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Urban channel incision and stream flow subsidies have contrasting effects on the water status of riparian trees

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Abstract

The water relations of riparian trees are often closely tied to stream hydrology and channel morphology, which can be altered by urban development. In regions with limited precipitation, urban water use can generate or augment dry-season stream flows, potentially providing a water subsidy to riparian trees. However, urbanization is also associated with high storm flows that cause stream channel incision, or downcutting, which could limit the effect of flow subsidies by lowering riparian water tables. We investigated the effects of urban dry-season flow subsidies and stream channel incision on the water status of streamside trees in Sacramento, California, which has a Mediterranean climate with a distinct and lengthy dry season. For two common facultative riparian species, *Quercus lobata* (valley oak) and *Fraxinus latifolia* (Oregon ash), we analyzed both midday stem water potential (Ψ_{stem}) measurements and leaf carbon isotope signatures ($\partial^{13}C$) to determine whether channel incision and dry-season flow had interacting effects on seasonal midday water stress and longer-term water use efficiency. We found that stream flow could substantially reduce dry-season water stress in both tree species, but only at low levels of channel incision. Leaf $\partial^{13}C$ signatures for *Q. lobata* suggested increased water use efficiency in trees growing along incised streams and those lacking dry-season flow. Urban management decisions that affect both dry-season base flows and channel incision can thus influence the growth and health of riparian trees, potentially leading to broader changes in riparian ecosystems.

Keywords Hydrology · Stream morphology · *Quercus lobata* · Water stress · Mediterranean climate

Introduction

Urban development can cause changes in watershed hydrology and stream channel morphology that may affect the water relations of riparian trees. Urban water use can change the source and timing of water inputs to streams (Paul and Meyer 2001), potentially shifting both the amount and the seasonality of water available to trees growing along streambanks. While these changes could have a marked effect on tree water status, the response may be limited where stream channels are incised. Channel incision is common in urban areas due to increased impervious surfaces and infrastructure that route stormwater directly into streams, causing flashy storm flows that downcut streambeds (Booth 1990; Walsh et al. 2005). This deepening of the stream channel effectively increases the elevation of trees above stream base flows and associated water tables, limiting water availability in the primary rooting zone (Loheide and Gorelick 2007). Thus, in urban areas, channel incision may interact with changes in stream base flow to affect the growth, health, and productivity of riparian trees, ultimately influencing the ecological functioning of both riparian ecosystems and the streams they border.

Changes in the seasonality of stream flow due to urbanization could have a particularly strong effect on riparian trees in Mediterranean climate regions, where many streams are naturally intermittent due to the near-complete absence of precipitation during the summer dry season. Urban water subsidies from sources including landscape irrigation and wastewater treatment plants have been shown to substantially increase dry-season stream flow in Mediterranean-climate cities, sometimes converting intermittent streams to perennial streams (White and Greer 2006) and occasionally contributing so much water that dry-season base flows exceed wet-season base flows (Solins et al. 2018). Such a dramatic increase in dry-season base flows could alleviate seasonal water stress for riparian trees (Swift et al. 2008), and could be particularly

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important for the establishment of young trees that cannot rely on deeper groundwater (Dawson and Ehleringer 1991). Along incised channels, though, the positive impact of these dry-season flow subsidies may be limited or negated. In addition, channel incision could impede the ability of trees to access stream water year-round, leading to chronically higher levels of water stress.

Different assessments of tree water stress can help to elucidate both periodic and persistent effects of factors like channel incision and dry-season stream flow. The instantaneous measurement of stem water potential (Ψ_{stem}), which assesses the amount of tension on water in the tree's xylem, reflects environmental conditions at the time of sampling and can thus provide insight into seasonal levels of water stress if measured at different times of year (Shackel and Gross 2002). Measuring Ψ_{stem} at midday, when water stress is at its diurnal peak, has proven to be a reliable metric of tree water status (McCutchan and Shackel 1992; Shackel and Gross 2002) and has also shown strong associations with physiological responses to water stress (Shackel et al. 1997, 2000; Naor 2000).

While each midday Ψ_{stem} measurement provides a snapshot of a tree's condition, the $\partial^{13}C$ signature of its tissues reflects its water use efficiency (WUE) over time, indicating longer-term water status (Farquhar et al. 1982, 1989). Tissues of C_3 plants are generally highly depleted in ^{13}C compared to ambient air because photosynthesis discriminates against heavier $^{13}CO_2$ molecules. However, increased WUE due to stomatal closure or increased photosynthetic rates creates a lower concentration of CO_2 at the site of carboxylation, which leads to reduced discrimination against $^{13}CO_2$ and thus higher (less negative) values of $\partial^{13}C$ in tissues (Farquhar et al. 1982, 1989). Stomatal closure in water-stressed plants is thus generally associated with higher values of $\partial^{13}C$ (Cernusak et al. 2013). Leaf properties that influence photosynthesis and gas exchange can also affect the $\partial^{13}C$ of leaf tissues. Nitrogen, a key component of photosynthetically important compounds, is expected to be positively related to $\partial^{13}C$ (Chaves et al. 2004; Cernusak et al. 2013), while specific leaf area (SLA)—the leaf area to mass ratio—is expected to be negatively related to $\partial^{13}C$ because of reduced CO_2 diffusion in thicker or denser leaves (Vitousek et al. 1990; Kogami et al. 2001; Gerdol et al. 2018).

Leaf $\partial^{13}C$ is primarily determined as leaves are formed (Chaves et al. 2004); however, due to the incorporation of both stored carbohydrates and new photosynthates in the creation of leaf tissues (Damesin et al. 1998), $\partial^{13}C$ signatures in mature leaves of deciduous trees could reflect a combination of conditions from previous summers and the early part of the current growing season. Examining $\partial^{13}C$ along with instantaneous Ψ_{stem} measurements that are sensitive to short-term changes in water availability can provide a more complete picture of how environmental variables affect a tree's water status over time.

