ($\Delta^{13}C_{leaf}$), but did not increase biomass more in drier treatments than wetter treatments.
- The moderate positive effects of elevated CO_2 on riparian seedlings are unlikely to counteract the large negative effects of increased aridity projected under climate change. Our results suggest that increased aridity will reduce riparian seedling growth despite elevated CO_2, and will reduce growth more for native *Salix* and *Populus* than for drought-tolerant exotic species.

Introduction

Riparian ecosystems in arid and semiarid western North America may be dramatically altered by increased water stress under climate change (Rood *et al.*, 2008; Stromberg *et al.*, 2010; Perry *et al.*, 2012). Most climate models of the southwestern USA predict increased aridity over the next century as a result of greater evapotranspiration and less precipitation (Seager & Vecchi, 2010). In addition, warmer temperatures are reducing snowpacks and increasing winter runoff, and thus reducing late spring and summer streamflows in western North America (Christensen *et al.*, 2004; Stewart *et al.*, 2005; Maurer, 2007; Miller & Piechota, 2008). These changes are likely to increase riparian plant water stress, which can hinder tree seedling recruitment (Mahoney & Rood, 1998; Shafroth *et al.*, 1998; Horton & Clark, 2001; Amlin & Rood, 2002) and alter plant community composition (Rood *et al.*, 2003; Auble *et al.*, 2005; Lite & Stromberg, 2005; Strom *et al.*, 2011). In particular, greater water stress may reduce the abundance of dominant, mesic, native *Populus* (cottonwood) and *Salix* (willow) species (Rood *et al.*, 2003), and favor more drought-tolerant, exotic species, including *Tamarix ramosissima* Ledeb., *T. chinensis* Lour., and *T. ramosissima* × *chinensis* hybrids (tamarisk or saltcedar; Stromberg *et al.*, 2010) and *Elaeagnus angustifolia* L. (Russian olive; Reynolds & Cooper, 2010).

Increased atmospheric CO_2 concentrations (hereafter [CO_2]), however, may offset the effects of increased aridity on riparian plants. Atmospheric [CO_2] rose from 280 to 368 ppm during the 20th century and may rise to > 700 ppm by the end of the 21st century (IPCC, 2007). Elevated [CO_2] reduces stomatal conductance and increases water-use efficiency (WUE) in many plants, particularly under dry conditions, thus reducing their overall demand for water (Wand *et al.*, 1999; Ainsworth & Long, 2005). In semiarid grasslands, elevated [CO_2] can reduce transpiration enough to completely counteract the negative effects of moderate warming on soil water availability, and increases plant growth most strongly in dry years (Morgan *et al.*, 2004, 2011). However, potential effects of elevated [CO_2] on plant growth and WUE have not been considered in most predictions of climate change effects on semiarid riparian ecosystems (e.g. Rood *et al.*, 2008; Stromberg *et al.*, 2010; Yarnell *et al.*, 2010), and research is lacking on riparian plant responses to elevated [CO_2].

Predicting how elevated [CO_2] might affect riparian plants is difficult, because responses to elevated [CO_2] vary considerably among species (Leakey *et al.*, 2009). For *Populus deltoides* Bartram

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ex. Marsh spp. *deltoides* (eastern cottonwood), a dominant eastern North American riparian tree, elevated [CO_2] (720–1000 ppm) decreased stomatal conductance by 25–50% and increased instantaneous WUE by 20–30%, net photosynthesis by 20–60%, and growth by 25–80% (Will & Teskey, 1997; McDonald *et al.*, 2002; Barron-Gafford *et al.*, 2005; Murthy *et al.*, 2005; Lewis *et al.*, 2010). If western North American riparian species respond similarly, then elevated [CO_2] may mitigate the negative effects of lower water availability on riparian plants under climate change. Further, if riparian species vary in their responses to elevated [CO_2], then elevated [CO_2] could favor some species over others, potentially altering community composition.

Riparian species responses to elevated [CO_2] could vary as a result of interspecific differences in direct effects on photosynthesis, effects on stomatal conductance, or indirect effects of stomatal conductance on growth. There are no previous data to suggest that particular riparian plant species are likely to be more responsive than others to direct effects of elevated [CO_2]. Species with greater drought tolerance, however, may benefit less from indirect effects of reduced stomatal conductance on growth, because they are less water-stressed than other species when water is moderately limited. For example, *Tamarix* spp. are better able to access shallow soil water, maintain turgor through osmotic adjustments, and avoid xylem cavitation than *Populus* and *Salix* spp. (Smith *et al.*, 1998; Rood *et al.*, 2003), and may benefit less from reduced stomatal conductance.

Effects of increased aridity and elevated [CO_2] on seedlings may be particularly important for riparian tree populations. Seedling mortality strongly limits native riparian tree abundance (Lytle & Merritt, 2004). Riparian *Populus* and *Salix* seedlings establish on bare, moist surfaces created by floods and exposed by flood recession, growing roots rapidly downward to maintain contact with soil moisture from the declining water table (Mahoney & Rood, 1998; Shafroth *et al.*, 1998). Most seedlings die in their first 12 months from water stress or flood and ice scour (Stromberg *et al.*, 1991; Cooper *et al.*, 1999; Johnson, 2000), and successful establishment occurs only once every 5 to >60 yr depending on streamflow and geomorphology (Scott *et al.*, 1996). Increased aridity as a result of climate change may further reduce the probability of establishment (Perry *et al.*, 2012). Understanding how elevated [CO_2] interacts with increased aridity to influence seedling water stress and growth is critical for predicting how climate change will alter riparian plant communities.

We conducted a glasshouse experiment to test the effects of elevated [CO_2] and water availability on seedling growth, physiology, and drought tolerance of five western North American woody riparian species, including the two most common native species (*Salix exigua* Nutt. (sandbar willow) and *Populus deltoides* Bartram ex. Marsh spp. *monilifera* (Aiton) Eckenwalder (plains cottonwood)), the two most common exotic species (*Tamarix* spp. and *Elaeagnus angustifolia*), and an increasingly common exotic species (*Ulmus pumila* L. (Siberian elm)) (Friedman *et al.*, 2005; Zalapa *et al.*, 2010). Our objectives were to evaluate the potential for elevated [CO_2] to offset increases in water stress in riparian woody seedlings; and favor establishment by some species more than others. We predicted that elevated [CO_2] would increase seedling WUE, and therefore increase growth more for the relatively drought-intolerant, native species than for the exotic species, and more in treatments with lower water availability.

Materials and Methods

We grew seedlings of the five study species (hereafter, *Salix*, *Populus*, *Tamarix*, *Elaeagnus*, and *Ulmus*) in a glasshouse under ambient (440 ± 48 (SD) ppmv) and elevated (752 ± 85 ppmv) [CO_2] and with four water-table decline rates (0.5, 1.5, 3.0, and 4.0 cm d^{-1}). Each of the 40 treatment combinations (five species × two [CO_2] treatments × four water treatments) was replicated eight times.

The experiment was arranged in a blocked, split-plot design, with water treatments in 'whole pots', species in 'subpots', and [CO_2] treatments in separate glasshouse bays. One bay received CO_2 inputs sufficient to maintain the elevated [CO_2] treatment during 16 h, lighted days. Because it was not possible to apply [CO_2] treatments at the whole-pot or subpot level, the experiment lacked true replication of the [CO_2] treatment. To minimize the likelihood of spurious effects of location, we used wheeled platforms to rotate the [CO_2] treatments between the two bays weekly, except during an 11 d period of equipment failure starting in the 10th week. Within each bay, the pots were divided into eight blocks, each consisting of four whole pots (one per water treatment). When rotating the [CO_2] treatments, we also rotated the block locations within each bay, and the whole-pot locations within each block.

