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Original article

Responses of drought-tolerant *Tipuana tipu* trees to long-term irrigation: A tree-ring study in Lisbon, Portugal

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ABSTRACT

Tree planting is a key strategy for the adaptation of cities to climate change. However, cities in semi-arid and Mediterranean climates struggle to sustain tree growth, often relying on irrigation systems. Literature suggests that irrigation enhances tree growth and ecosystem service provision at the cost of structural and physiological adjustments that can lead to lower wood density, compromising tree's mechanical stability and pathogen resistance. Yet, the response of trees to irrigation is species dependent, raising uncertainty about its possible costs and benefits. We investigate how drought-tolerant *Tipuana tipu* trees – a common species in Lisbon and other cities worldwide – responded to six years of irrigation using a multi-proxy tree-ring approach. We examined even sized and aged trees growing under comparable conditions in the Duque de Saldanha Square, differing only in irrigation regime. The strong positive relationship between growth and oxygen stable isotopes of control trees suggests that growth is associated with high atmosphere demand during the warm and dry season. Starting in 2017, the irrigation alleviated the stomatal conductance limitations in the treatment trees, as evidenced by the significant decrease in stable carbon isotope values and a twofold increase in growth rate compared to control trees. Notably, irrigation did not result in any significant wood density reduction. These findings challenge the assumption of wood density reduction under irrigation and further highlight this drought-tolerant species capacity to increase growth rate and maintain wood density. A trait combination likely to enhance ecosystem services delivery without compromising mechanical stability under long-term irrigation.

1. Introduction

Climate change is one of the main challenges humanity faces this century, exposing billions of people to unsustainable living conditions (Fletcher et al., 2024), particularly in cities (United Nations, U.N,2014). Urban populations are already grappling with heat (Han et al., 2023; Kim and Brown, 2021) and increased frequency and intensity of droughts and floods – currently among the worst natural hazards in cities worldwide – impacting human mortality, morbidity, and economic vulnerability (Alves et al., 2024; Doocy et al., 2013). Urban

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resilience can be achieved through ecosystem services provided by green areas and trees (Elmqvist et al., 2015; United Nations, U.N,2015), like the provision of thermal comfort and rainfall interception. However, urban environments often impair tree function and subsequent ecosystem services provision through plant hydraulics and photosynthesis limitations, particularly under adverse climate conditions (Fini et al., 2022; López et al., 2021). Under such unfavourable conditions, urban planners are increasingly investing in irrigation systems (Rambhia et al., 2023), whose benefits are still poorly documented worldwide (Esperon-Rodriguez et al., 2025).

Automated irrigation systems have become a common strategy supporting urban tree development (Vico et al., 2014), mitigating the limited access to soil moisture that results from impervious surfaces and compacted urban soils (Mullaney et al., 2015; Smith et al., 2024). Adequate soil moisture through irrigation aid trees to sustain sap flow even under water limitation, supporting higher tree leaf area, transpiration, carbon assimilation, and growth (Ibsen et al., 2023; López et al., 2021; Luketich et al., 2019; Xi et al., 2021). Better performing trees through irrigation can improve the provision of ecosystem services and population's well-being (Lafortezza and Chen, 2016; Wei et al., 2021).

Artificial water input through irrigation also brings challenges. The primary drawback is financial and environmental costs (Parween et al., 2021; Spulber and Sabbaghi, 2012), particularly in precipitation-scarce environments. Using water for irrigation raises bioethical concerns in arid regions or during drought events, as water scarcity requires prioritizing human needs over other uses (Sørup et al., 2020; United Nations, U.N,2015). Discussions of these drawbacks often overlook the impacts of irrigation on urban tree function like the potential trade-off between tree growth rate and wood density observed within species (e.g. Arsić et al., 2021). Rapid growth is typically associated with greater investment in cell division and expansion – often resulting in wider vessels to support high evapotranspiration rates – and reduced allocation to secondary compounds and cell-wall thickening during xylogenesis (Ziemińska et al. 2013, Zheng and Martínez-Cabrera, 2013). This combination potentially leads to lower wood density, and consequently reduced wood stiffness and strength within species (Hoffmeyer, Pedersen,1995, Lachenbruch et al. 2010) making trees more vulnerable to pathogens and mechanical failure that impacts both urban insfrastructure and human life (Larjavaara and Muller-Landau, 2010; Niklas and Spatz, 2010; Van Duong et al., 2023). Trees can only maintain optimal wood properties under irrigation if leaf assimilation meets the higher carbon demands of xylogenesis (Eckert et al., 2019).