This study assesses the influences of dry-season stream flow and channel incision on the water status of urban riparian trees in the metropolitan region of Sacramento, California, USA. We chose the endemic valley oak (*Quercus lobata*) as the focal species for this study, and added Oregon ash (*Fraxinus latifolia*) as a comparison because it has a shallower rooting structure (Lewis and Burgy 1964; Owston 1990). We hypothesized that 1) dry-season stream flow would reduce water stress in streamside trees during the summer; 2) channel incision would limit the benefit of dry-season flow and also increase water stress in the wet season; and 3) channel incision would have a greater effect than dry season stream flow on leaf $\partial^{13}C$ values due to its influence throughout the growing season. We further predicted that all effects would be stronger in smaller trees due to higher reliance on moisture in the upper soil layers, and also stronger in *F. latifolia* due to its shallower root system.

Methods

Study area description

Study sites were located in residential neighborhoods in the metropolitan area of Sacramento, California. This region is characterized by a Mediterranean climate with a January mean minimum temperature of 3.2 °C, and a July mean maximum temperature of 33.7 °C (WRCC 2016). Precipitation falls almost exclusively in the cool winter months between October and April, and mean annual precipitation since 1941 is 438 mm. The area is characterized by deep alluvial soils (Soil Survey Staff 2018) and low water tables that have been further depressed due to municipal groundwater pumping in some areas, with depths exceeding 30 m across much of the study area (Criss and Davisson 1996; Sacramento Groundwater Authority 2016). However, on the eastern edge of the study area, water tables may be within 3–5 m of the surface (California DWR (Department of Water Resources) 2014), and some soils are less than a meter deep (Soil Survey Staff 2018). Most small streams in the region were historically intermittent or ephemeral, but urban water subsidies now create perennial flows or provide sporadic dry-season water subsidies in some stream reaches (Solins et al. 2018). Stream channel incision occurs throughout the study region, but not every stream is incised.

Species descriptions

Both *Q. lobata* and *F. latifolia* are winter-deciduous, facultative riparian species common across the study area. *Quercus lobata*, the largest North American oak, is endemic to California and is the dominant tree species in two major plant communities: valley oak woodland and valley oak riparian forest (Howard 1992). There is evidence that *Q. lobata* can grow deep taproots or other vertical roots to reach groundwater (Griffin 1973), perhaps in excess of 20 m (Lewis and Burgy 1964). *Fraxinus latifolia* has a smaller stature than *Q. lobata* and lacks taproots, instead growing an extensive and fibrous shallow root system. Distributed from California's Central Valley north to Puget Sound in Washington, it is commonly found in riparian zones, although it can also grow in upland forests, old fields, and roadsides (Owston 1990).

Study design

Based on extensive field reconnaissance in 2014 at publicly-accessible sites along small streams (1st to 4th order; Strahler 1957), we identified eight study sites for sampling *Q. lobata* trees (Fig. 1). The sites were chosen to create a gradient of channel incision, considered as the height of the stream bank above the thalweg of the stream (Groffman et al. 2002), and also to include contrasting dry-season flow conditions across that gradient. Stream reaches at some sites had continuous flow in late summer and some were completely dry; others included both pools of water and dry or damp stretches (Table 1). After more detailed vegetation studies revealed that *F. latifolia* also occurred with sufficient frequency to create a similar gradient of incision and flow conditions, we added seven study sites for *F. latifolia* trees in summer of 2015 (Table 1 and Fig. 1).

In this study, we define "riparian" based on proximity to the stream. Across the study sites, we identified a total of 48 trees of each species growing near the stream bank's edge, at a maximum distance of 7 m. Individuals within each study site ranged from saplings to mature trees (Table 1). In sites where there were more suitable trees than necessary, we chose healthy individuals that would create the widest and most even size gradient. For both species, we sampled a range of tree sizes across the full gradient of incision for each dry-season stream flow category. For each tree, we measured diameter at breast height (DBH) to the nearest cm, the distance from the base of the trunk to the edge of the stream bank, and the width of the stream at that location. As a metric for channel incision, we measured the vertical distance from the stream's thalweg to the tree's root crown (henceforth "root crown elevation"). All distance metrics were measured to the nearest 0.25 m.

Water potential

We measured midday Ψ_{stem} (McCutchan and Shackel 1992; Shackel and Gross 2002) in *Q. lobata* at the end of the dry season in both 2014 and 2015 (19-Aug to 04-Sept and 17-Aug to 26-Aug, respectively), as well as at the end of the wet season in 2015 (01-May to 21-May). We added measurements of *F. latifolia* at the end of the dry season in 2015 (30-July to 07-Aug). Both 2014 and 2015 were drought years with approximately the same severity at the time of dry-season sampling (Dai and National Center for Atmospheric Research Staff 2017).

We used a Scholander-type pressure chamber to measure Ψ_{stem} between 13:00 and 16:00, the time of greatest transpirational demand in this region. On each tree, we chose three healthy, shaded leaves between 1 and 4 m above ground level, located close to the trunk or scaffold branches. We enclosed each leaf (or terminal leaflet for *F. latifolia*) in a watertight foil bag for 15–30 min to stop transpiration and allow the leaf to equilibrate to the tree's stem water potential (Shackel and Gross 2002). We then excised each leaf and determined its

