Species-specific plant water status responses to land surface temperature vary across three cities with different precipitation patterns

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Abstract

As urbanization intensifies and global climate warms, people are exposed to high urban temperatures. Mature trees can reduce human exposure to extreme heat; however, urban forests also experience hot temperatures that may affect their physiological function. To investigate how urban heat, specifically land surface temperature (LST), vapor pressure deficit (VPD), and city-level precipitation regimes affect tree function, we measured stem water potential and stomatal conductance on street trees (eight species) in three U.S. cities with comparable annual temperatures but different precipitation profiles; Sacramento,

CA, Raleigh, NC, and New Orleans, LA. LST negatively affected water potential and stomatal conductance in Sacramento, and only for certain species, with these effects shifting across the growing season: early-season trees showed larger declines in stem water potential under heat without restricting stomatal conductance, while late-season trees restricted conductance sharply under heat and maintained stable water potential. Neither Raleigh nor New Orleans showed comparable heat effects on stem water potential, though a few species in Raleigh showed a positive stomatal conductance response to LST. VPD was linked to both water potential and stomatal conductance, though the direction and strength of these responses varied by species. Species differed considerably in their sensitivity: *U. parvifolia* showed no heat effects in any city, while *P. calleryana* was the most heat- and drought-sensitive species. Our findings linking tree physiological function to urban heat exposure can inform urban planning decisions on species selection and tree placement in the context of increasingly warm and dry urban climates.

Introduction

As heatwaves intensify due to climate change (Meehl and Tebaldi 2004) and urban development (Ward et al. 2016), residents experience increased risk of mortality (García-Herrera et al. 2010, Zhao et al. 2021). Individual trees can reduce local land surface temperatures by up to 6°C (Ossola et al. 2021), providing critical cooling in urban heat islands (Ballinas and Barradas 2016, Jato-Espino 2025), but face physiological stress under high heat and limited water availability (Tabassum et al. 2021). Urban forest canopies worldwide are dominated by a few cosmopolitan species planted across vastly different climatic zones (Ossola et al. 2020). Species such as *Ginkgo biloba*, *Acer rubrum*, and *Pyrus calleryana* occur in cities ranging from arid to humid climates, yet whether they can maintain physiological function across such diverse conditions remains largely untested.

If precipitation is the main water source for mature urban trees (Mincey and Vogt 2014), the mismatch between species distributions and local climate suitability creates critical uncertainty about urban forest resilience under climate change (Cunha et al. 2025, Esperon-Rodriguez et al. 2025). The effects of heat

and drought vary by species, with physiological function driven by the interplay between vapor pressure deficit (VPD) and soil water availability (Novick et al. 2022, Torres-Ruiz et al. 2024). When soil water availability is sufficient to meet atmospheric demand, trees in warmer conditions can maintain open stomata, supporting elevated photosynthesis, growth, and ecosystem services such as cooling (Kumarathunge et al. 2019). However, open stomata lose water via evapotranspiration at rates that increase with VPD, creating water stress when atmospheric demand outpaces soil water supply (Grossiord et al. 2020). Under such conditions—whether from high VPD, limited soil water, or both—plants close their stomata, reducing associated ecosystem services (Grossiord et al. 2020). While the individual effects of temperature and water availability on tree physiology are well established in natural and agricultural systems, field-based assessments of how their interaction affects mature urban trees across contrasting precipitation regimes and the multifaceted abiotic conditions that characterize urban environments are limited. Baseline measurements of urban tree water stress are absent across diverse climates and pavement conditions and physiological thresholds for most urban species are uncharacterized.

Existing mature trees planted across urban heat gradients offer an opportunity to determine how temperature affects diverse tree species in situ (Dale and Frank 2014). Cities experiencing extreme heat and aridity may reveal which species possess mechanisms to maintain function as climate change intensifies, while wetter cities provide contrasts to test whether adequate precipitation buffers trees from heat stress. However, confounding urban variables such as soil compaction or imperviousness around planting sites can alter infiltration and root growth, potentially preventing trees from accessing water even in high-precipitation cities (Day and Bassuk 1994, Kozlowski 1999, Rahman et al. 2011). Previous research has addressed tree responses to climate change through experimental manipulations (Marchin et al. 2020, Meineke and Frank 2018), climatic niche models (Kendal et al. 2018), and urban-rural comparisons (Pretzsch et al. 2017, Smith et al. 2019). While informative, these approaches cannot capture how widely planted species perform under real urban conditions across contrasting climates, a critical gap for predicting which trees will sustain ecosystem services as cities warm.

The goal of this study is to test whether commonly planted urban tree species maintain physiological function across land surface temperature (LST) gradients in three cities with contrasting precipitation regimes, and to identify the role of LST and VPD in regulating tree water status. Specifically, we asked: 1) Do effects of urban heat on tree function vary across cities with diverse precipitation regimes? and 2) Does vapor pressure deficit (VPD) predict tree hydration status in urban systems? Beyond these two questions, we tentatively explored the relationship between city-level precipitation and tree hydration status, acknowledging that inter-annual variation in sampling may confound cross-city comparisons. We measured stem water potential and stomatal conductance as indicators of tree water status. We expected trees in the hottest locations to display lower stem water potential and stomatal conductance, with this effect most pronounced in the driest city (Rivera et al. 2017). Because focal species differ in their native niches, we expected them to respond differently to urban heat gradients (Rahman et al. 2014, 2024), though we had no a priori predictions about which would maintain function in warmer areas. Our study contributes empirical evidence on how changing environmental conditions affect urban tree physiology, with the aim of identifying which common species might persist and function as heat islands intensify.

Materials and Methods

Study site and tree selection:

This study was conducted in Sacramento, California (38.5816° N, 121.4944° W), Raleigh, North Carolina (35.7796° N, 78.6382° W) and New Orleans, Louisiana (29.9509° N, 90.0758° W), USA. We chose these cities because of their similar thermal regimes, but contrasting precipitation patterns (Appendix 1; Figure S1), and because each city hosts five of the most common street tree species planted globally (Ossola et al. 2020). To guide tree selection and quantify patterns of urban warming in each city, we mapped LST from 2014 - 2022 using LANDSAT C2 U.S. Analysis Ready Data (ARD) (Figure 1; U.S. Geological Survey, 2023) (Appendix 1; Text S1).

We obtained the most current urban tree inventories from the urban foresters of Sacramento, Raleigh, and

New Orleans from the year 2021. We then chose five tree species shared among the three cities; Southern magnolia (*Magnolia grandiflora*), Red maple (*Acer rubrum*), Callery pear (*Pyrus calleryana*), Chinese elm (*Ulmus parvifolia*) and Mulberry (*Morus alba*), as well as trees that only occur in each city; London plane (*Platanus* × *hispanica*) in Sacramento, Willow oak (*Quercus phellos*) in Raleigh, and Southern live oak (*Quercus virginiana*) in New Orleans.