Whole pots were 30-cm-diameter × 100-cm-deep PVC pipes, capped at the bottom, equipped with a flexible drainpipe near the base, and filled with water. Whole pots served as water reservoirs for five sand-filled subpots (one per species) arranged inside each whole pot (Supporting Information, Fig. S1). Subpots were 8-cm-diameter × 105-cm-deep (5275 cm^3) PVC pipes, capped at the bottom, with four, 1-cm-diameter holes drilled 3 cm above the base, covered with fine screen. Similar pot dimensions have been used in many studies of riparian tree seedlings (Mahoney & Rood, 1991; Rood *et al.*, 2000; Horton & Clark, 2001), because riparian tree seedling roots grow primarily downward to follow declining water tables (Mahoney & Rood, 1998). Subpots were filled with 5 cm of medium/fine gravel (predominantly 5–8 mm particles) at the bottom, then 92 cm of medium/coarse alluvial sand (predominantly 0.4–2.0 mm particles) mined from the Cache la Poudre floodplain (LaFarge North America, Fort Collins, CO, USA), then 5 cm of medium/coarse alluvial sand mixed with Scotts osmocote plus fertilizer (Scotts Professional, Geldermalsen, the Netherlands), and finally 1 cm of a finer medium/coarse sand (predominantly 0.2–1.0 mm particles). The fertilizer was a 3- to 4-month-duration, slow-release fertilizer, with 15% nitrogen (N), 9% phosphorus, 12% potassium, 1.9% calcium, 1.4% magnesium, 4% sulfur, and trace elements. It was applied at a rate of 4 mg N kg^{-1} to mimic a 10 mg N kg^{-1} yr^{-1} mineralization rate, based on N mineralization on sandbars with establishing riparian trees (6.5–32.9 mg kg^{-1} yr^{-1}) (Adair *et al.*, 2004).

Salix and *Populus* seeds were collected in Fort Collins, and *Tamarix* seeds were collected in Loveland, CO. Most North

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American *Tamarix* are *Tamarix ramosissima* × *T. chinensis* hybrids (Gaskin & Kazmer, 2009), which are morphologically indistinguishable from the parent species, so the species identity of the *Tamarix* is uncertain. *Elaeagnus* seeds, collected in Montana, were purchased from F. W. Schumacher Co., Inc. (Sandwich, MA, USA). *Ulmus* seeds, collected in North Dakota, were purchased from Lawyer Nursery (Plains, MT, USA). Because *Elaeagnus* seeds are dormant and germinate more slowly than the other species, *Elaeagnus* seeds were stored in moist sand at 4°C for 80 d, and then planted in flats filled with moist sand 28 d before the start of the experiment. One week before the start of the experiment, three *Elaeagnus* seedlings, just emerging from the seed coat, were transplanted into one subpot in each whole pot. All other species were sown into subpots at the start of the experiment. *Ulmus* seeds were covered with a 0.25 cm layer of sand after sowing. Seedlings were thinned to the largest three seedlings per subpot 1 wk after sowing, and to one per subpot (the mid-sized seedling) 3 wk after sowing.

For the first week after sowing, water levels in the whole pots were maintained daily at 5 cm below the subpot soil surface. After 1 wk, water levels in the whole pots were lowered by 0.5, 1.5, 3.0, or 4.0 cm daily by lowering the position of the drain-pipe. We used declining water tables for the water treatments because *Salix*, *Populus* and *Tamarix* germination and establishment commonly occur during flood recession on riparian floodplains (Fenner *et al.*, 1985; Mahoney & Rood, 1998; Shafroth *et al.*, 1998). River stage decline rates of 0.5–4.0 cm d^{-1} are realistic during flood recession (Mahoney & Rood, 1991; Shafroth *et al.*, 1998), and *Salix*, *Populus*, and *Tamarix* seedling survival is often poor with water-table decline rates > 4.0 cm d^{-1} (Mahoney & Rood, 1991; Segelquist *et al.*, 1993; Horton & Clark, 2001; Amlin & Rood, 2002; Stella & Battles, 2010). Water-table declines continued throughout the experiment for the 0.5 cm d^{-1} treatment and continued down to a 98 cm depth for the 1.5, 3.0 and 4.0 cm d^{-1} treatments (reached at 69, 38 and 31 d, respectively).

Soil moisture was determined as a function of height above the water table in two unoccupied subpots with the water table maintained at 64 cm below the soil surface. After 1 wk, soil was collected from each subpot in 64, 1-cm-deep increments down to the water table. The samples were weighed, dried at 105°C, and reweighed to determine soil moisture. Soil moisture in each water treatment was estimated by calculating the daily mean soil moisture for the entire soil column above the water table, accounting for the changing position of the water table over time. Mean soil moisture over the course of the experiment was 12.2, 7.7, 6.2, and 5.8% in the 0.5, 1.5, 3.0, and 4.0 cm d^{-1} treatments, respectively. Soil moisture at field capacity (−0.033 MPa) and at the wilting point (−1.5 MPa) was determined for two samples by the Colorado State University Soil Testing Laboratory, Fort Collins, to assess approximate full and depleted soil water conditions.

The glasshouse bays were maintained at a temperature (± SD) of 27 ± 3°C during the day and 18 ± 2°C at night, with a 16 h photoperiod, to approximate the June to August climate in Fort Collins (Western Regional Climate Summaries; http://www.wrcc.dri.edu). Relative humidity was 28 ± 6% during the day and 52 ± 8% at night. Each bay was lit by 12 high-pressure sodium lamps. Midday photosynthetic photon flux density at the soil surface before sowing, averaged across subpots, was 517 ± 60 μmol m^{-2} s^{-1}.

The experiment was maintained for 12 wk, similar to the duration of a typical first growing season for *Populus*, *Salix* and *Tamarix* in Colorado (Cooper *et al.*, 1999). Seedling survival and height were measured weekly. In the 10th week, the percentage of each plant's leaf surface area composed of necrotic tissue was estimated by counting the number of leaves within different classes (0, 1–5, 5–25, 25–50, 50–75, and 75–100% necrotic tissue) and averaging the percent midpoints of all leaves. Above-ground and below-ground biomass was harvested in the 12th week, dried at 60°C, and weighed. During the harvest, predawn and midday stem xylem water potentials (hereafter Ψ_{pd} and Ψ_{md}) were measured for whole plants (above ground) using a Scholander pressure chamber (Model 1505D, PMS Instruments, Albany, OR, USA). Ψ_{pd} was measured between 02:30 and 05:00 h for four randomly selected blocks, and Ψ_{md} was measured between 11:00 and 14:00 h for the remaining four blocks. Roots were harvested by gently emptying the subpot into a sieve and rinsing away the sand. Harvested roots were straightened over a meter stick to estimate maximum root length, but rooting depths within the subpots were not measured. Small leaf sizes, especially in the faster water-table decline treatments, prevented measurements of photosynthesis, stomatal conductance, and leaf (rather than stem) water potentials.