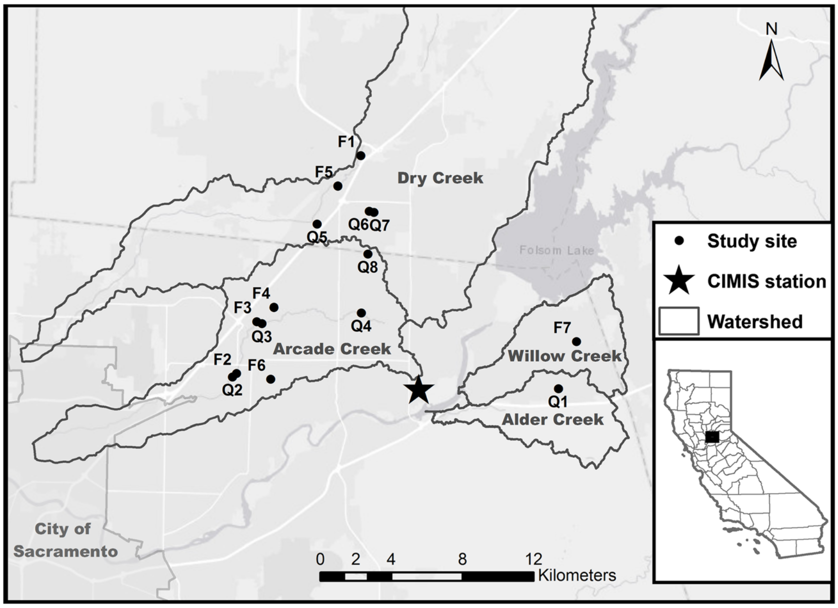

Fig. 1 Map of the study area showing the location of study sites, boundaries of the watersheds in which they are located, and the location of the California Irrigation Management Information System (CIMIS) station from which we retrieved atmospheric data. We sampled *Quercus lobata* at study sites that start with a "Q" and *Fraxinus latifolia* at sites that start with an "F"

Table 1 Description of the fifteen sampling sites, including the number of individual trees sampled (*n*), the range of their diameters at breast height (DBH), and the range of two measures of channel morphology: root crown elevation (RCE) and channel width. In addition, the dry-season stream flow status is shown for each year that dry-season Ψ_{stem} was sampled. When a single site included portions of a stream reach that differed in flow status, the number of trees adjacent to each category of flow is noted in parentheses. We sampled *Q. lobata* at study sites that start with a "Q" and *F. latifolia* at sites that start with an "F"

Site	*n*	DBH (cm)		RCE (m)		Channel width (m)		Dry-season stream flow	
		min	max	min	max	min	max	2014	2015
Q1	6	5	82	0.5	1.25	2	4.5	flowing	flowing
Q2	6	3	113	2	4	4	6.5	flowing (4); moist (2)	dry
Q3	6	4	69	2	3	4.5	6.5	dry	dry
Q4	6	3	52	1.25	2	1.5	3	flowing (4); dry (2)	flowing (2); dry (4)
Q5	6	3	106	2	2.5	6	8	flowing	flowing (1); moist (1); dry (4)
Q6	6	3	47	1.25	2	1	1.5	flowing	dry
Q7	6	2	49	0.5	1.25	1.5	8	flowing	flowing
Q8	6	5	48	1.5	1.75	1	2	dry	dry
F1	7	3	21	0.5	1	1.5	3		flowing
F2	7	7	35	1.5	2.75	4.5	8		moist (3); dry (4)
F3	7	2	31	1.5	2.5	3.5	7.5		moist
F4	7	5	33	0.75	2.5	3.5	5.5		moist (6); dry (1)
F5	7	6	57	2	2.5	10.5	14		flowing
F6	8	3	22	0.25	0.5	1	3		flowing (3); moist (1); dry (4)
F7	5	1	32	0.5	0.75	2.5	3.5		dry

balancing pressure in a humidified pressure chamber within 5 min of excision; leaves were kept bagged until measurement to prevent water loss. We assigned each tree the mean of its three Ψ_{stem} readings for analysis.

At the time of sampling, we measured the depth of the stream water in the channel directly in front of each tree. For analysis of dry-season measurements, we categorized each tree as being adjacent to a stretch that was dry, flowing (water depth was measurable, even if it was in an isolated pool), or moist (channel substrate was damp, indicating some recent water inputs). To account for differences in transpirational demand, we used a digital psychrometer to record the temperature and relative humidity (RH) at the time of excision for each tree and calculated vapor pressure deficit (VPD) following Abtew and Melesse (2013). We also acquired hourly data for reference evapotranspiration (ET_o) and solar radiation from the California Irrigation Management Information System (CIMIS) station number 131 in Fair Oaks, CA (Fig. 1). The reference surface for ET_o at this station is well-watered grass (CIMIS 2018). We also recorded the number of days since the last precipitation event for our wet-season sampling of *Q. lobata*.

$\partial^{13}C$ and leaf properties

We took leaf samples the year after sampling dry-season Ψ_{stem} in both species to see whether the $\partial^{13}C$ signal reflected conditions from the previous dry season due to use of stored carbohydrates in the construction of new leaves. We collected leaves soon after they reached maturity, between 21-May-2016 and 07-Jun-2016. Five *Q. lobata* trees and four *F. latifolia* trees were damaged or felled by the time of sampling, so these trees were excluded from analysis. We used a pole pruner to collect at least two small branches from different locations in the outer canopy of each tree to keep sun exposure as consistent as possible. We chose six leaves from these branches with the least damage and cleaned them with DI water. To determine SLA, we scanned the leaves to calculate leaf area and then dried them at 50 °C to constant dry weight before measuring mass. We excluded the petiole and rachis from *F. latifolia's* compound leaves, but included individual leaflet petiolules and the petioles of *Q. lobata* leaves. We then pulverized the composited leaves from each tree for chemical analysis. Leaf samples were analyzed for $\delta^{13}C$ (reported in ‰ relative to the Vienna PeeDee Belemnite international standard) and N content by mass using an elemental analyzer interfaced to a continuous flow isotope ratio mass spectrometer at the UC Davis Stable Isotope Facility.