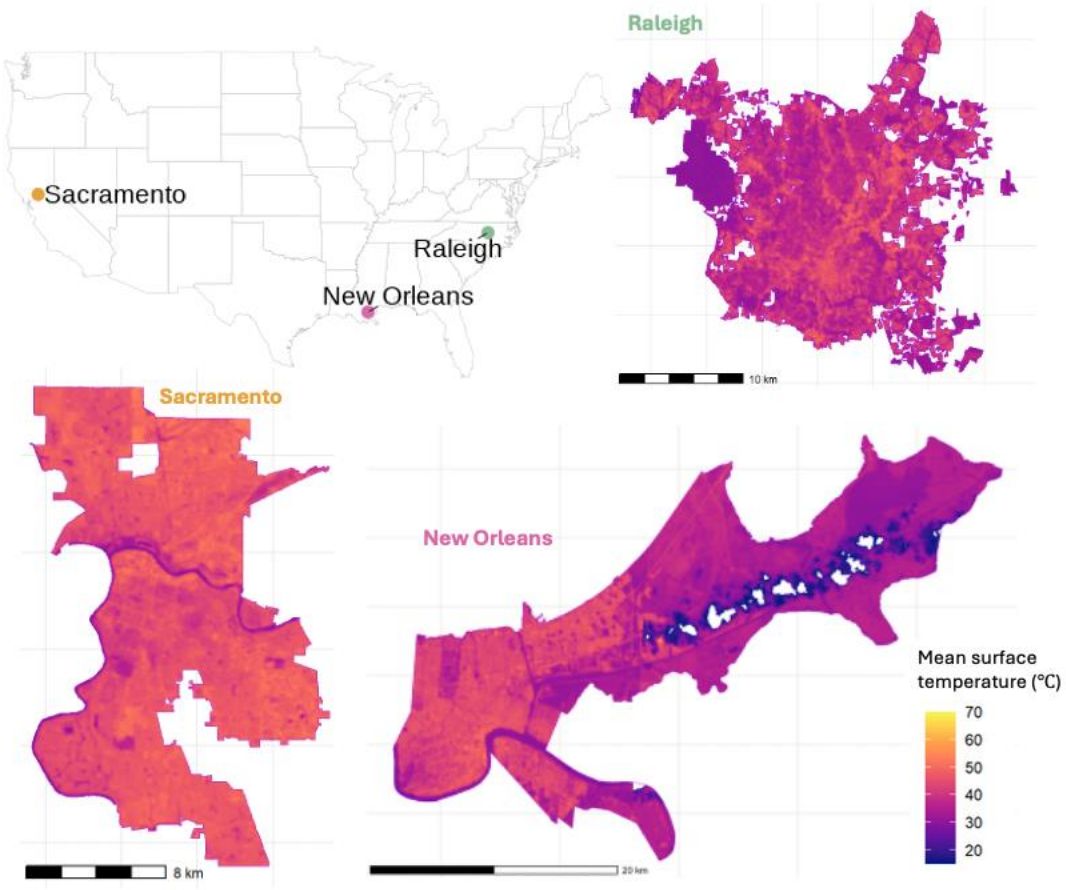

Figure 1. **LST gradient in focal cities**. The focal cities of Sacramento, Raleigh and New Orleans overlaid with mean LST from June – September in the years 2014-2022. Lighter yellow colors represent warmer areas, and purple colors represent cooler areas. LST values were obtained from LANDSAT C2 U.S. Analysis Ready Data (ARD) (U.S. Geological Survey, 2023).

Figure 1 (Land surface temperature gradient in focal cities): Alt text: *Three side-by-side maps of Sacramento, Raleigh, and New Orleans, each colored on a yellow-to-purple gradient showing summer LST, with lighter yellow areas indicating hotter zones and darker purple areas indicating cooler zones across each city.*

From the tree inventories provided by the cities, we selected trees that measured 10-75 cm Diameter at Breast Height (DBH), avoiding damaged or heavily pruned trees and saplings. To assign a mean LST to each individual tree, we overlaid the tree inventories with the LST maps described above. Within our DBH range, we selected trees at random prior to fieldwork, resulting in a sample of trees with land LST 33.69-49.7 °C. We sampled a total of 340 trees across Sacramento (n=113), Raleigh (n=120), and New Orleans (n=107). For selected trees, we took our own measurement of DBH and height as an indicator of tree size. Because many trees in Sacramento might be watered directly or indirectly, we recorded which trees were potentially being watered by noting which trees were growing amongst green grass. Most precipitation in Sacramento falls in winter, such that green grass in summer might indicate anthropogenic water input.

Measurement of tree physiological variables:

Tree hydration and function are often understood through measures of stem water potential (MPa) and stomatal conductance (gs; mmol m^{-2} s^{-1}). Stem water potential is a direct measurement of tree hydration, such that trees with lower stem water potential are less hydrated (Shackel et al. 2021). Stomatal conductance is a measure of water loss from stomata opening (Horton and Hart 1998). We measured stem water potential and stomatal conductance during the summer between June 28th and August 11th of 2023 in Sacramento, between June 5th and July 11th of 2024 in Raleigh, and between August 14th and September 17th of 2024 in New Orleans. Sampling dates varied among cities due to logistical constraints of coordinating fieldwork across three distant sites, though all measurements were taken during periods of high regional temperatures. Following sampling methods from Meineke and Frank (2018), we clipped branches from the lower outer canopy of each tree, with one branch from each cardinal direction, between 11:00 and 14:00 to measure midday stomatal conductance and stem water potential.

To measure stomatal conductance, we used a porometer Li-600 (LI-COR, Lincoln, NE, USA). We chose the auto light adapted setting and surveyed the leaves under ambient conditions after the instrument was

stable. When possible, we measured stomatal activity (mmol m^{-2} s^{-1}) for all cardinal directions choosing two leaves per direction (eight leaves per tree). We measured midday stem water potential (Ψ_{MD}) on 1-3 mm diameter branches using a portable pressure chamber Model 615 D (PMS Instrument Company, Albany, OR, USA). For all tree species except *M. grandiflora* and *Platanus* × *hispanica* we clipped the lateral branches at the stem base and pressurized them. Due to the size of the branches in *M. grandiflora* and *Platanus* × *hispanica,* we clipped individual leaves to pressurize, thus the measurements from these two species correspond to leaf water potential. It is important to note that water potential is measured in negative numbers and lower numbers (far from zero) imply lower water hydration.

Additional variables:

For each collection day, we extracted precipitation (in), minimum and maximum air temperature (°C) from NOAA (2023 and 2024 Global Historical Climatology Network - Daily), and vapor pressure deficit (VPD), measured as vpdmax (hPa), from PRISM Climate Group (Oregon State University, http://prism.oregonstate.edu, [accessed January 30th, 2025]). We quantified imperviousness as the percentage of impervious surface surrounding each tree within its individually estimated catchment area (Appendix 1; Text S2) (Willaredt et al. 2026). For example, park trees had imperviousness values near 0%, while street trees in paved tree pits had values approaching 100% (Appendix 1; Figure S2).

Statistical analysis:

We analyzed our data in R Studio (Version 2024.04.1) (Posit Team 2025), R version 4.4.0 (R Core Team, 2015). Before running regression models, we examined variance inflation factors (VIF) and Pearson correlations among predictors and excluded any with correlation coefficients $|r| \geq 0.3$ (Appendix 1; Figure S3).

For the models including all three cities and city-specific models below, we built Bayesian Regression Models using Stan in the *brms* package (v2. 14.4; Bürkner, 2017). To determine if a variable is a predictor of stem water potential or stomatal conductance, we identified parameters with 95% credible intervals

that did not overlap zero. Credible intervals are used in Bayesian statistics as the 95% probability that the true estimate lies within the interval, given the observed data (Hespanhol et al. 2019). To improve model convergence, we z-score scaled numerical predictors and stem water potential. For model structure, prior specifications and sampling parameters, see supplemental methods (Appendix 1; Text S3).

LST models: We built separate Bayesian mixed-effects models for each city and each response variable (water potential and stomatal conductance), resulting in six models total. All models included mean LST, day of the year (Julian day), tree species, DBH, direction of the measurement, and an interaction between Julian day and mean LST, with tree identity included as a random effect. New Orleans models additionally included precipitation. For Sacramento, we included a binary variable indicating whether trees were likely to have received irrigation, inferred from the presence of green vegetation growing around the base of the tree. Urban foresters in Raleigh and New Orleans indicated that mature street trees in those cities are unlikely to receive irrigation, so this variable was not included in their models.

For model interpretation, we estimated marginal trends for the effect of mean LST on each response variable for each tree species (emtrends), and marginal mean values of each response variable per species and, where applicable, per irrigation status (emmeans). These estimated values represent predicted means or trends for the described metrics when all other covariates were held constant. We calculated the estimated marginal means (emmeans), marginal trends (emtrends), and further pairwise comparisons (pairs) in the *emmeans* package (Lenth 2025).

Further, to examine differences in stem water potential and stomatal conductance among cities, we built a Bayesian regression model for each response variable including mean LST, tree species, and city as fixed effects, with tree identity as a random effect. Day of the year and year of sampling were correlated with city identity and were therefore excluded from these models. These cross-city comparisons should be interpreted with caution, as trees were sampled in different years across cities, making it impossible to

fully disentangle the effects of city from those of year.

VPD model: To examine differences in stem water potential based on daily VPD values, we built a regression model that included DBH, VPD, and species as predictors, and an interaction of species and VPD (to test whether the slope of the VPD-water potential relationship varies among species). We excluded city, year, and day of the year from this model because these variables are confounded with each other in our sampling design. Despite these potential confounding variables, this model provides a high-level assessment of potential relationships between tree hydration and VPD in trees experiencing a range of on-the-ground conditions.

Results

Prior to model fitting, we assessed multicollinearity among predictors separately for each city using Pearson correlations and variance inflation factors (VIF). In all three cities, impervious surface cover was correlated with mean LST ($r = 0.31–0.38$) and was therefore excluded. In Sacramento, minimum temperature was also excluded due to correlations with day of the year ($r = 0.30$) and maximum air temperature ($r = 0.73$), and maximum air temperature was subsequently excluded as well. In New Orleans and Raleigh, both maximum and minimum air temperature were excluded due to correlations with day of the year ($|r| = 0.53–0.69$) and with each other ($r = 0.57$ and 0.76, respectively). In Raleigh, precipitation was additionally excluded due to its correlation with day of the year ($r = 0.41$), and to a lesser extent with minimum temperature ($r = 0.35$) (Appendix 1; Figure S3). Precipitation was excluded from Sacramento as no rainfall occurred during the sampling period. Final models retained mean LST and day of the year in all cities, with New Orleans additionally including precipitation.