Leaf tissue was analyzed for $\delta^{13}C$ to evaluate intrinsic WUE (C assimilation per unit stomatal conductance, iWUE; Farquhar *et al.*, 1988) and for C and N concentrations (hereafter [C] and [N]) to evaluate N limitation. Dried leaves were separated from stems and ground with a Wiley® mill (Thomas Scientific, Swedesboro, NJ, USA) equipped with a 1 mm screen, or cut with fine scissors for very small samples. Necrotic portions of *Populus* and *Salix* leaves were removed before grinding. For each plant, a 3–5 mg subsample was weighed to the nearest microgram, and analyzed for [C], [N], and $\delta^{13}C$ using a Carlo Erba NA 1500 elemental analyzer (Milano, Italy) and a VG Isochrom continuous-flow isotope ratio mass spectrometer (Isoprime Inc., Manchester, UK) at the Colorado State University Isotope Laboratory (observed precision for $\delta^{13}C = 0.2‰$).

An estimate of atmospheric $\delta^{13}C$ in the glasshouse was required to calculate $\Delta^{13}C_{leaf}$ from $\delta^{13}C_{leaf}$. Because the CO_2 source used to create the elevated [CO_2] treatment was depleted of ^{13}C ($\delta^{13}C \approx -39.9‰$), we calculated atmospheric $\delta^{13}C$ in the elevated [CO_2] treatment as

$$\delta^{13}C_{gh(elev)} = \frac{([CO_2]_{amb} \times \delta^{13}C_{gh(amb)}) + (([CO_2]_{elev} - [CO_2]_{amb}) \times \delta^{13}C_{CO2})}{[CO_2]_{elev}}$$

where $[CO_2]_{amb}$ is the [CO_2] in the ambient treatment (440 ppmv), $[CO_2]_{elev}$ is the [CO_2] in the elevated treatment (752 ppmv), $\delta^{13}C_{CO2}$ is the $\delta^{13}C$ of the CO_2 source for the elevated [CO_2] treatment (−39.9‰), and $\delta^{13}C_{gh(amb)}$ is the ambient

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atmospheric $\delta^{13}C$ in the glasshouse. We assumed that $\delta^{13}C_{gh(amb)}$ was −10‰, based on recent atmospheric $\delta^{13}C$ measurements in Salt Lake City, UT, USA (Pataki *et al.*, 2007), which is similar in population size to Fort Collins, but set within a denser metropolitan area. Atmospheric $\delta^{13}C$ in Salt Lake City ranged from −8 to −15‰ (mean *c.* −10.5‰) downtown and from −8 to −13‰ (mean *c.* −9.5‰) in a residential neighborhood. Given this uncertainty, we also conducted a sensitivity analysis in which we calculated $\Delta^{13}C_{leaf}$ with $\delta^{13}C_{gh(amb)}$ from −8 to −15‰. The estimate of $\delta^{13}C_{gh(elev)}$ assumes even mixing of ambient and injected CO_2 in the glasshouse. While imperfect mixing could lead to spatial variation in $\Delta^{13}C_{leaf}$ within the elevated [CO_2] treatment, this probably did not influence treatment effects, because the treatments were arranged in blocks and blocks were rotated frequently within bays.

Seedling measurements were compared among treatments with ANOVAs in Proc Mixed (SAS 9.2, Cary, NC, USA), with [CO_2], water, species and all interactions as fixed effects and block and block × water as random effects. Heights were analyzed with a repeated-measures ANOVA using a first-order autoregressive variance structure. The Kenward–Roger method was used to estimate degrees of freedom. To correct nonnormality and heteroscedasticity, total biomass and heights were cube-root-transformed, Ψ, $\Delta^{13}C_{leaf}$, [N], and C : N were log-transformed, root : shoot ratios were inverse cube-root-transformed, and percent cover of necrotic leaf tissue was arcsine, square-root-transformed for analysis.

Results

Growth and survival

Elevated [CO_2] increased mean total biomass by 15% (Fig. 1a–e; Table 1). The [CO_2] effect did not vary significantly among species or water treatments. Lower water availability in the faster water-table decline treatments (Fig. 2) reduced total biomass. *Salix* and *Populus* were the most strongly affected by lower water availability; they were the largest plants in the 0.5 cm d^{-1} treatment and the smallest in the 3.0 and 4.0 cm d^{-1} treatments (water × species interaction, Tables 1, S1).

Elevated [CO_2] increased mean root : shoot ratios by 4% (Fig. 1f–j; Table 1). The [CO_2] effect did not vary significantly among species or water treatments. Lower water availability affected root : shoot ratios of some species and not others (water × species interaction, Table 1). Specifically, lower water availability increased *Tamarix*, *Elaeagnus*, and *Ulmus* root : shoot ratios, but not *Salix* and *Populus* root : shoot ratios (Table S1). *Salix*, *Populus*, and *Ulmus* root : shoot ratios tended to be greater than *Tamarix* and *Elaeagnus* root : shoot ratios, but this difference decreased with lower water availability (Table S1).

Elevated [CO_2] increased shoot heights in most weeks of the experiment (Table 1), including a 19% increase in the final week (Fig. 3a–e). The effect of [CO_2] on heights varied with time for some water treatments and species, becoming more consistent later in the experiment (week × water × [CO_2] and week × [CO_2] × species interactions, Table 1). Specifically,

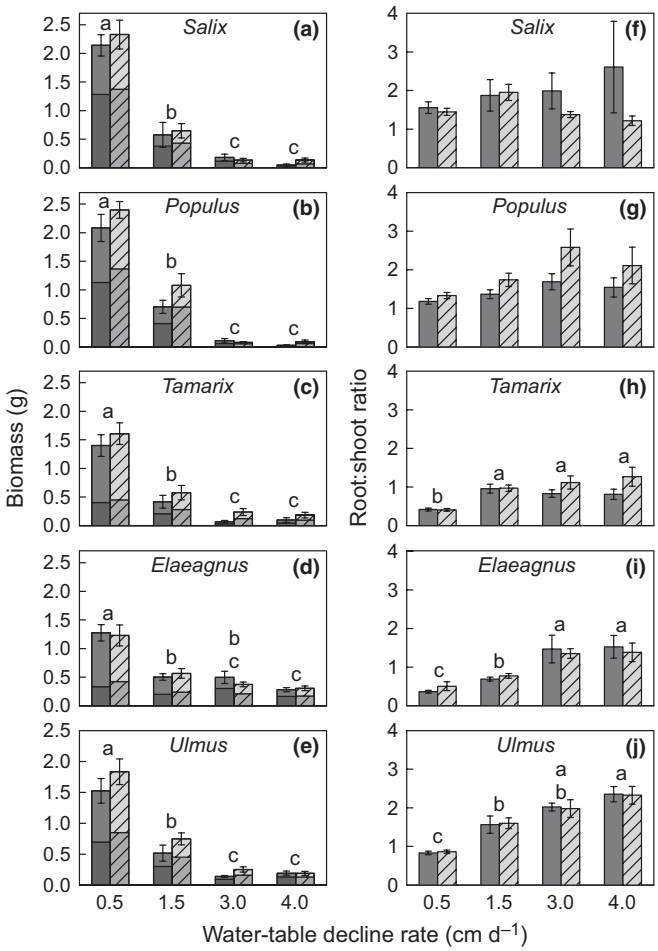

Fig. 1 Mean biomass and root : shoot ratio with each water-table decline rate and [CO_2] treatment combination for: (a, f) *Salix*, (b, g) *Populus*, (c, h) *Tamarix*, (d, i) *Elaeagnus*, and (e, j) *Ulmus*. In (a–e), the lower, darker portions of the stacked bars are below-ground biomass, the upper, lighter portions are above-ground biomass, and the error bars are for total biomass. ANOVA results are presented in Table 1. Different lower-case letters above the bars indicate significant differences in mean total biomass or root : shoot ratio among water treatments for each species (Tukey HSD, $P < 0.05$; Supporting Information Table S1). Error bars are one standard error of the mean.