Statistical analysis

We assessed the importance of stream channel variables in predicting Ψ_{stem} and $\delta^{13}C$ for each species using linear models, starting with full models that included all measured factors and interactions we hypothesized to be potentially influential (Table 2). For Ψ_{stem} models, we included only the

Table 2 Full and final models used to predict each response variable, presented in formula syntax used for the lme4 R package

Response	Full model	Final model
Dry-season Ψ_{stem} (*Q. lobata*)	Ψ_{stem} ~ RCE*flow*DBH + RCE*channel.width + DBH*bank.distance + temperature + water.depth + year + (1|site/tree)	Ψ_{stem} ~ RCE*flow + DBH*flow + temperature + year + (1|site/tree)
Dry-season Ψ_{stem} (*F. latifolia*)	Ψ_{stem} ~ RCE*flow*DBH + RCE*channel.width + DBH*bank.distance + evapotranspiration + water.depth + (1|site)	Ψ_{stem} ~ RCE*flow + evapotranspiration
Wet-season Ψ_{stem} (*Q. lobata*)	Ψ_{stem} ~ RCE*DBH + RCE*log(channel.width) + log(water.depth) + DBH*log(bank.distance) + temperature + DBH*days.rain + (1|site)	Ψ_{stem} ~ RCE*log(channel.width) + log(bank.distance) + temperature + days.rain + (1|site)
δ^{13}C (*Q. lobata*)	δ^{13}C ~ RCE*log(DBH) + RCE*2015.flow + RCE*channel.width + 2015.flow*log(DBH) + log(DBH)*bank.distance + pctN + SLA + (1|site)	δ^{13}C ~ log(DBH) + 2015.flow + pctN + SLA
δ^{13}C (*F. latifolia*)	δ^{13}C ~ RCE* log(DBH) + RCE*2015.flow + RCE*channel.width + 2015.flow* log(DBH) + log(DBH) *bank.distance + pctN + SLA + (1|site)	δ^{13}C ~ log(DBH) + SLA

Asterisks in equations denote interactions, and random effects are in parentheses

RCE root crown elevation, the height of the tree's root crown above the thalweg of the stream; *flow* categorical variable describing whether the stream was dry, moist, or flowing; *DBH* diameter at breast height; *channel.width* width of the bottom of the stream channel; *bank.distance* the distance of the tree's root crown from the edge of the stream bank; *water.depth* depth of stream water at the thalweg; *days.rain* days since the last precipitation event; *pctN* leaf nitrogen content by mass; *SLA* specific leaf area

atmospheric variable that had the highest correlation with Ψ_{stem} based on Kendall's τ, as many of the atmospheric variables were highly correlated with one another. We also included transformations for variables that had nonlinear relationships with the outcome variable based on scatter plots. Each full model included study site as a random intercept, and the full model for dry-season *Q. lobata* Ψ_{stem} measurements also included tree nested within site as a random intercept because it included two years of data. For *Q. lobata*, there were only three Ψ_{stem} measurements categorized as moist across both years, so we combined these measurements with the flowing category for analysis.

Starting with each full model, we used an automated function to construct an exhaustive set of candidate models and compared them using Akaike's information criterion with a correction for small sample size (AICc). We considered all models within two points of the lowest AICc score to see whether there was strong evidence for the importance of variables other than those retained in the model with the lowest AICc score. We also used graphical results to check for homoscedasticity of residuals and to ensure that outlying points weren't driving or masking trends. Based on these checks, we decided to exclude one tree from the late wet-season Ψ_{stem} model for *Q. lobata* and two trees from the δ^{13}C model for *Q. lobata*.

For each final model, we retained terms that were consistently included across top models and were consistent with graphical results. When random effects explained no variance, we removed them from the final model. We used maximum likelihood to fit full models for comparison via AICc, but fit top candidate models and final models with random effects using restricted maximum likelihood estimation.

In addition, we tested whether SLA and leaf N content were correlated with each other, and with root crown elevation and DBH, using Kendall's τ. We also compared values for SLA and leaf N content across flow conditions using Kruskal-Wallis rank sum tests. We performed all analyses using R statistical software version 3.5.0 (R Core Team 2018). We fit mixed effects models with the lme4 package (Bates et al. 2015), derived estimated *p*-values for mixed effects models with the lmerTest package (Kuznetsova et al. 2017), and constructed graphs and confidence intervals for regression results using the effects package (Fox and Weisberg 2018). We used the MuMIn package (Bartoń 2018) to construct and compare candidate models, and to estimate the variance explained by fixed and random effects in mixed models.

Results

Dry-season Ψ_{stem}

Midday Ψ_{stem} measurements for *Q. lobata* at the end of the dry season ranged from −3.5 to −1.4 MPa in 2014 and from

−3.6 to −1.0 MPa in 2015, while those for *F. latifolia* in 2015 had a wider range, from −5.7 to −0.8 MPa. See Table S1 for full ranges of all measured variables. For both species, the final models predicting dry-season Ψ_{stem} (Table 2) included a highly significant interaction between dry-season flow and root crown elevation (*Q. lobata* estimated $p = 0.008$ and *F. latifolia* $p < 0.001$). At low root crown elevations, Ψ_{stem} measurements were substantially greater when the stream was flowing, indicating less water stress in trees growing along streams with dry-season flow; however, at high root crown elevations, Ψ_{stem} measurements were not significantly different for trees located along flowing and dry streams (Fig. 2, a and b). For *F. latifolia*, the negative relationship between Ψ_{stem} and root crown elevation was very similar for trees along moist and flowing streams, but the trees along flowing streams were less stressed relative to those along moist streams (Fig. 2b). Along dry streams, root crown elevation had a weak negative relationship to Ψ_{stem} for *Q. lobata* (Fig. 2a), but the relationship was positive for *F. latifolia*, indicating that trees along dry streams with low banks were actually more stressed than those along incised, dry streams (Fig. 2b).