Results reported in the main text are constrained to predictors with 95% credible intervals that did not cross zero. Throughout our results, we report the raw beta estimates from the regression coefficients ± standard error and 95% credible intervals (CI) for model outputs. Appendix 2 includes unscaled (original units) outputs from the regression models, estimated marginal means and trends, and pairwise

comparisons.

Do effects of urban heat on tree function vary across cities with diverse precipitation regimes?

In Sacramento, LST had no credible effect on stem water potential (β = -0.31 ± 0.27; 95% CI [-0.84, 0.23]). However, this effect was modulated by the day of the year (interaction β = 0.53 ± 0.24; 95% CI [0.05, 0.98]), such that the effect of LST on hydration became more negative earlier in the season and weakened as the season advanced. For stomatal conductance, LST likewise showed no credible main effect (β = -0.38 ± 0.20; 95% CI [-0.78, 0.02]), though the interval only narrowly included zero. This effect was modulated by day of year in the opposite direction (interaction β = -0.54 ± 0.17; 95% CI [-0.87, -0.20]), indicating that the negative effect of LST on stomatal conductance became more pronounced later in the growing season (Figure 2).

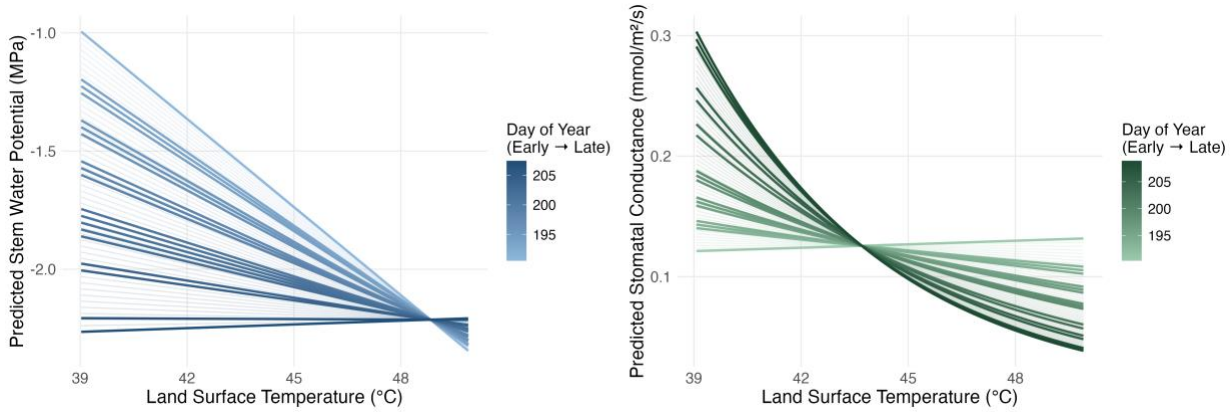

Figure 2**. Sacramento interaction between LST and day of the year for stem water potential and stomatal conductance**. Solid lines represent the days we measured trees, and light lines represent model predictions. Light blue/green lines represent days at the beginning of the measurement period and dark blue/green lines represent the last days of the measurements. Lines converge near the point where day-of-year has little influence on the outcome; away from this point, day-of-year effects diverge in opposite directions. The effect of LST on stem water potential weakens as the season progresses and the effect of LST on stomatal conductance becomes more pronounced as the season progresses.

Figure 2 (Sacramento LST and day interaction): Alt text: *Two line-plot panels for Sacramento showing predicted stem water potential and stomatal conductance across a range of LST, each with multiple overlaid lines colored on a light-to-dark blue or green gradient representing early to late days of the measurement season; the lines fan out from a shared crossing point, sloping in opposite directions further from that point, illustrating that the temperature effect weakens over the season for water potential and strengthens over the season for stomatal conductance.*

Regarding the effect of irrigation in Sacramento, stem water potential did not differ between irrigated and non-irrigated trees (irrigation $\beta = 0.42 \pm 0.33$; 95% CI [-0.22, 1.08]). However, irrigated trees maintained higher stomatal conductance as LST increased compared to non-irrigated trees (interaction $\beta = 0.52 \pm 0.20$; 95% CI [0.13, 0.91]) (Appendix 1; Figure S4). As LST increased by 1°C, stomatal conductance increased by approximately 4.3% in irrigated trees, but declined by approximately 10.8% in non-irrigated trees, indicating that irrigation might buffer trees against the reduction in stomatal conductance.

When examining species-specific responses to LST, only *P. calleryana* in Sacramento showed a credible decline in stem water potential with warming (emtrend = -0.36; 95% HPD [-0.71, 0.00]), corresponding to a decrease of approximately 0.05 MPa per 1°C increase in LST (Figure 3). No other species showed credible effects of LST on stem water potential in any city. For stomatal conductance, *Platanus x hispanica* in Sacramento showed a marginal negative response to LST (emtrend = -0.34; 95% HPD [-0.66, 0.01]). In Raleigh, both *M. alba* (emtrend = 0.30; 95% HPD [0.01, 0.59]) and *A. rubrum* (emtrend = 0.28; 95% HPD [0.01, 0.55]) showed credible positive responses to LST, corresponding to approximately 8% and 7.4% higher stomatal conductance per 1°C increase, respectively (Figure 3). No LST effects were detected for any species in New Orleans (Figure 3).

When comparing species, *P. calleryana* had consistently lower stem water potential than all other species in Sacramento. *M. grandiflora* and *M. alba* were the most hydrated species across all three cities. In Sacramento and Raleigh both species had significantly higher water potential than *A. rubrum* (estimates ranging from 0.75 to 0.81), and in Raleigh they also differed significantly from *P. calleryana*, *U. parvifolia*, and *Q. phellos*. In New Orleans, *M. alba* had higher water potential than *P. calleryana*, *U. parvifolia*, and *A. rubrum*, while *M. grandiflora* was better hydrated than *A. rubrum* and *Q. virginiana* (Appendix 2).

For stomatal conductance, *P. calleryana* showed consistently high stomatal conductance across cities, differing significantly from *M. grandiflora* and *A. rubrum* in Sacramento, and from all other species in

Raleigh. *A. rubrum* consistently showed the lowest stomatal conductance, differing significantly from multiple species in all three cities. In New Orleans, *M. grandiflora* and *A. rubrum* had the lowest stomatal conductance, both differing significantly from *M. alba* and *Q. virginiana* (Appendix 2).