Although a trade-off between growth and wood density at the species level remains contentious (Fajardo et al., 2022, 2024), lower wood density can be expected under particular growth conditions. Factors like fertilization, which can negatively affect the wood mechanical properties (Akello et al., 2024), and irrigation that promotes plastic wood anatomy changes to cope with the higher water availability and, consequently, increased hydraulic efficiency (Wimmer et al., 2002; Drew et al., 2009; 2011) can lead to reduced wood density. Species-specific growth strategies, such as those of heliophilous fast-growing trees (Chen et al., 2017), may cause similar effects on wood density. Despite being phylogenetically determined (Li et al., 2024), wood density exhibits substantial plasticity within individuals (e.g. Bastin et al., 2015; González-Melo, 2021; Ortega-Rodriguez et al., 2023), among individuals, and across environmental gradients (e.g. Hornink et al., 2025; Pompa-García et al., 2024), resulting in intra-specific variation of 40 % or more (e.g. Ibsen et al., 2023).

Most of the insights on the effects of irrigation are based on relatively short-term laboratory and field experiments (e.g. de Luis et al., 2011; Rossi et al., 2013). Few studies have assessed the responses of mature urban trees under real conditions (Vitali et al., 2024) due to the challenges of monitoring trees over prolonged periods (Roman et al., 2013). Particularly for drought-tolerant species, defined as trees that survive, grow, and reproduce under water limitation by avoiding or tolerating hydraulic stress through stomatal control and xylem adjustments (e.g. Allen et al., 2010; Klein, 2014). These physiological and structural adjustments can be accurately assessed through tree-ring studies. The tree-ring width reflects the radial annual growth (Stokes and Smiley, 1996), which varies according to the ontogenetic phase, climatic conditions, and disturbances that may either enhance or suppress growth over extended periods (Barton, 2024). Trees from the same species can adjust their growth and hydraulic architecture by modulating the tree-ring wood density in response to the environment conditions (e.g. Ortega-Rodriguez and Tomazello-Filho, 2019; Waite et al., 2023).

Tree rings provide additional insights into physiological processes like assimilation rate and stomatal conductance through stable isotope measurements (Miyahara and Locosselli, 2024; Song et al., 2022). For example, C_3 plants favour ^{12}C to the detriment of ^{13}C during the CO_2 diffusion through the stomata and Rubisco activity (McCarroll and Loader, 2004). Based on the ratio between ^{12}C and ^{13}C (tree-ring $\delta^{13}C$), one can infer the past physiological status of trees. A positive relationship between growth and $\delta^{13}C$ values suggests growth limitations by assimilation, whereas negative relationships suggest limitation by stomatal conductance (Brienen et al., 2022). The oxygen isotope signature ($\delta^{18}O$) can also point to a preferential transpiration of the lighter isotope (McCarroll and Loader, 2004; Andreu-Hayles et al., 2022). In addition, a positive association between $\delta^{18}O$ and growth suggests that growth variability may be influenced by stomatal regulation under high atmospheric demand (Cintra et al., 2019). The combination of these proxies strengthens the interpretation of the mechanisms underlying trees' growth and even a limited sample size (between 3 and 6 trees) can yield site-representative insights (Leavitt, 2010).

To better understand how urban trees coordinate xylogenesis and leaf-level physiology under different irrigation regimes, we studied the heliophilous (Tortorelli, 2009) and drought-tolerant (Locosselli et al., 2014) *Tipuana tipu* (Benth.) Kuntze (Fabaceae) in Lisbon, Portugal. Using a multi-proxy tree-ring analysis – including tree-ring width, wood density, and stable carbon and oxygen isotopes – we tested the following hypotheses: I) Trees exhibit a significant increase in growth rate following the irrigation. II) Irrigated trees display reduced wood density to cope with the additional water supply. III) Irrigation increases stomatal conductance, resulting in lower $\delta^{13}C$ and $\delta^{18}O$ values. By addressing these hypotheses, we aim to support decision-making in urban forestry management regarding tree species selection and irrigation systems.