DBH was also an important predictor of dry-season Ψ_{stem} for *Q. lobata*, and showed a highly significant ($p = 0.001$) interaction with dry-season flow (Fig. 2c). Larger *Q. lobata* trees were generally less stressed than smaller trees, and this trend was greater for trees growing along dry streams than for those growing along flowing streams. While stream flow had a substantial influence on the Ψ_{stem} of small trees, the Ψ_{stem} of the largest trees—those with a DBH greater than about 75 cm—was not strongly influenced by stream flow.

Both species exhibited strong relationships between Ψ_{stem} and atmospheric variables, but not the same ones. For *Q. lobata*, Ψ_{stem} was negatively related to temperature ($p < 0.001$), while for *F. latifolia*, Ψ_{stem} was negatively related to ET_o ($p < 0.001$). Temperature and VPD, which were almost perfectly correlated, had nearly the same effect on Ψ_{stem} for *Q. lobata*, and the same was true of ET_o and solar radiation for *F. latifolia*. *Quercus lobata* Ψ_{stem} showed no strong relationship to ET_o or solar radiation, and *F. latifolia* Ψ_{stem} showed no strong relationship to temperature or VPD. The final model predicting dry-season Ψ_{stem} for *Q. lobata* also included a strong effect of year (estimated $p < 0.001$), showing that trees were typically less stressed in 2015. This full model explained approximately 80% of the variance, with fixed effects explaining approximately 75% of the variance. For *F. latifolia*, the adjusted R^2 value for final model was 0.79.

Wet-season Ψ_{stem}

When all streams were flowing in late spring, Ψ_{stem} measurements for *Q. lobata* ranged from −1.8 to −0.3 MPa. At this time, Ψ_{stem} showed a strong negative relationship with root crown elevation along narrow streams, but not along wider streams (Fig. 3a), with an estimated *p* value of 0.02 for this interaction. The final model (Table 2) also included a positive relationship between Ψ_{stem} and the log distance of the tree from the bank's edge (estimated $p < 0.001$), showing that trees close to the edge were more stressed (Fig. 3b). Temperature and the number of days since the last rainfall were both negatively related to Ψ_{stem} (estimated $p = 0.003$ and $p = 0.09$, respectively). Fixed effects in this model explained approximately 73% of the variance, while the full model explained approximately 77% of the variance.

∂^{13}C and leaf properties

We found a considerable range of values for ∂^{13}C in both species: −31.8 to −28.3 for *Q. lobata* and − 32.3 to −27.4 for *F. latifolia*. For both species, ∂^{13}C had a strong negative relationship with SLA (Fig. 4, a and c; $p < 0.001$) and a weak positive relationship with DBH (Fig. 4, b and d; $p = 0.008$ for *F. latifolia* and $p = 0.03$ for *Q. lobata*). For *Q. lobata*, ∂^{13}C was also negatively related to nitrogen content (Fig. 4e; $p = 0.002$), and was lower in trees growing along streams that had been flowing the previous summer (Fig. 4f; $p = 0.04$). Adjusted R^2 values for final models (Table 2) were 0.61 for *Q. lobata* and 0.42 for *F. latifolia*.

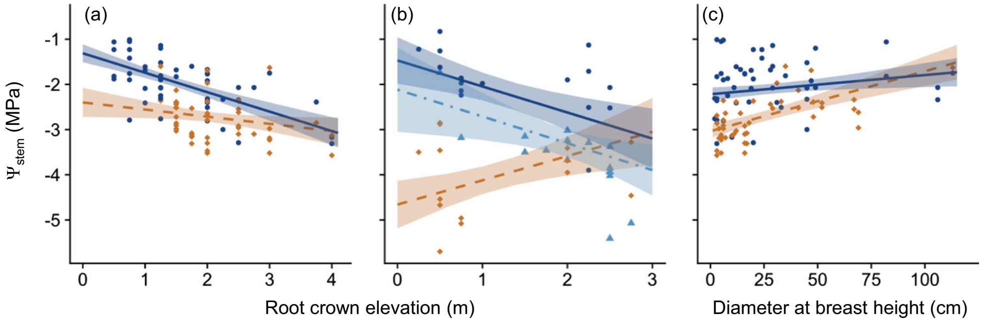

Fig. 2 Response of dry-season stem water potential (Ψ_{stem}) to interactions between (**a**, **b**) stream flow and the elevation of the tree's root crown above the thalweg of the stream and (**c**) stream flow and diameter at breast height (DBH) for (**a**, **c**) *Q. lobata* individuals and (**b**) *F. latifolia* individuals. The results for *Q. lobata* include data collected for the same individuals in both 2014 and 2015. There was no clear relationship between Ψ_{stem} and DBH for *F. latifolia*, so this graph is not shown

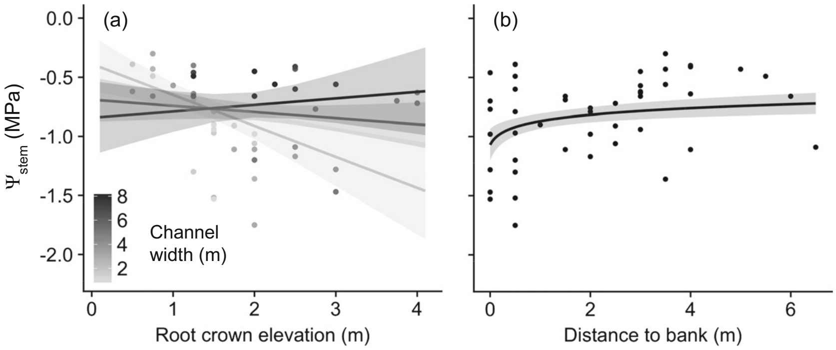

Fig. 3 Late wet-season Ψ_{stem} for *Q. lobata* individuals as a function of (**a**) the interaction between channel width and the elevation of the tree's root crown above the thalweg of the stream and (**b**) the distance of the tree's root crown to the edge of the bank

Leaf N content by mass and SLA were not significantly correlated with each other in either species, and neither species showed significant relationships between SLA and root crown elevation or the previous season's stream flow status. SLA was negatively correlated with DBH in both species ($\tau = -0.22$, $p = 0.04$ for *Q. lobata*; $\tau = -0.26$, $p = 0.01$ for *F. latifolia*).