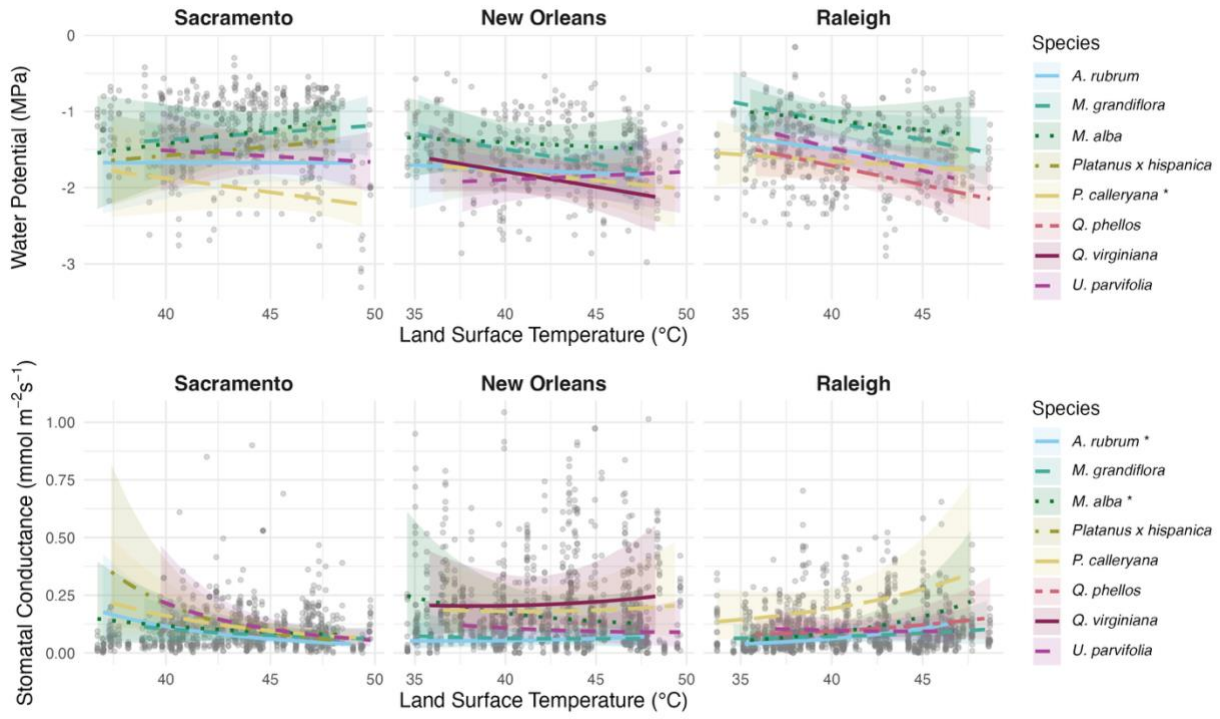

Figure 3. **Relationship between mean LST and stem water potential (top) and stomatal conductance (bottom) for eight urban tree species across Sacramento and New Orleans**. Lines represent model-predicted slopes from city-specific Bayesian mixed-effects models, with shaded ribbons indicating 95% highest posterior density intervals. Points show individual observations from the raw data. Asterisks (*) indicate species for which the 95% credible interval of the LST effect did not overlap zero. More negative water potential values indicate greater water stress, while lower stomatal conductance indicates more closed stomata.

Figure 3 (Species responses to LST): Alt text: *A two-row, two-column grid of scatter plots with fitted trend lines and shaded confidence ribbons, showing stem water potential (top row) and stomatal conductance (bottom row) plotted against LST for Sacramento (left column) and New Orleans (right column). Each panel contains eight differently colored and patterned lines, one per tree species, with raw data points scattered behind them.*

Does vapor pressure deficit (VPD) predict tree hydration status in urban systems?

Mean VPD during measurement days was 3.96 ±0.08 kPa in Sacramento (maximum: 6.28 kPa), 2.57 ±0.04 kPa in Raleigh (maximum: 3.72 kPa), and 1.99 ±0.06 kPa in New Orleans (maximum: 3.01 kPa).

VPD alone did not predict stem water potential in the model including all species and all cities (β −0.03 ± 0.06; 95% CI −0.15 − 0.08, R^2 0.40) but did predict stomatal conductance (β −0.31 ± 0.07; 95% CI −0.43 − −0.18, R^2 0.38). When examining the marginal trends, increased VPD had positive effects on *U. parvifolia* (emtrend 0.30, 95% CI 0.19 − 0.40), *M. grandiflora* (emtrend 0.27, 95% CI 0.17 − 0.36), *M. alba* (emtrend 0.25, 95% CI 0.14 − 0.35), *A. rubrum* (emtrend 0.13, 95% CI 0.04 − 0.23), and *Q. virginiana* water potential (emtrend 0.53, 95% CI 0.23 − 0.83), and a negative effect on *Q. phellos* (emtrend −0.53, 95% CI −0.83 − −0.22). This result indicates that as VPD increased (increase in air dryness), *U. parvifolia, M. grandiflora, M. alba, A. rubrum,* and *Q. virginiana* became more hydrated, while *Q. phellos* became less hydrated (Figure 4). VPD did not predict water potential in *P. calleryana* (emtrend −0.03, 95% CI −0.14 − 0.09) or *Platanus x hispanica* (emtrend −0.11, 95% CI −0.33 − 0.11). In the marginal trends from stomatal conductance, VPD had a negative effect on *P. calleryana* (emtrend −0.31, 95% CI −0.44 − −0.18) and *M. alba* (emtrend −0.22, 95% CI −0.36 − −0.07; Figure 4).

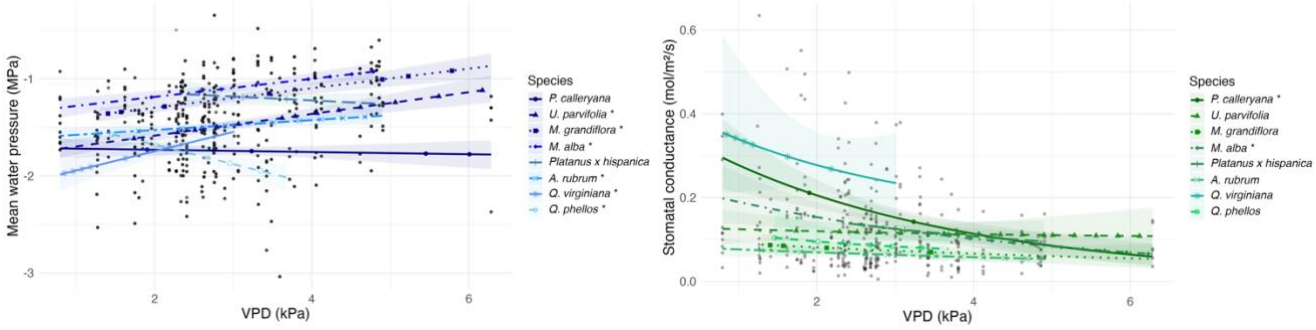

Figure 4. **Species-specific responses of stem water potential and stomatal conductance to vapor pressure deficit (VPD)**. Lines represent posterior mean predictions from the fitted models, with shaded ribbons denoting 95% credible intervals. Species marked with an asterisk (*) indicate a credible VPD effect, defined as a 95% credible interval for the species-specific marginal trend that did not overlap zero.

Figure 4 (Species responses to VPD): Alt text: *Two scatter plots with fitted trend lines and shaded confidence ribbons, showing stem water potential and stomatal conductance plotted against vapor pressure deficit, each with eight differently colored and patterned lines representing tree species. Several species names in the legend are marked with an asterisk indicating a statistically credible VPD effect.*

Combined-city model: species and city effects on stem water potential and stomatal conductance

When examining all cities together, we expected trees in Sacramento to be less hydrated and have lower stomatal conductance than those in the other cities, though these comparisons should be interpreted cautiously as trees were sampled in different years across cities. Overall stem water potential did not differ significantly among cities (Sacramento $\beta = -0.04 \pm 0.20$; 95% CI [-0.43, 0.34]; $R^2 = 0.68$), and meaningful species × city interactions suggested that city-level differences in hydration were species-specific rather than consistent across focal tree species. Trees in Sacramento showed 32% lower stomatal conductance than those in New Orleans (Sacramento emmean = 0.079 mmol m^{-2} s^{-1} vs. New Orleans emmean = 0.115 mmol m^{-2} s^{-1}; $\beta = -0.79 \pm 0.18$; 95% CI [-1.16, -0.44]; $R^2 = 0.54$), a pattern driven largely by *M. alba* (Sacramento − New Orleans = -0.85, 95% CI [-1.29, -0.39]) and *P. calleryana* (Sacramento − New Orleans = -0.79, 95% CI [-1.15, -0.43]) rather than a consistent citywide response, as *A. rubrum, M. grandiflora*, and *U. parvifolia* showed no credible difference between these two cities (Appendix 2).

Discussion

The ecosystem services provided by urban street trees depend on tree physiological function, particularly their ability to remain hydrated and to transpire. Urban heat may stress trees and reduce their function, but rather than widespread loss of function, we found nuanced effects of heat that differed among species and cities. When considering all species combined, the effect of LST on stem water potential and stomatal conductance was only detected in Sacramento. In the other two cities, Raleigh and New Orleans, we detected no effects of urban warming on either variable at the aggregate level.

The seasonal modulation of LST effects on stem water potential and stomatal conductance was unique to Sacramento. This city-specific pattern may reflect the pronounced Mediterranean climate of Sacramento, where a prolonged dry season coincides with peak summer heat, creating a progressively intensifying water deficit as the season advances. Early in the season, stomatal conductance barely responds to LST, and stem water potential declines sharply instead (Figure 2); later in the season, this reverses, conductance drops sharply with LST while stem water potential stays comparatively stable. This points to

a shift toward stronger stomatal restriction under higher LST as the dry season progresses, though we interpret this cautiously since the two responses come from separate models rather than a joint trade-off model. In contrast, Raleigh and New Orleans showed no comparable seasonal LST-induced pattern. The importance of water availability in mediating urban heat responses was further underscored by the irrigation results: although irrigation did not alleviate heat-related stress at the level of stem water potential, irrigated trees maintained substantially higher stomatal conductance as LST increased suggesting that supplemental water supply supports continued gas exchange under increased LST even when it does not translate into measurable improvements in whole-plant water status. If urban tree species exhibit heat and/or drought tolerance, artificial watering could compromise acclimation, leaving trees more vulnerable to climate extremes in the likely event of future water scarcity in the American West (Madrigal-González et al. 2025, Rissanen et al. 2025).