elevated [CO_2] did not affect heights in the 0.5 cm d^{-1} treatment in the first 7 wk (*post-hoc* week × [CO_2], $F_{9,632} = 3.4$, $P = 0.0004$) and did not affect *Tamarix* and *Ulmus* heights in the first 2 wk (*post-hoc* week × [CO_2], $F_{9,502} = 3.3$, $P = 0.0006$; $F_{9,504} = 4.3$, $P < 0.0001$, respectively). Lower water availability reduced mean heights of all species starting in the fifth week (week × water × species interaction, Table 1), and reduced *Salix*, *Populus*, and *Tamarix* heights more than *Elaeagnus* and *Ulmus* heights (*post-hoc* water × species, $P < 0.0001$ for weeks 6–11). At the start of the experiment (week 2), *Elaeagnus* and *Ulmus* were considerably taller than *Populus*, *Tamarix*, and *Salix* across all treatments (7.7 ± 0.2 and 5.5 ± 0.1 compared with 1.5 ± 0.1, 0.39 ± 0.03, and 0.29 ± 0.02 cm, respectively) (*post-hoc* species, $F_{4,273} = 1684.0$, $P < 0.0001$). At the end of the experiment (week 11), species differences in height varied among water treatments (*post-hoc* water × species, $F_{12,249} = 7.6$, $P < 0.0001$). In the 3.0

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Table 1 ANOVA results for effects of water, [CO_2] and species on seedling growth

		Total biomass			Root : shoot ratio			Maximum root length			Height		
Factor	ndf	ddf	*F*	*P**	ddf	*F*	*P*	ddf	*F*	*P*	ddf	*F*	*P*
Water	3	28	332.6	**< 0.0001**	21	55.5	**< 0.0001**	21	28.2	**< 0.0001**	320	232.6	**< 0.0001**
[CO_2]	1	249	15.6	**0.0001**	249	4.7	**0.03**	246	11.0	**0.001**	320	50.0	**< 0.0001**
Water × [CO_2]	3	249	0.7	0.6	249	0.2	0.9	246	0.4	0.7	320	0.9	0.5
Species†	4	249	5.3	**0.0004**	249	71.3	**< 0.0001**	246	14.5	**< 0.0001**	320	300.8	**< 0.0001**
Water × species	12	249	9.2	**< 0.0001**	249	9.6	**< 0.0001**	246	3.1	**0.0003**	320	4.6	**< 0.0001**
[CO_2] × species	4	249	1.6	0.2	249	1.9	0.1	246	1.5	0.2	320	0.7	0.6
Water × [CO_2] × species	12	249	0.9	0.6	249	1.0	0.4	246	1.3	0.2	320	1.2	0.3
Week‡	9										2493	973.4	**< 0.0001**
Week × water	27										2509	76.0	**< 0.0001**
Week × [CO_2]	9										2493	5.5	**< 0.0001**
Week × species	36										2510	44.8	**< 0.0001**
Week × water × [CO_2]	27										2509	1.8	**0.006**
Week × water × species	108										2505	3.0	**< 0.0001**
Week × [CO_2] × species	36										2510	1.7	**0.008**
Week × water × [CO_2] × species	108										2505	1.2	0.06

Post-hoc ANOVA results for the significant water × species interactions are provided in Supporting Information Table S1.
*Significant effects are in bold ($P < 0.05$).
†*Salix exigua*, *Populus deltoides* spp. *monilifera*, *Tamarix* spp., *Elaeagnus angustifolia*, *Ulmus pumila*.
‡Weeks 2–11.
ndf, numerator degrees of freedom; ddf, denominator degrees of freedom.

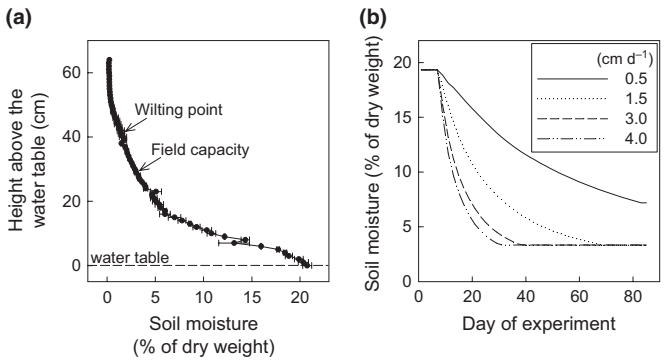

Fig. 2 (a) Mean soil moisture in each cm of soil above a static water table 64 cm below the soil surface. Heights above the water table for soil moisture (± SD) at field capacity (−0.033 MPa; 3.0 ± 0.4% moisture) and the wilting point (−1.5 MPa; 1.6 ± 0.1% moisture) are indicated with arrows. Error bars are one standard deviation. (b) Estimated mean soil moisture above the water table in each water treatment over the course of the experiment (calculated from the data in (a)).

and 4.0 cm d^{-1} treatments, *Elaeagnus*, *Ulmus* and *Tamarix* were taller than *Populus* and *Salix*, whereas in the 0.5 cm d^{-1} treatment, *Tamarix* was taller than *Elaeagnus* and *Elaeagnus* was taller than *Ulmus*, *Populus*, and *Salix* (Fig. 3a–e).

Elevated [CO_2] increased mean maximum root lengths by 12% (Fig. 3f–j; Table 1). The [CO_2] effect did not vary significantly among species or water treatments. Effects of the water treatments on maximum root lengths varied among species (water × species interaction, Table 1). Mean maximum root lengths were longer in the 1.5 cm d^{-1} treatment than in all other water treatments for *Populus* and *Ulmus*; longer in the 1.5 cm d^{-1} treatment than in the 0.5 and 4.0 cm d^{-1} treatments for *Elaeagnus*; and longer in the 1.5 cm d^{-1} treatment than in the 4.0 cm d^{-1} treatment for *Tamarix* and *Salix* (Table S1). *Elaeagnus* and *Ulmus* maximum root lengths were shorter than the other species in the 0.5 cm d^{-1} treatment, and *Elaeagnus* maximum roots lengths remained relatively short in the 1.5 cm d^{-1} treatment (Table S1). *Salix* maximum root lengths were longer than all other species in the 0.5 cm d^{-1} treatment.