2. Materials and methods

2.1. Sampling site and species

Lisbon (Fig. 1 A) has a population of 507,220 people, as reported in 2018 by the Portuguese National Statistical Institute, with approximately 58,000 street trees within the municipality (Câmara Municipal de Lisboa / Direção Municipal da Estrutura Verde, Ambiente e Energia, 2025). Lisbon has a Mediterranean climate according to the Köppen classification (Köppen, 1931) and is characterized by wet winters and dry summers (Fig. 1B). Sampling took place in the Duque de Saldanha Square (38°44'01.7"N; 9°08'41.4"W – Fig. 1 C), one of the main squares in the central axis of the city connecting key avenues. It comprises a roundabout with two concentric tree lawns. The inner lawn depends solely on precipitation for water supply, while the outer lawn is irrigated using a drip-based automatic system (Fig. 1D) installed in the summer of 2017. The irrigation system lies on a 4.20 m wide tree lawn and consists of a network of seven lines of 16 mm low-density polyethylene pipes with perforations spaced every 40 cm (Figure S1 in Supplementary Material). It has a maximum water flow of 4 litres per hour, running twice a day for 30 min. The soil in this site is sandy, with medium organic matter content (4.62 % ± 0.69), slightly alkaline pH (8.2 ± 0.0), and low electrical conductivity (0.25 mS/cm ± 0.01). This specific site represents a unique condition to evaluate the response of comparable mature trees (Table 1) to the long-term effect of irrigation. It contrasts