Responses to LST were species- and city- specific. In Sacramento, *P. calleryana* demonstrated a negative relationship between LST and stem water potential, declining by approximately 0.054 MPa per 1°C increase with its stem water potential approaching TLP (Turgor Loss Point) values at high temperatures, suggesting this species is operating nearer to its physiological limit (Sjöman et al. 2018). For stomatal conductance, *Platanus* × *hispanica* in Sacramento showed a similar, though only marginally credible, negative trend with LST (95% HPD interval narrowly overlapping zero). This pattern would be consistent with the isohydric strategy previously documented for *Platanus* × *hispanica*, in which early stomatal closure limits water loss and helps maintain stem water potential under drought (Claude et al. 2024), but given the borderline credibility of this effect, we treat this interpretation as tentative rather than a confirmed finding. In Raleigh, by contrast, *M. alba* and *A. rubrum* both showed credible increases in stomatal conductance with rising LST, suggesting these species may sustain rather than restrict gas exchange under heat in a wetter-summer climate.

Without further physiological and anatomical measurements it remains unclear whether decreased stem

water potential reflects acclimation or a stress response. Although trees can display morphological plasticity under warmer conditions to avoid canopy damage when water is available (Tang et al. 2025), species-specific water and heat stress thresholds for urban species have not been as well characterized as agricultural crops, where both optimal baselines (water potential under well-watered conditions) and stress thresholds have been established for economically important species like *Olea europea* or *Prunus domestica* (Shackel et al. 2021). In these agricultural systems, baseline water potentials under full irrigation provide reference points to assess when declining values indicate mild, moderate, or severe stress. For most urban tree species, such baselines remain unknown, making it difficult to determine whether observed water potentials represent normal fluctuations or concerning departures from optimal performance.

Although effects of LST in Sacramento alone were as expected in the current study, other studies have demonstrated similar effects of LST on the stem water potential of *A. rubrum* and *Q. phellos* in Raleigh. Dale and Frank (2017) report that stem water potential decreased as temperature increased for *A. rubrum* in 2014, and Meineke and Frank (2018) also observed a negative effect of LST on stem water potential in *Q. phellos*. It is possible that the dynamic complexity of the urban forest could mitigate the effects of LST some years or that our study also included older mature trees that have access to underground water. However, in past studies, most trees that experienced drought stress had a smaller diameter to the trees included in the current study (Dale and Frank 2017, Meineke and Frank 2018, Marchin et al. 2022). Inter-annual differences in the relationships between tree function and local climate highlight the context-dependency of tree responses to urban heat stress and underscore that species-level sensitivity to LST may only manifest under specific combinations of heat and water deficit, rather than being a consistent feature of a given species or city.

Beyond their responses to LST, species differed in their water status and gas exchange. *Pyrus calleryana* stood out as the least hydrated species in Sacramento, showing lower stem water potential than all other

423 species, yet maintaining relatively high stomatal conductance across cities. At the opposite end, *M.*
424 *grandiflora* and *M. alba* were the most hydrated species across all three cities. *Acer rubrum* consistently
425 showed among the lowest stomatal conductance across all cities. Together, these contrasts suggest that
426 species vary considerably in their water use strategies, with some maintaining high gas exchange despite
427 low water potential, a pattern that warrants further investigation in the context of urban heat tolerance.
428 Notably, *A. rubrum*'s low conductance appears to be a baseline trait rather than a heat-induced decline,
429 since its only credible LST response (Raleigh) was an increase (Figure 3). Given this chronic low
430 conductance combined with enhanced pest pressure under urban warming, *A. rubrum* may still be a poor
431 fit for future climate scenarios. This species is a favorite for planting because of its distinct fall coloration,
432 but multiple lines of evidence now point to it as a poor choice for urban plantings as the climate warms
433 (Dale and Frank 2017). Similarly, given *P. calleryana*'s poor performance in hot areas within Sacramento,
434 and its documented susceptibility to branch failure (Kane 2007), this species appears to be a poor choice
435 across cities as the intensity of storms and warming intensify. *Ulmus parvifolia* showed no detectable
436 response to LST for either variable across cities, consistent with its documented physiological resilience
437 to extreme heat and drought with minimal crown dieback and no mortality under heatwaves (Marchin et
438 al. 2022). However, its growth has been shown to decline in response to local climatic conditions in some
439 cities (Esperon-Rodriguez et al. 2025), suggesting that while *U. parvifolia* may maintain water status and
440 gas exchange under urban heat gradients, longer-term growth performance may still be sensitive to
441 climate.
442
443 Does vapor pressure deficit (VPD) predict tree hydration status in urban systems?
444 Sacramento experiences higher VPD (~4 kPa) compared to Raleigh (~2.6 kPa) and New Orleans (~2
445 kPa). Vapor pressure deficit predicted overall stomatal conductance (trees closed stomata as air got drier)
446 but not stem water potential, suggesting that trees might be regulating water loss through stomatal control
447 rather than passively losing water (Grossiord et al. 2020). Species-specific VPD responses revealed
448 different possible water management strategies. *Ulmus parvifolia* maintained higher stem water potential

under elevated VPD, a pattern that may reflect access to deeper water sources that buffer whole-plant water status even as atmospheric demand increases. In contrast, *Q. phellos* showed the expected negative response, becoming less hydrated as air dried. *Pyrus calleryana* and *M. alba* closed stomata as VPD increased, a response that may represent a compensatory mechanism to limit water loss; however, in *P. calleryana* this stomatal response appears insufficient to fully buffer water potential, consistent with its overall vulnerability in hotter urban areas documented elsewhere in this study. The divergent responses of *U. parvifolia* and *Q. phellos* under the same atmospheric conditions highlight that species vary considerably in their capacity to maintain water status under high evaporative demand, likely reflecting differences in rooting depth, hydraulic architecture, or physiological acclimation (Martínez-Vilalta et al. 2009).

Differences when comparing cities

Contrary to expectations, precipitation regime did not appear to drive urban tree hydration status. Although cross-city comparisons should be interpreted cautiously given that trees were sampled in different years and seasons, the summers during which measurements were taken were climatically representative of typical conditions for each city (Appendix 2). Based on the sampling sequence, we would have expected Sacramento trees to appear less hydrated than those in Raleigh, as Sacramento was sampled later in the season, meaning trees had experienced more cumulative days without rain and higher seasonal heat stress by the time of measurement. This pattern suggests that factors beyond rainfall and atmospheric demand, such as soil properties, irrigation, or species-specific water use strategies, may buffer (or exacerbate) regional water limitations for urban trees.

Limitations and Ways Forward

Our tree selection was based on LANDSAT LST measurements at 30m resolution, this resolution provided a LST gradient that represented diverse urban environments and neighborhoods with higher imperviousness and lower tree density where summer temperatures tend to be higher in the summer

compared to other areas. While VPD probably varies by tree location, measuring microclimate-scale data (e.g., tree sensors) was not within the scope of this study. Yet the city-level measurements successfully captured a VPD gradient (2-6 kPa) that revealed the likelihood of species-specific possible drought tolerance mechanisms. Future studies incorporating tree-level microclimate sensors would allow finer-scale characterization of the atmospheric conditions each individual tree experiences. Further, our study provides instantaneous measurements of tree water status during peak summer stress periods, not assessments of long-term performance or functional failure thresholds. These snapshot measurements reveal immediate responses but cannot predict sustained performance under chronic stress. City-specific recurrent measurements across seasons and years, combined with growth and anatomical data, are needed to assess long-term function and climate adaptation (Velasquez-Camacho et al. 2025).

Critical belowground factors such as soil texture and water holding capacity, infrastructure water inputs (e.g., leaky water mains), root access to groundwater, and management practices, were not measured or controlled. While we measured imperviousness surrounding trees, we could not directly assess soil volume or belowground root space availability. However, despite experiencing similar atmospheric conditions, species showed different water status responses. For instance, *U. parvifolia* became more hydrated under high VPD, indicating that species-specific mechanisms, whether belowground traits or physiological acclimation to local conditions, might override atmospheric drivers in this study. Unmeasured root-level factors, including differences in rooting depth, root density, mycorrhizal associations and physiological acclimation may help explain observed species differences across cities. Our results document tree performance under realistic urban conditions where these factors interact, revealing that species responses to VPD and precipitation are not uniform and likely reflect multiple interacting mechanisms.