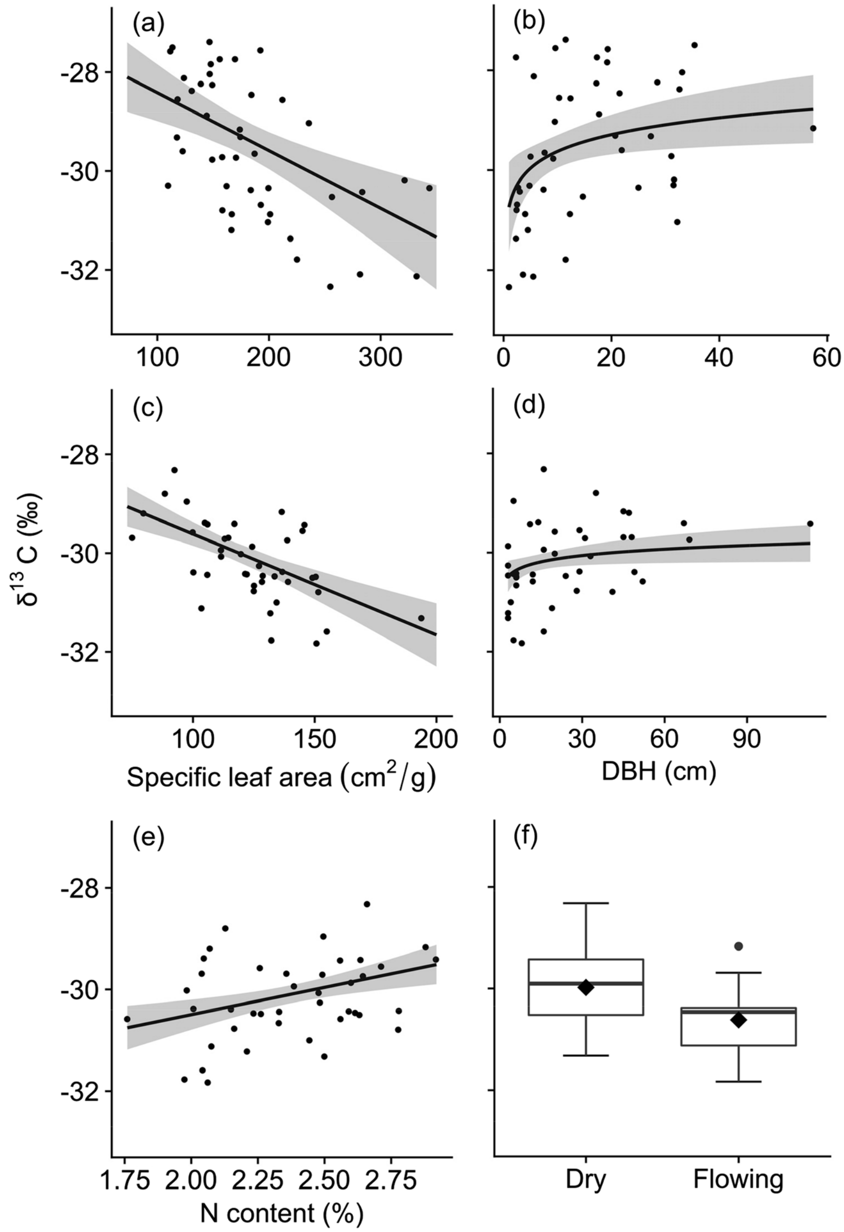

Fig. 4 Relationship between ∂^{13}C in leaf tissues and predictors included in the final models for (**a**, **b**) *F. latifolia* individuals and (**c**–**f**) *Q. lobata* individuals, with regression lines and 95% confidence intervals plotted for all continuous variables. Trends for DBH were stable when the largest tree was removed from the model for both species. For plot **f**, boxes show median values bounded by 1st and 3rd quartile values, with whiskers extending to the smallest and largest values at most 1.5 times the interquartile range; diamonds show mean values

Leaf N content was not significantly related to DBH in either species, nor with root crown elevation or flow for *F. latifolia*. However, we did observe significantly higher ($p = 0.004$) leaf N content in *Q. lobata* trees growing along streams that had been dry the previous summer, as well as a significant positive correlation ($\tau = 0.30$, $p = 0.007$) between root crown elevation and leaf N content in this species.

Discussion

Our results show that altered urban hydrology can have substantial effects on riparian trees in a Mediterranean climate. As hypothesized, the two contrasting consequences of urbanization we studied—dry-season flow subsidies and stream channel incision—interacted to affect the dry-season water status of streamside trees. For both of our study species, the presence of dry-season flow was associated with a marked decrease in water stress for trees growing along streams that were not incised, but increasing channel incision reduced the influence of these water subsidies to the point that trees growing at high levels of incision were highly stressed regardless of flow. Springtime Ψ_{stem} measurements show that channel incision can also cause chronically higher water stress in these trees. Thus, urban design and management decisions that affect the magnitude of both dry-season base flows and wet-season storm flows associated with channel incision can influence the growth and health of riparian trees.