At harvest, the water table in the 1.5, 3.0, and 4.0 cm d^{-1} treatments was 98 cm below the soil surface. Estimating from Fig. 2a, soil with moisture at field capacity (3.0 ± 0.4%; −0.033 MPa) was *c.* 70 cm below the soil surface, and soil with moisture at the wilting point (1.6 ± 0.1%; −1.5 MPa) was *c.* 57 cm below the soil surface. The water table in the 0.5 cm d^{-1} treatment was 44 cm below the soil surface and soil with moisture at field capacity was *c.* 15 cm below the soil surface. Mean maximum root lengths at harvest were long enough to reach the water table for all species in the 0.5 cm d^{-1} treatment and for *Populus*, *Salix*, and *Tamarix* (under elevated [CO_2]) in the 1.5 cm d^{-1} treatment (Fig. 3f–j). Mean root lengths in the 3.0 cm d^{-1} treatment were too short to reach the water table, but long enough to reach depths with moisture > 3.0%, or at least > 1.6%. Mean root lengths in the 4.0 cm d^{-1} treatment were long enough to reach depths with 3.0% moisture only for *Salix* under elevated [CO_2], and were too short to reach depths with 1.6% moisture for several species × [CO_2] treatment combinations. However, maximum root length may be an overestimate or underestimate of maximum root depth, because the root length may have been concentrated near the soil surface, or deep, fine roots may have been broken and not measured.

Most *Populus* (90% of plants) developed necrotic lesions on their leaves that appeared to result from pathogen infection (Fig. S2). Elevated [CO_2] increased abundance of the necrotic lesions, tripling mean percent cover on *Populus* leaves (22 ± 3% compared with 7 ± 2%) ([CO_2], $F_{1,28} = 20.0$, $P = 0.0001$). Many *Salix* (66% of plants) developed smaller necrotic lesions, and also

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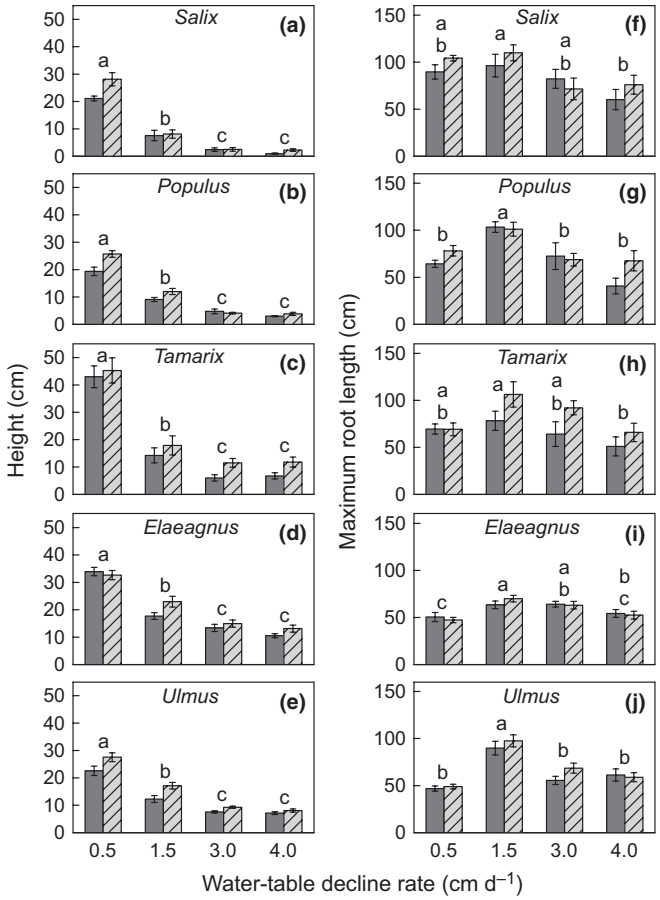

Fig. 3 Mean heights in week 11 and maximum root lengths at harvest with each water-table decline rate and [CO_2] treatment combination for: (a, f) *Salix*, (b, g) *Populus*, (c, h) *Tamarix*, (d, i) *Elaeagnus*, and (e, j) *Ulmus*. ANOVA results for heights across all weeks and maximum root lengths are presented in Table 1. Different lower-case letters above the bars indicate significant differences in mean height or maximum root length among water treatments for each species (Tukey HSD, $P < 0.05$; *post-hoc* ANOVA results for heights across all weeks and maximum root lengths are presented in Supporting Information Table S1). Error bars are one standard error of the mean.

exhibited greater percent cover of the lesions under elevated [CO_2] than under ambient [CO_2] (4 ± 1% compared with 2 ± 1%) ([CO_2], $F_{1,28} = 5.5$, $P = 0.03$). A few *Elaeagnus* (8% of plants) had small necrotic regions on some leaves under elevated [CO_2] (2 ± 1%), but not under ambient [CO_2]. Minor leaf necrosis on most *Ulmus* (89% of plants) did not differ significantly between [CO_2] treatments (4 ± 1%). *Tamarix* did not exhibit leaf necrosis.

Only three of the 320 study plants died during the experiment. All three received ambient [CO_2], including two *Salix* (4.0 cm d^{-1} treatment) and one *Populus* (3.0 cm d^{-1} treatment).

Water potential and tissue chemistry

Elevated [CO_2] affected Ψ_{pd} and Ψ_{md} at harvest for some species in some water treatments (water × [CO_2] × species interaction, Table 2; Fig. 4). Specifically, elevated [CO_2] increased *Ulmus* Ψ_{pd} and Ψ_{md}, particularly in the 0.5 and 1.5 cm d^{-1} treatments, although the water × [CO_2] interaction was not quite significant, and decreased *Tamarix* Ψ_{pd} and Ψ_{md} in the 4.0 cm d^{-1} treatment, but did not affect Ψ_{pd} and Ψ_{md} of any other species (Table S2). Lower water availability also affected Ψ_{pd} and Ψ_{md} for only some species (water × [CO_2] × species interaction, Table 2). Lower water availability reduced *Elaeagnus* and *Ulmus* Ψ_{pd} and Ψ_{md} and *Populus* Ψ_{pd}; increased *Tamarix* Ψ_{pd} and Ψ_{md} under ambient [CO_2]; and did not affect *Salix* Ψ (Table S2). Many of the *Salix* in the 3.0 and 4.0 cm d^{-1} treatments were too small to measure in the pressure chamber, which reduced the power to detect a water effect on *Salix* Ψ. Differences in Ψ among species depended on water treatment and time of day (time × water × species interaction, Table 2). In the 0.5 and 1.5 cm d^{-1} treatments, *Populus* Ψ_{pd} was greater than all other species and *Tamarix* Ψ_{pd} was lower than all other species (Table S2). Further, in the 0.5 cm d^{-1} treatment, *Elaeagnus* Ψ_{md} was greater than *Tamarix* Ψ_{md}. In the 3.0 cm d^{-1} treatment, Ψ_{pd} and Ψ_{md} were greater for *Populus* than for all other species, and in the 4.0 cm d^{-1} treatment, Ψ_{pd} and Ψ_{md} were greater for *Populus* than for *Tamarix* and *Ulmus* (Table S2). Ψ_{pd} was greater than Ψ_{md} except for *Populus* in the 3.0 and 4.0 cm d^{-1} treatments (time × water × species interaction, Table 2).