Our results provide a baseline of how mature urban trees function in different cities. By studying commonly planted species across cities, our approach tests whether popular urban tree selections maintain

physiological function across diverse environments and LST. Based on our findings, we recommend the following future research directions as promising for further characterizing tree responses to urban heat gradients: 1) quantify additional urban water sources (infrastructure inputs, irrigation systems) that could influence tree acclimation and performance; 2) increase species screening through evaluation of hydraulic strategies, wood density, and foliar traits to identify species adaptable to current and future urban conditions (Madrigal-González et al. 2025, Rahman et al. 2024); 3) examine past growth of young and mature trees in relation to long-term climate trends and extreme events (Camarero et al. 2018); and 4) develop predictive frameworks for early stress detection and proactive urban forest management (Anderegg et al. 2019).

Unlike natural forests, the species composition of urban forests emerges from the decision-making of a wide range of stakeholders over years or even decades (Roman et al. 2018). These stakeholders typically have preferences for the types of trees they plant and manage, which include aesthetic value, food production, shade, and maintenance needs (Buffam et al. 2022). Such preferences are likely to be decoupled from which species can survive and function as the climate warms and urbanization intensifies. Stakeholders' decisions about the urban forest are therefore not integrated with information about tree performance under warming conditions (Tabassum et al. 2023) or underground soil and water information. A knowledge base about which trees are likely to continue to function under climatic and urban pressures is urgently needed to ensure urban forests for future generations.

From our species, *U. parvifolia* stands out as a strong candidate for a drought- and heat-tolerant species, given its consistent lack of detectable LST response across all three cities. *Platanus* × *hispanica* may be a tentative additional candidate, though its marginal stomatal response to LST in Sacramento warrants confirmation before drawing firm conclusions. Characterizing the duration and frequency of water potential drops below turgor loss point and prolonged stomatal closure that trees can tolerate before incurring irreversible physiological damage would help establish species-specific stress thresholds across

a range of water availability conditions, particularly relevant given documented episodes of leaf abscission during heat waves (Sanusi and Livesley 2020). Additionally, future studies could identify other tree species with similar tolerance and ecosystem services to diversify future urban forest plantings. On the contrary, *P. calleryana* may be poorly suited for hot, dry cities like Sacramento, where it may be operating near its physiological limits, trading water for gas exchange.

Conclusions

As city populations increase, urban forests become critical providers of ecosystem services that extend beyond heat mitigation. Species identity and local conditions determined tree responses to urban heat and atmospheric drought. Certain species (*P. calleryana*) approached physiological thresholds under combined stress, while others (*U. parvifolia*) demonstrated better physiological function across diverse conditions. Building resilient urban forests will require city-specific risk assessments accounting for atmospheric and belowground factors and evidence-based species selection guided by physiological performance under current and future climates rather than aesthetic preferences alone.

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Contributions:

- Contributed to conception and design: ECM, AO, EM
- Contributed to acquisition of data: ECM, OR, ML, MW
- Contributed to analysis and interpretation of data: ECM, EY, ML, MW, AO, EM
- Drafted and/or revised the article: ECM, EY, ML, MW, AO, OR, SC, EM
- Approved the submitted version for publication: ECM, EY, MW, AO, OR, SC, EM

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Competing interests

The authors declare that they have no competing interests, including financial interests or personal relationships that could have influenced the work reported in this research paper.

AI disclosure statement

The authors used Claude Sonnet 4.6 to assist with grammar. All AI-generated content was reviewed and edited by the authors.

Appendix 1

Appendix 1 is included in a separate file (Appendix 1.doc).

Appendix 2

Appendix 2 is included in a separate file (Appendix 2.xlsx).

Data accessibility statement

The data that support the findings of this study will be made openly available upon acceptance of this manuscript. All datasets will be deposited in the Dryad Digital Repository (https://datadryad.org).

Figures

This manuscript contains 4 figures:

Figure 1. Land surface temperature gradient in focal cities. The focal cities of Sacramento, Raleigh and New Orleans overlaid with mean surface temperature from June – September in the years 2014-2022. Lighter yellow colors represent warmer areas, and purple colors represent cooler areas. Land surface temperature values were obtained from LANDSAT C2 U.S. Analysis Ready Data (ARD) (U.S. Geological Survey, 2023).

Figure 2. Sacramento interaction between mean surface temperature and day of the year for stem water potential and stomatal conductance. Solid lines represent the days we measured trees, and light lines represent model predictions. Light blue/green lines represent days at the beginning of the measurement period and dark blue/green lines represent the last days of the measurements. Lines converge near the point where day-of-year has little influence on the outcome; away from this point, day-of-year effects diverge in opposite directions. The effect of LST on stem water potential weakens as the season progresses and the effect of LST on stomatal conductance becomes more pronounced as the season progresses.

Figure 3. Relationship between mean land surface temperature and stem water potential (top) and stomatal conductance (bottom) for eight urban tree species across Sacramento and New Orleans. Lines represent model-predicted slopes from city-specific Bayesian mixed-effects models, with shaded ribbons indicating 95% highest posterior density intervals. Points show individual observations from the raw data. Asterisks (*) indicate species for which the 95% credible interval of the LST effect did not overlap zero. More negative water potential values indicate greater water stress, while lower stomatal conductance indicates more closed stomata.

Figure 4. Species-specific responses of stem water potential and stomatal conductance to vapor pressure deficit (VPD). Lines represent posterior mean predictions from the fitted models, with shaded ribbons denoting 95% credible intervals. Species marked with an asterisk (*) indicate a credible VPD effect, defined as a 95% credible interval for the species-specific marginal trend that did not overlap zero.

Appendix 1

for

Species-specific plant water status responses to land surface temperature vary across three cities with different precipitation patterns

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Contents

Text S1. Study site and tree selection

To guide tree selection and quantify patterns of urban warming in each city, we mapped land surface temperatures from 2014 - 2022 using LANDSAT C2 U.S. Analysis Ready Data (ARD) (Fig. 2; U.S. Geological Survey, 2023) acquired from Earth Explorer (U.S. Geological Survey, 2000). The criteria we used to select available surface temperature raster files included the thermal band type (band 10 in Landsat 8-9), observation date, location, and percent cloud cover (set between 0-10%). Though land surface temperature data were available before 2014, Landsat 4-7 employs a different satellite and calibration technique (thermal band 6). We therefore chose to omit previous years. We then extracted and converted units of land surface temperatures from selected raster files in ArcGIS (Esri, 2021) with the following equation: [("band_filename" * 0.00341802) + 149 - 273.15] (U.S. Geological Survey, 2021). Finally, we averaged the summer land surface temperatures across years (2014 - 2022) to calculate a mean surface temperature (Fig. 2).

Text S2. Extraction of additional variables

We extracted maximum and minimum temperature and humidity values from the National Oceanic and Atmospheric Administration (NOAA) (2023 and 2024 Global Historical Climatology Network - Daily) (Fig. S1) for days when each individual tree was measured in each city. We determined the imperviousness in the immediate surrounding of each tree using the dataset GHS-BUILT-S (Pesaresi M., Politis P. 2023) (Fig. S2). Around each tree, we defined a buffer in the size of the tree catchment, that is, the area covering the potential tree root zone, and calculated the weighted mean of all intersecting raster grid cells similar to the method described in Willaredt et al. (Willaredt et al. 2026).

Text S3. Statistical analysis

Models with water potential as the response variable were specified with a gaussian error distribution, and priors for fixed effect coefficients were specified as Normal (0, 1) with 1,500 warm-up iterations, 3,000 iterations, four chains, four cores, and a delta value of 0.9. The models including stomatal conductance as the response were specified with a gamma error distribution and with priors specified as Normal (0, 1) for categorical fixed effects, Normal (0, 0.5) for continuous variables, and Gamma (2, 0.1) for the shape parameter. We ran each model with 3,000 warm-up iterations, 8,000 iterations, four chains, four cores, and an increased delta of 0.99 to ensure convergence and eliminate divergent transitions.