Channel incision interacts with stream flow to affect late dry-season Ψ_{stem}

Along streams that were flowing at the end of the dry season, *Q. lobata* and *F. latifolia* responded remarkably similarly to channel incision. Trees with low root crown elevations showed values of Ψ_{stem} around −1.5 MPa, whereas at high levels of incision, models for both species predicted values of Ψ_{stem} closer to −3 MPa, suggesting substantial stress (Shackel and Gross 2002; Swift et al. 2008). In fact, our measurements of Ψ_{stem} for *Q. lobata* along highly incised streams were on average even lower than those for *Q. lobata* trees growing in an upland context (Knops and Koenig 1994, 2000). Crous et al. (2012) also found that increasing elevation above the channel of a flowing stream corresponded to lowered water potentials in riparian trees.

Along dry streams, in contrast, channel incision had no marked effect on late dry-season Ψ_{stem} for *Q. lobata* and actually showed a positive relationship with Ψ_{stem} in *F. latifolia*, indicating greater stress at lower levels of incision. This positive trend was driven by the extremely low Ψ_{stem} values for *F. latifolia* trees growing along dry streams with low banks, which may be related to recent changes in stream flow. Our field surveys show that these stream reaches received at least some flow the previous summer, and given that our sampling occurred during the height of a multiyear drought, it is likely that they were flowing in past non-drought summers as well. Thus, the trees along these unincised streams may never have experienced very low levels of soil moisture, leading them to respond particularly severely to the lack of stream flow in 2015. Conversely, trees along incised streams may have developed more drought-tolerant morphological and physiological characteristics, such as greater root-to-shoot ratios and root depth, in response to chronic water shortage (Brunner et al. 2015).

Dry-season flow substantially reduced water stress in smaller *Q. lobata* trees, while large trees were generally unaffected and were less stressed overall. This result may indicate differential access to groundwater (Dawson and Ehleringer 1991; Dawson 1996), although the very deep water tables in some parts of this region may be beyond the reach of even the largest trees. Large trees might also benefit from more extensive shallow root systems. There was no differential effect of tree size on Ψ_{stem} in *F. latifolia*, suggesting that this species is similarly sensitive to dry-season stream flow and channel incision as it matures, possibly reflecting its lack of taproots to access groundwater. The smaller stature of mature *F. latifolia* trees and the paucity of very large individuals in our study sites may also have contributed to this result.

The extremely low water potentials we measured in some *F. latifolia* trees suggest that *F. latifolia* may be more susceptible to drought stress than *Q. lobata*. In addition to *F. latifolia*'s lack of taproots, its generally greater SLA could make it more sensitive to low-moisture conditions. Lower midday Ψ_{stem} values for *F. latifolia* could also indicate that it has a less conservative stomatal response to high xylem tension than *Q. lobata*. This conjecture is supported by our finding that Ψ_{stem} in *F. latifolia* was much more strongly related to ET_o—reference evapotranspiration measured under well-watered conditions—and levels of solar radiation than it was to temperature and VPD. Tree species show a range of stomatal responses to reductions in water potential, varying from the early use of stomatal closure to maintain high leaf water potential to the continuation of gas exchange at relatively low leaf water potential (Klein 2014), and *F. latifolia* may tend more toward the latter strategy than *Q. lobata*. While we are unaware of any studies that have investigated embolism resistance in *F. latifolia*, the lowest Ψ_{stem} values we measured likely indicate a serious loss of hydraulic conductivity (Choat et al. 2012).

Effects of channel incision are present in the late wet season

In the late wet season, *Q. lobata*'s water status appears to reflect conditions in the upper soil layers that affect its shallow roots, as trees of all sizes were responsive to the number of days since the last precipitation event in addition to channel incision. We found that the effect of root crown elevation was reduced on wider streams, possibly reflecting the lower degree of entrenchment—for streams with the same bank height, overbank flooding would be more likely on wider streams carrying more water. Counterintuitively, we found that trees growing very close to the stream channel were generally more stressed. Such close proximity to the channel may have caused root damage or general constraints to root growth that impacted their water status. However, neither this effect of distance nor the effect of channel width were corroborated by the results for $\partial^{13}C$. These factors may thus have become important after leaves had matured, or were more marked when we sampled in 2015 at the height of the drought than after a wetter winter in 2016.

$\partial^{13}C$ signatures primarily reflect leaf characteristics

The strongest predictor of $\partial^{13}C$ for both species was SLA, and this relationship may reflect both causal and non-causal factors (Damesin et al. 1997). Low SLA (thicker or denser leaves) has been associated with reduced mesophyll conductance of CO_2, which reduces discrimination against $^{13}CO_2$ at the site of carboxylation and leads to higher values of $\partial^{13}C$ (Vitousek et al. 1990; Kogami et al. 2001; Gerdol et al. 2018). In addition, both $\partial^{13}C$ and SLA can be affected by tree size, position in the canopy, and the structure of the surrounding forest in ways that tend to negatively covary. Larger trees generally have higher $\partial^{13}C$ values and lower SLA, in part due to increased hydraulic constraints with greater branch length (Chaves et al. 2004; McDowell et al. 2011), and this effect of tree size was reflected in the small positive relationship we found between $\partial^{13}C$ and DBH in both species, as well as the negative correlation between SLA and DBH. In addition, when atmospheric mixing is low, $\partial^{13}C$ values lower in the canopy can be reduced due to refixation of respired CO_2 already depleted in ^{13}C compared to the ambient air, and these lower-canopy leaves are likely to also have greater SLA due to low irradiance (Broadmeadow and Griffiths 1993). The wide ranges of values we found for $\partial^{13}C$ and SLA are likely linked to these sources of variation, as our study included trees of varying sizes situated in riparian forests with differing structures and extents. We were able to account for much of this variation by including SLA in the models predicting $\partial^{13}C$.