Assuming that ambient atmospheric $\delta^{13}C$ in the glasshouses ($\delta^{13}C_{gh(amb)}$) was between −8 and −10‰, elevated [CO_2] reduced $\Delta^{13}C_{leaf}$ across all water treatments and species (Fig. 5a–e; Table 2). The magnitude of this effect was smaller for *Elaeagnus* than for the other species ([CO_2] × species interaction, Table 2), and was smaller in the drier treatments than in the wetter treatments (water × [CO_2] interaction, Table 2). The sensitivity analysis indicated that the negative effect of elevated [CO_2] on $\Delta^{13}C_{leaf}$ was robust to assumptions of a more negative $\delta^{13}C_{gh(amb)}$, except for *Elaeagnus* if $\delta^{13}C_{gh(amb)} \leq -11$‰ and for the 3.0 and 4.0 cm d^{-1} treatments if $\delta^{13}C_{gh(amb)} \leq -12$‰. The $\delta^{13}C_{gh(amb)}$ would have to have been ≤ -15‰ for elevated [CO_2] not to have significantly reduced $\Delta^{13}C_{leaf}$ for the other species and water treatments. Effects of water-table decline rate on $\Delta^{13}C_{leaf}$ differed among [CO_2] treatments and species (water × [CO_2] and water × species interactions, Table 2). Specifically, lower water availability reduced $\Delta^{13}C_{leaf}$ under ambient [CO_2] but not elevated [CO_2] (across species), and for *Elaeagnus* but not other species (across [CO_2] treatments) (Table S3).

Elevated [CO_2] decreased mean leaf [N] by 7%, from 1.29 ± 0.03 to 1.20 ± 0.03% (Fig. S3; Table 2), and increased mean leaf C : N by 8% (Fig. 5f–j; Table 2). Lower water availability increased leaf [N] by 36%, from 1.06 ± 0.02% in the 0.5 and 1.5 cm d^{-1} treatments to 1.44 ± 0.04% in the 3.0 and 4.0 cm d^{-1} treatments, and decreased leaf C : N for most species, but did not significantly affect *Elaeagnus* leaf C : N (water × species interaction, Tables 2, S4). *Elaeagnus* leaf [N] was less than in the other species (0.97 ± 0.04% compared with 1.32 ± 0.03%), and *Elaeagnus* leaf C : N was greater than in the other species, particularly in the drier treatments (Table S4).

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Table 2 ANOVA results for effects of water, [CO_2] and species on seedling water potentials and tissue chemistry

		Stem water potential			$\Delta^{13}C_{leaf}$			Leaf C : N			Leaf [N]		
Factor	ndf	ddf	*F*	*P**	ddf	*F*	*P*	ddf	*F*	*P*	ddf	*F*	*P*
Water	3	26	2.4	0.09	269	18.0	**< 0.0001**	21	36.1	**< 0.0001**	21	30.3	**< 0.0001**
[CO_2]	1	201	0.6	0.5	269	209.9	**< 0.0001**	249	7.5	**0.007**	249	6.9	**0.009**
Water × [CO_2]	3	200	3.2	**0.03**	269	5.5	**0.001**	249	0.4	0.7	249	0.6	0.6
Species†	4	201	50.4	**< 0.0001**	269	159.7	**< 0.0001**	249	24.7	**< 0.0001**	249	17.7	**< 0.0001**
Water × species	12	200	3.5	**0.0001**	269	9.0	**< 0.0001**	249	1.9	**0.04**	249	1.6	0.1
[CO_2] × species	4	200	2.3	0.06	269	6.8	**< 0.0001**	249	0.2	0.9	249	0.4	0.8
Water × [CO_2] × species	12	200	1.8	**0.04**	269	1.4	0.2	249	0.9	0.6	249	0.7	0.8
Time‡	9	28	117.7	**< 0.0001**									
Time × water	27	27	2.6	0.07									
Time × [CO_2]	9	200	0.1	0.7									
Time × species	36	201	5.8	**0.0002**									
Time × water × [CO_2]	27	199	0.2	0.9									
Time × water × species	108	200	2.1	**0.02**									
Time × [CO_2] × species	36	200	0.3	0.9									
Time × water × [CO_2] × species	108	199	0.8	0.6									

Post-hoc ANOVA results for the significant interactions are provided in Supporting Information Tables S2–S4.
*Significant effects are in bold ($P < 0.05$).
†*Salix exigua*, *Populus deltoides* spp. *monilifera*, *Tamarix* spp., *Elaeagnus angustifolia*, *Ulmus pumila*.
‡Predawn vs midday.
ndf, numerator degrees of freedom; ddf, denominator degrees of freedom.

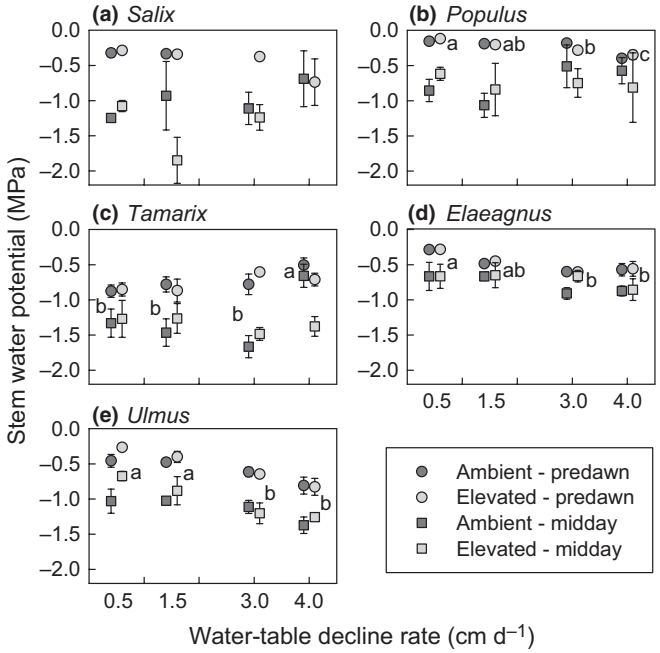

Fig. 4 Mean predawn and midday stem water potentials (Ψ_{pd} and Ψ_{md}) with each water-table decline rate and [CO_2] treatment combination in week 12 of the experiment for: (a) *Salix*, (b) *Populus*, (c) *Tamarix*, (d) *Elaeagnus*, and (e) *Ulmus*. Ambient and elevated [CO_2] treatments are offset horizontally to facilitate viewing. ANOVA results are presented in Table 2. Different lower-case letters in (b) indicate significant differences in *Populus* Ψ_{pd} among water treatments, averaged across [CO_2] treatments (Tukey HSD, $P < 0.05$; Supporting Information Table S2). Different lower-case letters in (c) indicate significant differences in *Tamarix* Ψ among water treatments under ambient [CO_2], averaged across times of day. Different lower-case letters in (d) and (e) indicate significant differences in *Elaeagnus* and *Ulmus* Ψ among water treatments, averaged across [CO_2] treatments and times of day. Error bars are one standard error of the mean.

Discussion

Water and [CO_2] effects on seedling growth

Increased drought and lower summer streamflows predicted under climate change may reduce riparian plant growth and recruitment, and favor drought-tolerant species, including exotics, in semiarid western North America (Stromberg *et al.*, 2010; Perry *et al.*, 2012). The large negative effects of faster water-table decline rates on seedling biomass (70–97%) support the prediction that lower water availability under climate change will severely limit riparian seedling growth. Our results do not, however, support the hypothesis that elevated [CO_2] will ameliorate these effects by increasing plant WUE. Instead, the small positive effect of elevated [CO_2] on biomass (15%) suggests that increases in seedling growth and WUE under elevated [CO_2] will be insufficient to offset the negative effects of increased aridity. Where aridity does not increase, however, seedling growth may increase moderately under elevated [CO_2].