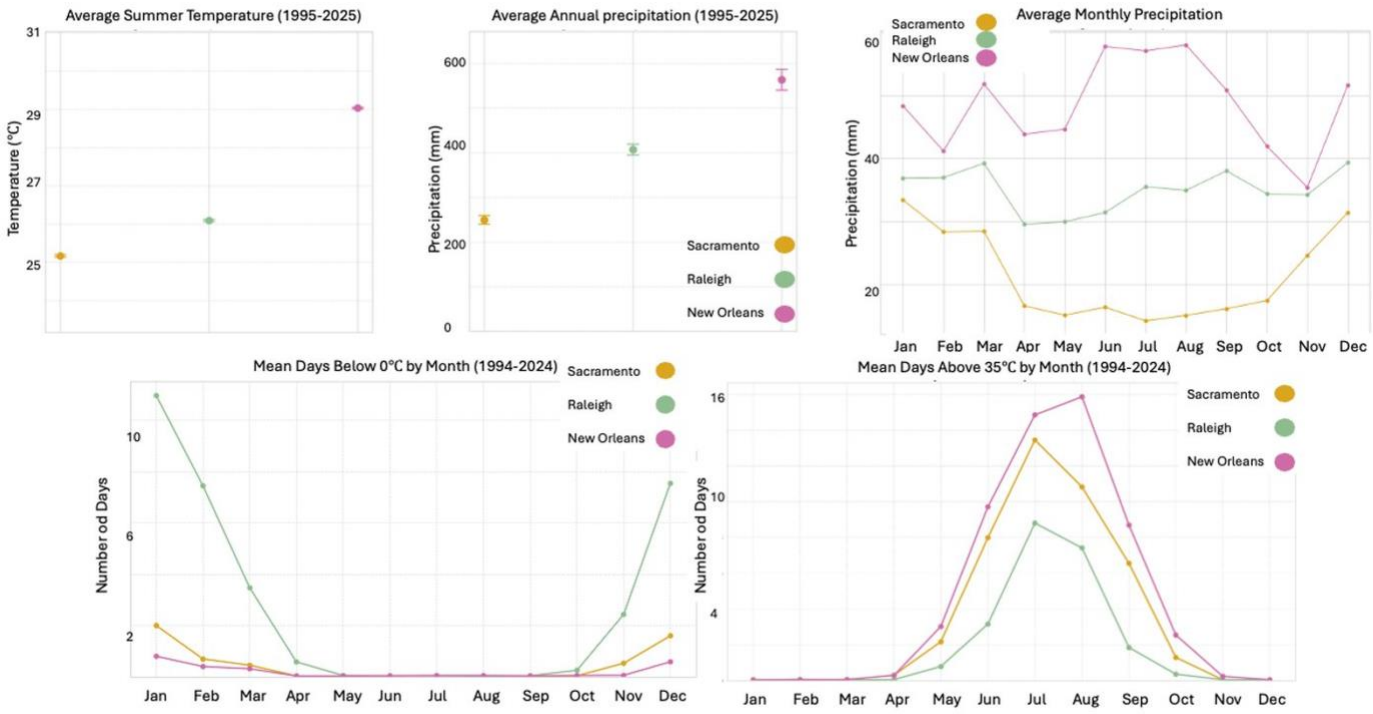


Figure S1. Climatic patterns from Sacramento, CA, Raleigh, NC, and New Orleans, LA, USA from the last 30 years (National Oceanic and Atmospheric Administration). Data obtained from the Global Historical Climatology Network – Daily dataset https://www.ncdc.noaa.gov/cdo-web/datasets

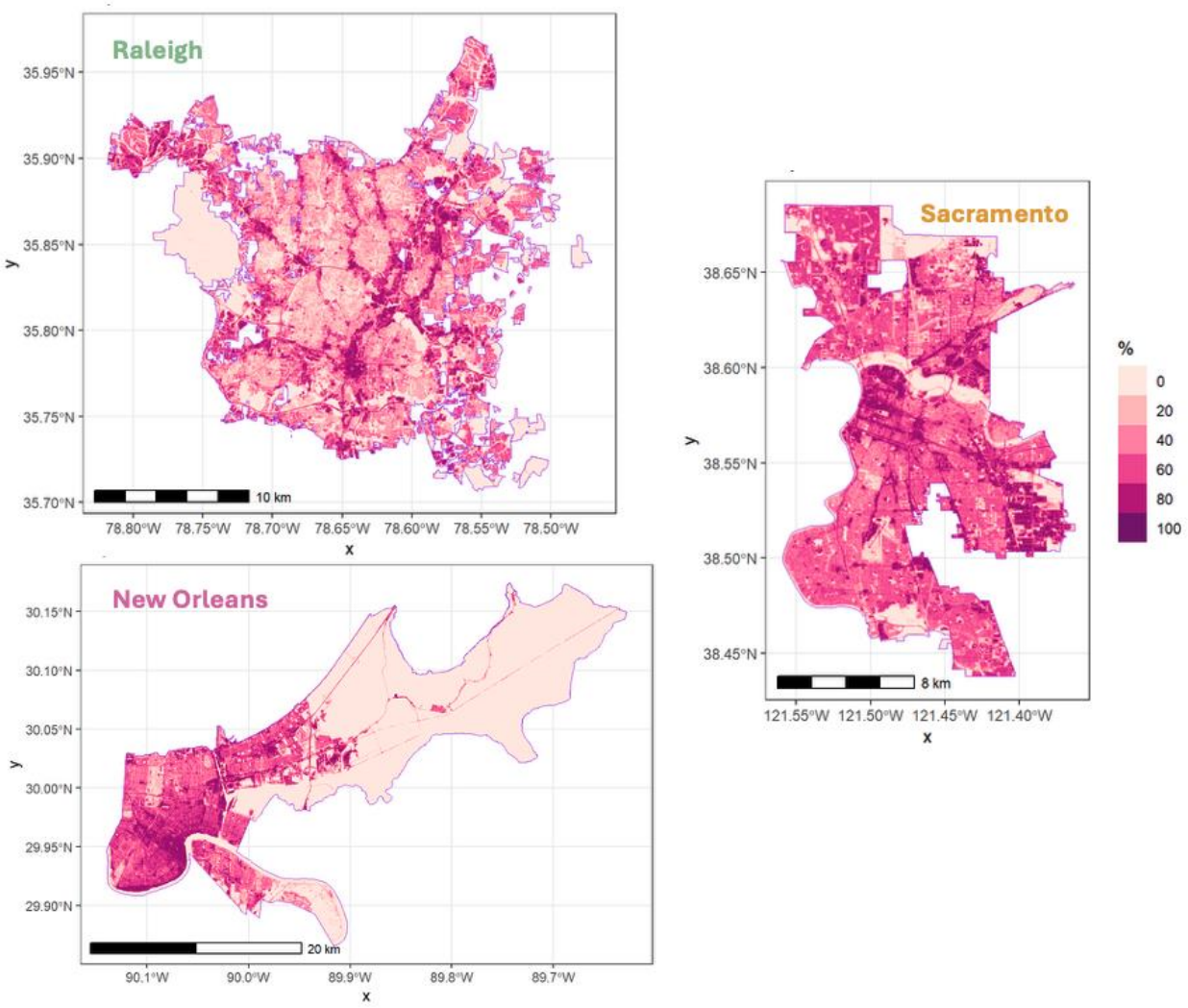


Figure S2. Imperviousness gradient per city from GHS-BUILT-S (Pesaresi M., Politis P. 2023) as a measure of urbanization. Light colors indicate low imperviousness, and dark colors indicate high imperviousness.

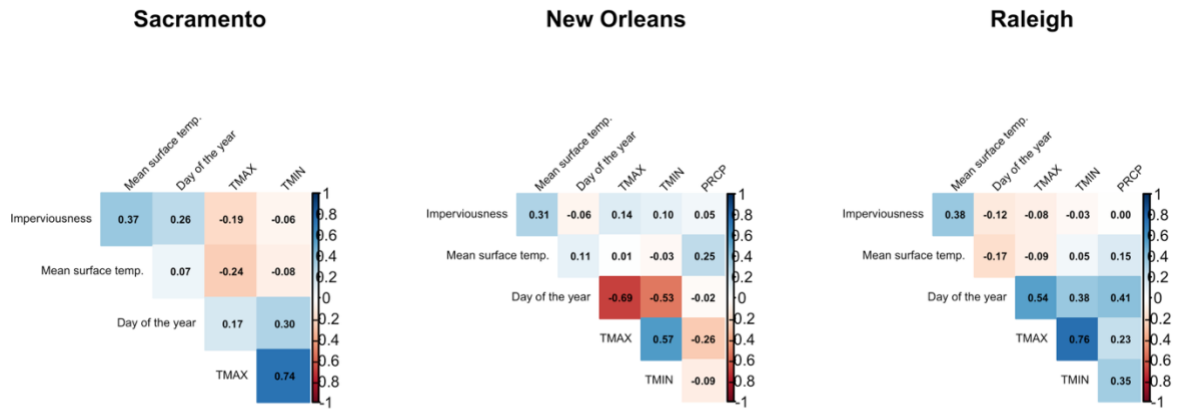


Figure S3. Pearson correlation matrices among candidate predictors for each city (Sacramento, New Orleans, and Raleigh). Color intensity reflects the strength of the correlation, with red indicating negative and blue indicating positive relationships. Numbers indicate correlation coefficients. Variables with $|r| \geq 0.3$ were considered collinear and excluded from subsequent regression models.