Counter to our predictions, though, we did not detect a direct influence of channel incision on leaf $\partial^{13}C$ values for either species. For *F. latifolia*, we found no relationship between $\partial^{13}C$ and root crown elevation or flow. If, as we have conjectured, *F. latifolia* does not respond strongly to water stress with stomatal closure, conditions during the dry season may not have greatly affected the $\partial^{13}C$ signature of its stored carbohydrates. Furthermore, leaves of deciduous trees can start photosynthesizing early in their development (Hoch et al. 2003), potentially masking the signal of the carbohydrate reserves mobilized in their initial creation. Conversely, we found that $\partial^{13}C$ values in *Q. lobata* were lower in trees located along streams that had been flowing the previous dry season, suggesting a perceptible contribution of stored carbohydrates and a stronger effect of flow than channel incision during the previous dry season. Although incision had a strong effect when we measured Ψ_{stem} at midday, stream flow may have had a greater impact on the trees' overall water status by allowing them to rehydrate overnight. Safety concerns prevented us from measuring predawn Ψ to test this hypothesis.

The highly significant positive correlation we found between root crown elevation and leaf N content in *Q. lobata* suggests that incision contributed to WUE indirectly via its influence on photosynthetic capacity, as leaf N content was positively linked to $\partial^{13}C$ in this species. Higher leaf N content may also reflect an investment in thicker cell walls, which could aid leaves in withstanding strong drought stress (Onoda et al. 2017). Other tree species have been shown to respond to drought stress with increased leaf N content (Weih et al. 2011). We found no relationship between leaf N content and $\partial^{13}C$ in *F. latifolia*, and results from other studies also point to N content having variable importance in predicting $\partial^{13}C$ (Sparks and Ehleringer 1997; Damesin et al. 1997; Hoffmann et al. 2005; Sun et al. 2016; Gatica et al. 2017).

For both species, differences in $\partial^{13}C$ likely also reflect environmental and structural factors that we did not capture, such as differences in soil properties and root architecture. The negligible explanatory power of study site in our models suggests that differences at the level of the individual tree account for more of the unexplained variation. This finding may be due to microscale variation in topography and soils in riparian zones, which can create heterogeneous patterns of water availability within small areas (Naiman et al. 2005; Duncan et al. 2013). Individual trees growing in close proximity may therefore experience different levels and durations of water stress despite similar metrics of stream flow and incision, as well as exposure to the same precipitation and temperature regimes. There may also be a genetic component influencing $\partial^{13}C$ (Cernusak et al. 2013).

Consequences for tree growth and riparian ecosystems

Our results suggest that dry-season stream flow due to urban water subsidies can markedly alleviate water stress in riparian trees, potentially increasing tree growth, productivity, and carbon storage beyond pre-development rates. Other studies have linked riparian tree growth to the amount and permanence of stream flow in water-limited environments (Stromberg and Patten 1990; Stromberg 2001). However, channel incision caused by the absence of effective stormwater management can limit the influence of dry-season flow and contribute to high and possibly damaging levels of water stress. Many of the dry-season water potentials we measured for trees growing along incised streams were indicative of extreme water stress that could lead to a loss of hydraulic conductivity (Swift et al. 2008; Choat et al. 2012). Ring-porous species like *Q. lobata* and *F. latifolia* also tend to show a dramatic reduction in gas exchange, and thus carbon assimilation, when leaf water potentials reach −3 MPa (Klein 2014), which was common for both species along incised streams in the dry season. Channel incision was also associated with lower water potentials in the late wet season along smaller streams, suggesting a persistent impact over the course of the summer. However, the ∂^{13}C values we measured are characteristic of mesic conditions (Stewart et al. 1995), showing that these trees avoid some consequences of the annual Mediterranean summer drought period by putting on new growth when water is generally plentiful in the spring. In places like Sacramento that have highly variable annual precipitation, channel incision and flow subsidies could have particularly strong effects on growth in years with low rainfall.

For this study, we necessarily chose facultative riparian species that can grow across a range of flow and channel conditions. Even in these relatively tolerant and adaptable trees, we found sizeable influences of both dry-season flow and channel incision. For riparian trees with greater moisture requirements, the low water availability along dry and incised streams is likely to be too severe. Wetland-associated trees were found to be far less common along incised streams in Sacramento, and may require dry-season stream flow to regenerate, while drought-tolerant upland species appear to benefit competitively along deeply incised streams (Solins and Cadenasso 2019). Thus, water management practices could alter not only the productivity of urban riparian forests, but also their composition, influencing ecosystem services such as nutrient cycling, habitat value, and carbon storage.

In water-scarce regions, urban water conservation measures such as limitations on landscape irrigation are becoming increasingly common, and may have unintended consequences for riparian trees by reducing dry-season flow subsidies. Flow cessation could be particularly problematic for riparian trees where unincised streams have been flowing perennially for years, allowing riparian trees to mature without experiencing intense summer water shortages. While a return to intermittency in these streams could be viewed as a desirable measure toward restoring pre-development riparian ecosystem function, the maintenance of perennial flows could also be beneficial from a broader restoration perspective. Runoff-derived urban stream flows offer the opportunity to foster the higher levels of primary productivity typically found in riparian forests along perennial streams and rivers in California (Holstein 1984), which have largely been lost (Katibah 1984).

The benefits of runoff-boosted riparian productivity need to be weighed against the potential for urban water subsidies to promote the invasion of nonnative species. However, nonnative woody plants appear to respond more strongly to channel incision than the presence of dry-season stream flow in Sacramento (Solins and Cadenasso 2019). In general, dry-season stream flow subsidies become less consequential for riparian trees as channel incision increases, and channel incision is a challenging problem to address. Restoring incised streams in urban environments tends to be expensive and disruptive, and is generally only effective in the long term when accompanied by effective stormwater management throughout the upstream watershed (Bernhardt and Palmer 2007). As a potential compromise where such restoration is impracticable, municipalities could prioritize water conservation in areas draining to streams that are already incised, and thus unlikely to provide ample water subsidies for riparian trees regardless of dry-season flow subsidies, while prioritizing the maintenance of good stormwater management practices in areas where incision can still be prevented.

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