Our results also support the prediction that increased aridity will hinder seedling recruitment of native *Salix* and *Populus* spp. more than exotic woody riparian species. The larger negative effects of the drier treatments on *Salix* and *Populus* biomass than on exotic species biomass support previous studies on *Tamarix* and *Elaeagnus* (Shafroth *et al.*, 1995; Glenn & Nagler, 2005; Lite & Stromberg, 2005; Reynolds & Cooper, 2010) and suggest that *Ulmus* is also more drought-tolerant than the native species. The similar responses of the native and exotic species to elevated [CO_2] suggest that elevated [CO_2] will not ameliorate the lower drought tolerance of the native species relative to the exotics.

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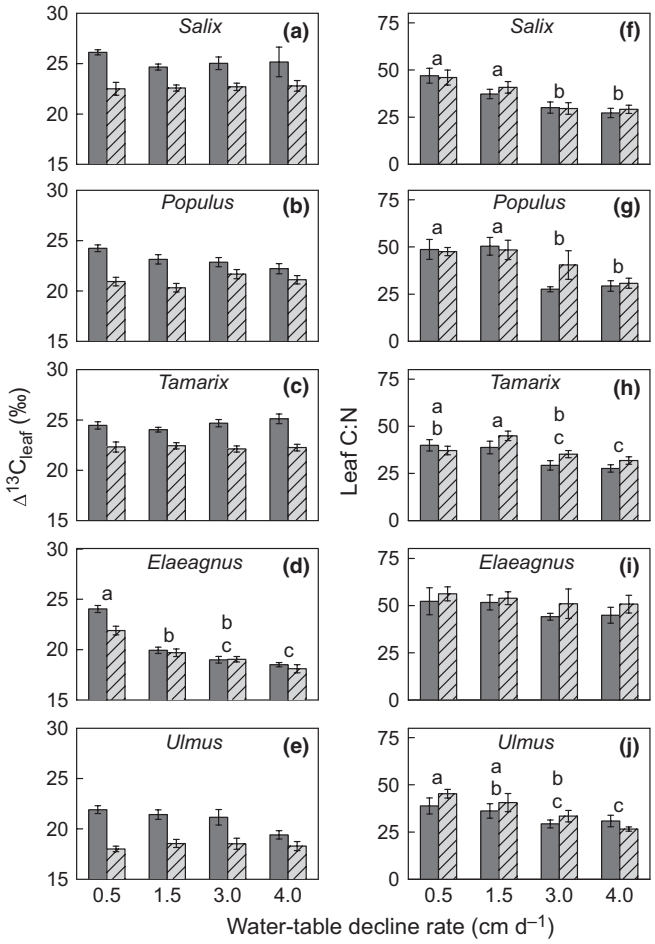

Fig. 5 Mean $\Delta^{13}C_{leaf}$ and leaf C : N ratio with each water-table decline rate and [CO_2] treatment combination for: (a, f) *Salix*, (b, g) *Populus*, (c, h) *Tamarix*, (d, i) *Elaeagnus*, and (e, j) *Ulmus*. ANOVA results are presented in Table 2. Different lower-case letters above the bars indicate significant differences in mean $\Delta^{13}C_{leaf}$ or C : N among water treatments (Tukey HSD, $P < 0.05$; Tables S3, S4). Error bars are one standard error of the mean.

Although quantitative predictions of riparian soil moisture under climate change are not available, the differences in soil moisture among our water treatments were similar in scale to projected changes in summer streamflows in western North America under climate change. Summer streamflows, which strongly influence riparian soil moisture (Naiman *et al.*, 2005), declined by as much as 20% in the last century (Miller & Piechota, 2008; Rood *et al.*, 2008) and are projected to decline by up to 50% in the next century (Christensen *et al.*, 2004; Dettinger *et al.*, 2004; Maurer, 2007), as a result of smaller snowpacks and earlier snowmelt at the headwaters. Similarly, estimated soil moisture in the 4.0 cm d^{-1} treatment was 25% less than in the 1.5 cm d^{-1} treatment and 52% less than in the 0.5 cm d^{-1} treatment.

[CO_2] effects on WUE and water status

Contrary to expectations, lower water availability did not reduce seedling growth less under elevated [CO_2] than under ambient [CO_2], except temporarily for heights in the first 7 wk of the experiment. Although plant growth in grasslands often responds positively to elevated [CO_2] through improved water relations (Volk *et al.*, 2000; Morgan *et al.*, 2004, 2011), exceptions to this pattern do occur (Morgan *et al.*, 2004; Hovenden *et al.*, 2008). Plants exposed to a single, prolonged water stress event, such as naturally occurs in Mediterranean grasslands (Morgan *et al.*, 2004) or the present experiment, may only briefly experience the moderate water stress that seems optimal for plant response to elevated [CO_2] (Nowak *et al.*, 2004), and may therefore exhibit little increase in growth from water savings.

Lower $\Delta^{13}C_{leaf}$ under elevated [CO_2] suggests that elevated [CO_2] increased seedling iWUE by reducing stomatal conductance and/or increasing photosynthetic capacity, a common plant response (Polley *et al.*, 2002; Morgan *et al.*, 2004; Nelson *et al.*, 2004; Leakey, 2009; Onoda *et al.*, 2009). The increase in iWUE, however, was smaller in the drier treatments than in the wetter treatments, which may explain in part why elevated [CO_2] did not improve growth more in the drier treatments. Very low soil water content can override effects of [CO_2] on stomatal conductance and growth (Hunt *et al.*, 1996; Knapp *et al.*, 1996; Smith *et al.*, 2000; LeCain *et al.*, 2003). The floodplain sand and gravel bars where pioneer riparian species often establish are well drained, and soil moisture can decline rapidly during flood recession, especially in the absence of precipitation (Shafroth *et al.*, 1998; Cooper *et al.*, 1999; Taylor *et al.*, 1999; Hultine *et al.*, 2010). Very low soil moisture in the drier treatments may have limited seedling responses to elevated [CO_2].

Although elevated [CO_2] appeared to increase iWUE, it did not increase Ψ for most species at the time of harvest. Measured Ψ values were similar to published values for moderately water-stressed *Salix*, *Populus*, and *Ulmus* (Foster & Smith, 1991; Cooper *et al.*, 2003; Dulamsuren *et al.*, 2009; Hultine *et al.*, 2010) but greater than published values for *Tamarix* and *Elaeagnus* (Busch & Smith, 1995; Horton *et al.*, 2001b; Gong *et al.*, 2006; Zhao *et al.*, 2007). Elevated [CO_2] may have increased growth mainly by increasing photosynthesis directly (Drake *et al.*, 1997) rather than by improving water status. Alternatively, the larger seedlings under elevated [CO_2] may have had less stomatal conductance per unit leaf area but greater total transpiration, resulting in unchanged Ψ (Morison, 1993).

Increased seedling root allocation and maximum root lengths under elevated [CO_2] also did not alleviate effects of lower water availability in this experiment. Such effects may increase growth and survival under some conditions, however, by increasing access to water and reducing flood mortality (Mahoney & Rood, 1998; Cooper *et al.*, 1999). Conversely, such effects might decrease growth and survival when water is abundant, by reducing canopy production and competitive ability for light (Sher *et al.*, 2000).