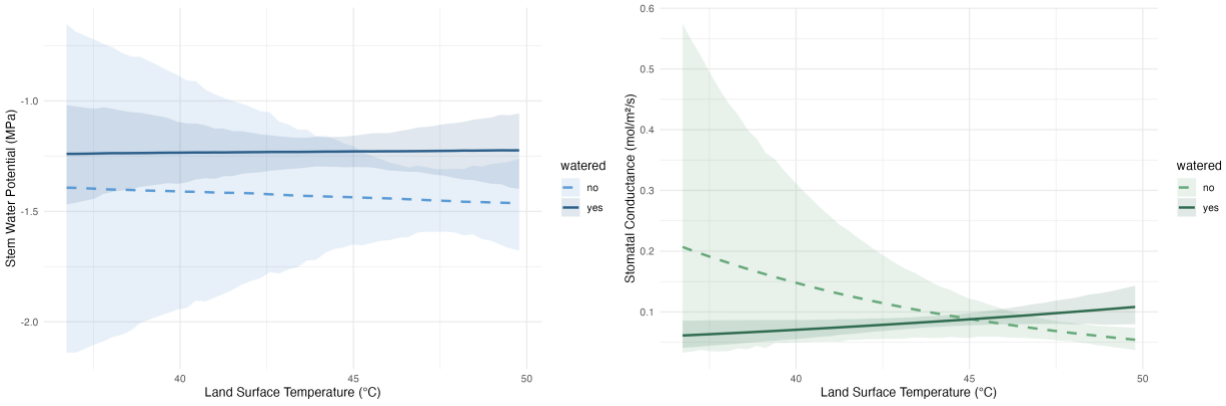
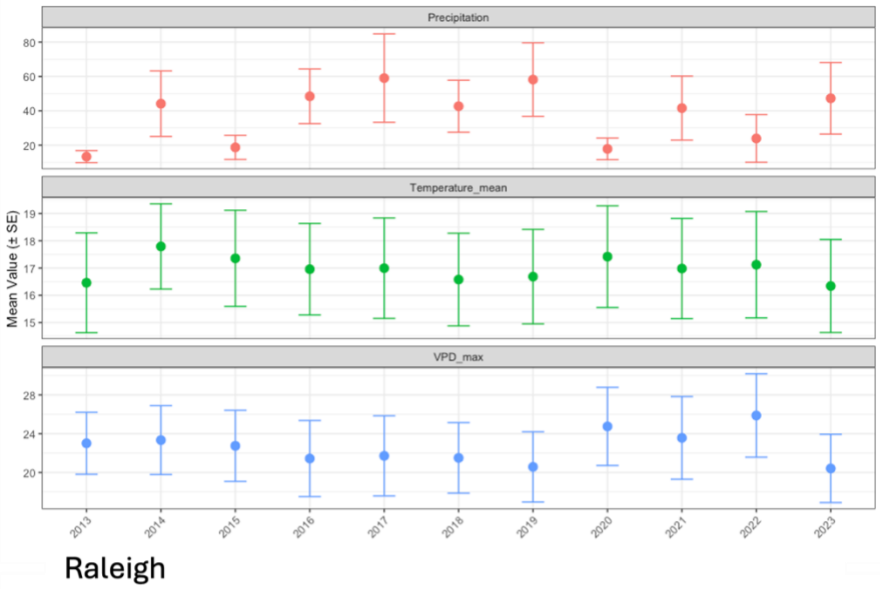
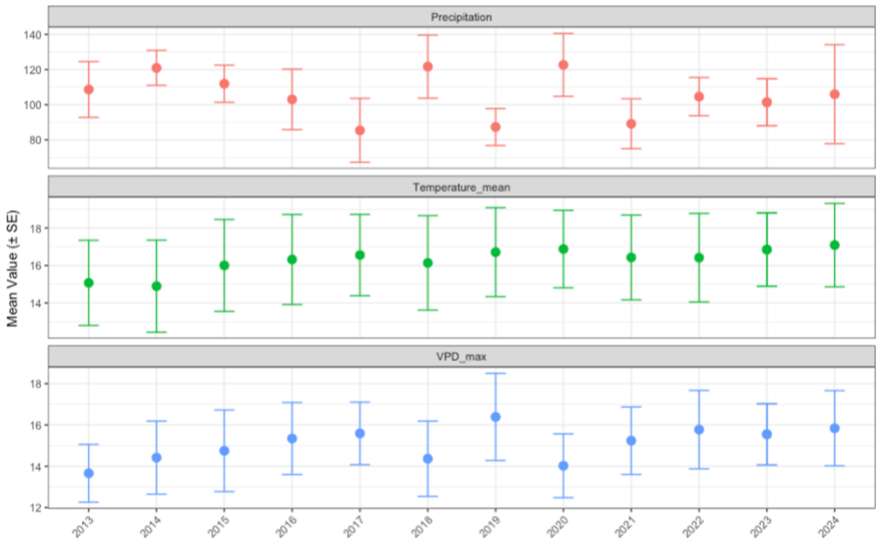


Figure S4. Sacramento interaction between land surface temperature and irrigation status for stem water potential and stomatal conductance. Dashed lines represent non-irrigated trees, and solid lines represent irrigated trees; shaded bands represent 95% credible intervals. Stem water potential did not differ between irrigated and non-irrigated trees across the range of surface temperatures measured. In contrast, irrigated trees maintained higher stomatal conductance as surface temperature increased, while non-irrigated trees showed a decline.

Sacramento



Raleigh



New Orleans

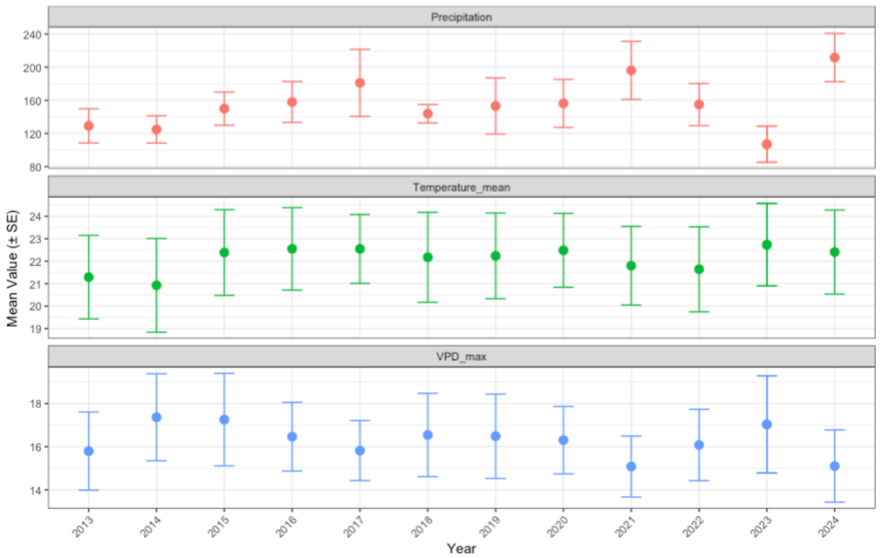


Figure S5. Precipitation (mm), mean temperature (°C), and maximum vapor pressure deficit (hPa) for Sacramento, Raleigh, and New Orleans (2013-2023/2024). Annual means calculated across all 12 months with standard error bars. Statistical comparisons using two-sample t-tests revealed no significant differences between recent years and 2023 (for Sacramento) and 2024 (for Raleigh and New Orleans). Sacramento 2023: VPD decreased by 2.4 hPa ($t = -0.66$, $p = 0.52$), temperature decreased by 0.7°C ($t = -0.39$, $p = 0.70$), and precipitation increased by 10.5 mm ($t = 0.49$, $p = 0.63$). Raleigh 2024: VPD increased by 0.9 hPa ($t = 0.47$, $p = 0.65$), temperature increased by 0.9°C ($t = 0.41$, $p = 0.69$), and precipitation increased by 0.4 mm ($t = 0.02$, $p = 0.99$). New Orleans 2024: VPD decreased by 1.2 hPa ($t = -0.69$, $p = 0.50$), temperature increased by 0.4°C ($t = 0.21$, $p = 0.84$), and precipitation increased by 56.9 mm ($t = 1.88$, $p = 0.08$). All comparisons were non-significant at $\alpha = 0.05$. Climate data were obtained from the PRISM Climate Group (Oregon State University, http://www.prism.oregonstate.edu) at 2.5 arcmin (~4 km) spatial resolution

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