Factors limiting responses to [CO_2]

Low nutrient availability in the floodplain sand in our experiment may have reduced effects of elevated [CO_2] on growth (de Graaff *et al.*, 2006; Reich *et al.*, 2006; Lewis *et al.*, 2010; McCarthy *et al.*, 2010). High leaf C : N in our experiment

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(40 ± 13) suggests N limitation. Further, increased C : N and root allocation under elevated [CO_2] may reflect increased nutrient limitation (Reich *et al.*, 2006; Dewar *et al.*, 2009; Lewis *et al.*, 2010). In other experiments with greater nutrient availability, elevated [CO_2] increased *Populus deltoides* ssp. *deltoides* biomass by 40–100% (McDonald *et al.*, 2002; Barron-Gafford *et al.*, 2005; Lewis *et al.*, 2010), compared with the 21% increase in *Populus* biomass in our experiment. Nutrient availability is typically low in floodplain sandbars (Adair & Binkley, 2002; Adair *et al.*, 2004), but riparian areas with greater nutrient availability because of nutrient pollution (Carpenter *et al.*, 1998) or fine sediment accretion (Adair *et al.*, 2004; Naiman *et al.*, 2010) may have larger seedling responses to elevated [CO_2]. Older riparian saplings or adult trees could respond to elevated [CO_2] either more strongly because soil nutrient availability increases as riparian geomorphic surfaces age (Adair *et al.*, 2004), or less strongly because nutrient demand increases, and hence availability decreases, as forests age (Körner, 2006).

Elaeagnus growth appears to have been particularly N-limited in our experiment. *Elaeagnus* had lower leaf [N] and greater C : N than the other species and than reported in field studies (Follstad Shah *et al.*, 2010), the slowest growth in the wettest treatment, and the smallest changes in growth and $\Delta^{13}C_{leaf}$ under elevated [CO_2]. *Elaeagnus* is actinorhizal (i.e. forms associations with N-fixing *Frankia* bacteria), but we did not observe *Frankia* nodules on our *Elaeagnus* roots. Nodulated *Elaeagnus* with greater N availability, and plants growing near nodulated *Elaeagnus* (Follstad Shah *et al.*, 2010), may respond more strongly to elevated [CO_2].

Increased necrotic lesions on *Populus* leaves under elevated [CO_2] may also have reduced effects of elevated [CO_2] on *Populus* growth (Newcombe, 1996). We were unable to identify the pathogen responsible, and therefore cannot assess its ecological relevance. Effects of elevated [CO_2] on pathogen infection in other *Populus* species vary among host and pathogen species (Percy *et al.*, 2002; Scarascia-Mugnozza *et al.*, 2005; Chakraborty *et al.*, 2008; Eastburn *et al.*, 2011). More generally, effects of elevated [CO_2] on the study species might be different in more complex environments with competitors, herbivores, and pathogens (Körner, 1995; Navas, 1998).

Mechanisms of drought tolerance

Tamarix drought tolerance has been attributed to its ability to maintain turgor via osmotic adjustments, prevent xylem cavitation, and use both deep and shallow soil water (Busch & Smith, 1995; Smith *et al.*, 1998; Pockman & Sperry, 2000). As in other studies, *Tamarix* Ψ tended to be lower than for other species, and did not decline with lower water availability, perhaps because of low osmotic potential (Smith *et al.*, 1998; Horton *et al.*, 2001b, 2003; Gries *et al.*, 2003; Xu *et al.*, 2007). By contrast, *Populus* Ψ tended to be greater than for other species, and was similar at midday and predawn in the drier treatments, suggesting stomatal closure. *Populus* is vulnerable to xylem cavitation and relies on tight stomatal control to maintain adequate Ψ when water-stressed (Horton *et al.*, 2001a; Cooper *et al.*, 2003). *Populus* Ψ_{md} approached reported thresholds for 50% xylem cavitation (*c.* −1.0 MPa; Tyree *et al.*, 1994), whereas *Tamarix* Ψ did not (*c.* −4.5 MPa; Pockman & Sperry, 2000).

Mechanisms of *Elaeagnus* and *Ulmus* drought tolerance are less well understood. Our results suggest that they may benefit from larger seed size and greater plasticity in root allocation and iWUE. Large *Elaeagnus* and *Ulmus* seeds (87.9 and 6.3 mg seed^{-1} compared with 0.1, 1.3, and 0.1 mg seed^{-1} for *Salix*, *Populus*, and *Tamarix*, respectively) allowed them to grow faster initially, when water tables were still high in the drier treatments. Further, increases in root allocation with lower water availability in *Elaeagnus* and *Ulmus* (and, to a lesser degree, in *Tamarix*) may have increased access to soil water (Poorter & Nagel, 2000). Plasticity in root allocation has also been observed in other studies of *Elaeagnus* and *Ulmus* (Shafroth *et al.*, 1995; Park *et al.*, 2012), but also of *Salix* and *Populus* (Shafroth *et al.*, 1995; Kranjcec *et al.*, 1998; Stella & Battles, 2010), so this trait is not always limited to the exotic species. In addition, increases in iWUE (i.e. reduced $\Delta^{13}C_{leaf}$) with lower water availability in *Elaeagnus* may have increased water conservation and/or C assimilation (Farquhar *et al.*, 1989). Although plasticity in root allocation and iWUE can simply reflect variation in water stress, the fact that *Elaeagnus* and *Ulmus* biomass was greater than that of the other species in the drier treatments suggests that in this case it may reflect greater drought tolerance.

Rooting depth is an important predictor of riparian seedling survival, because seedling roots must maintain contact with moisture from declining water tables as streamflow decreases through the summer (Mahoney & Rood, 1998; Stella & Battles, 2010). Differences in rooting depth are unlikely to explain species differences in drought tolerance in our experiment, however, as maximum root lengths were similar among species in the drier treatments. Maximum root lengths were greatest with a moderate water-table decline rate (1.5 cm d^{-1}), presumably because root growth was stifled by low water availability in the drier treatments and by inundation (particularly for *Elaeagnus* and *Ulmus* and less for *Salix*) in the wettest treatment (Segelquist *et al.*, 1993; Kranjcec *et al.*, 1998; Horton & Clark, 2001; Amlin & Rood, 2002).

Conclusions

Global change effects on western North American riparian plants may involve interactions between increased aridity (resulting from greater evapotranspiration, lower streamflows, and shifts in streamflow timing), elevated [CO_2], increased heat stress (Grady *et al.*, 2011), and changes in flood regime and geomorphology (Perry *et al.*, 2012). Our results suggest that elevated [CO_2] is unlikely to counteract the negative effects of increased aridity on riparian woody seedling recruitment. Further, they corroborate previous research demonstrating that common exotic riparian species are more drought-tolerant than dominant native species, adding *Ulmus* to the list of drought-tolerant exotic species. Finally, they indicate that elevated [CO_2] is unlikely to benefit seedling recruitment of mesic native species over drought-tolerant exotics. Increased aridity is likely to favor recruitment of more

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drought-tolerant species, including the exotics *Tamarix*, *Elaeagnus* and *Ulmus*, over native *Salix* and *Populus* spp., despite elevated [CO_2].

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Depiction of whole-pot and subpot experimental setup.

Fig. S2 Photographs of necrotic lesions on *Populus* leaves.

Fig. S3 Mean leaf [N] for each treatment combination.

Table S1 *Post-hoc* ANOVA results for seedling growth

Table S2 *Post-hoc* ANOVA results for stem water potentials (Ψ)

Table S3 *Post-hoc* ANOVA results for $\Delta^{13}C_{leaf}$

Table S4 *Post-hoc* ANOVA results for leaf C : N

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