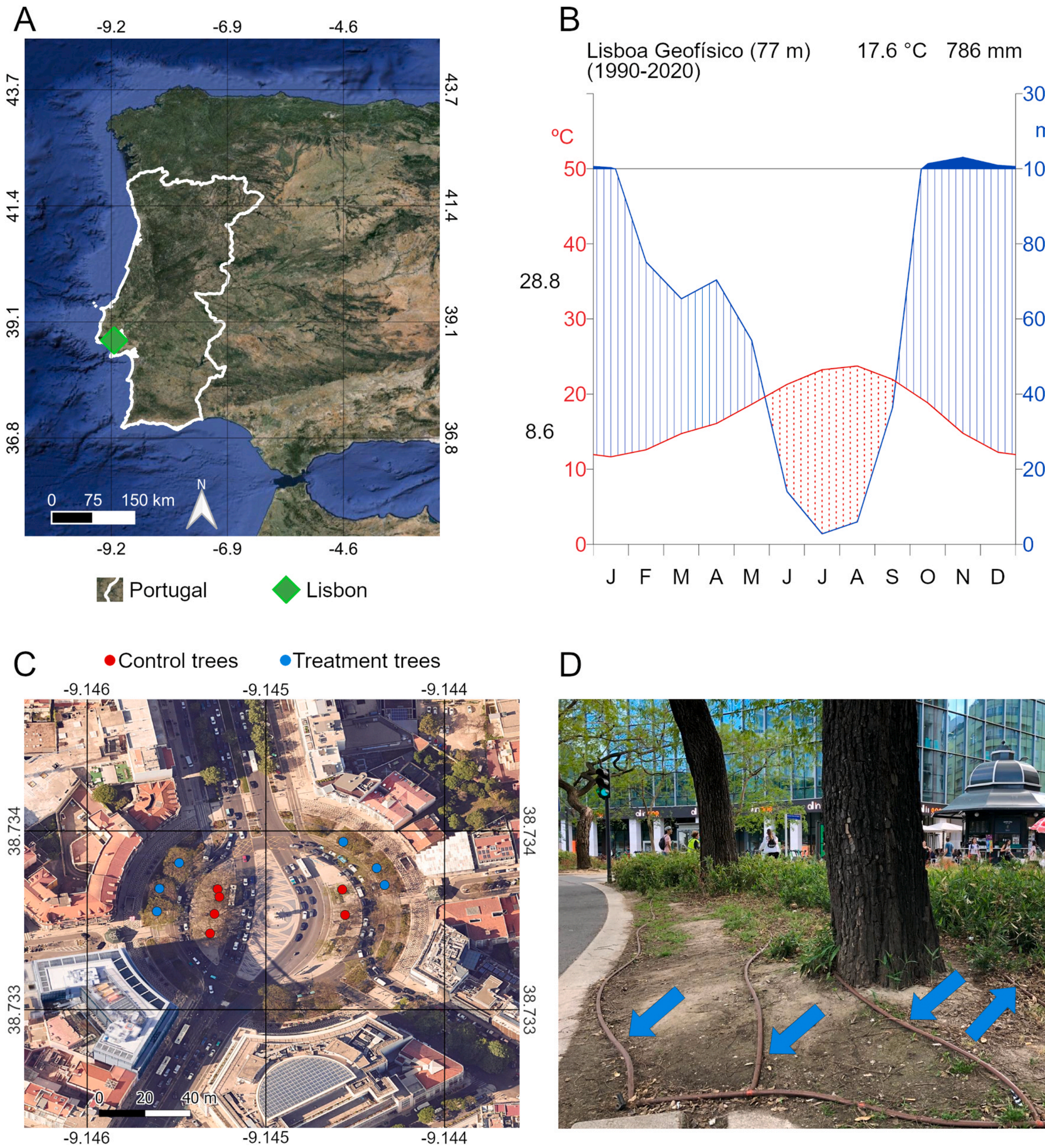

Fig. 1. (A) Location of Portugal in the Iberian Peninsula (white outline), and the city of Lisbon (green diamond). (B) Climate diagram for Lisbon, based on the data collected by the Portuguese Institute of Sea and Atmosphere (IPMA) at Lisboa Geophysical Station, from 1990 to 2020. (C) The Duque de Saldanha Square (38°44'01.7"N; 9°08'41.4"W) in Lisbon, with red dots indicating where the control trees are situated, and the blue dots indicate the irrigated, or treatment trees (see Table S1 in Supplementary Material for detailed information of each sampled tree). (D) Example of *Tipuana tipu* treatment trees and the automatic irrigation system at the study site.

with other sites usually found in the city where trees differ in size, age, and are either irrigated or not.

We studied *Tipuana tipu*, a native species to northern Argentina and southern Bolivia (Cattana et al., 2014) known for its drought tolerance by practitioners (e.g. Arizona Department of Water Resources, 2024), and previously proven increase in photosynthesis and growth during drought (Locosselli et al., 2024). This species has become widely planted worldwide (Moreira et al., 2018) and is among the most common street trees in Lisbon (Soares et al., 2024). It is a deciduous species (Zamproni et al., 2013) that produces clearly distinct semi-porous annual rings delimited by marginal parenchyma bands, successfully used in previous urban dendrochronological studies (e.g. Locosselli et al., 2019; 2024; Miyahara et al., 2022).

We sampled one or two increment cores per tree in May 2023, using 5 mm diameter increment borers. A total of 12 trees – six precipitation-dependent trees hereafter referred to as control, and six trees that started to be irrigated in 2017 hereafter referred to as treatment. Six trees is a standard sample size for stable isotopes dendroecological studies (Leavitt, 2010; Miyahara and Locosselli, 2024; Xu et al., 2020). Sampling injuries were plugged with natural cork. Samples were then mounted on wooden supports and left to air-dry for one week (Locosselli et al., 2019; 2020). Diameter at breast height (DBH), tree height (TruePulse 200, Laser Technology Inc), crown base height, crown diameter (North–South and East–West, Model R, Richter Messwerkzeuge), and the geographical coordinates for each tree were recorded in the field (see Table S1 in the supplementary material). Municipal guidelines stipulated that precipitation-dependent trees should not be pruned, while crown reduction was recommended for a subset of the irrigated trees (Câmara Municipal de Lisboa / Divisão de Manutenção de Espaços Verdes, Núcleo de Árvoredo,2015). Nonetheless, no evidence of

Table 1
Characterization of the sampled trees and their multi-proxy tree-ring series, with respective averages and standard errors for control and treatment trees. The letters indicate significant statistical differences: among periods within the same group (uppercase letters), and between groups within the same period (lowercase letters). See Tables S2 – S7 and Table S14 to access the detailed results of the statistical tests.

Parameter	Control	Treatment
N of trees (series)	6 (12)	6 (7)
Mean Diameter at Breast Height (cm)	54.80 ^{A} ± 4.04	55.33 ^{A} ± 1.38
Mean estimated tree age (years)	55.66 ^{A} ± 1.02	56.55 ^{A} ± 3.51
Mean Tree Height (m)	14.95 ^{A} ± 0.32	17.71 ^{A} ± 1.20
Mean Crown Base Height (m)	3.45 ^{A} ± 0.32	3.57 ^{A} ± 0.47
Mean Canopy Area Projection (m^2)	183.46 ^{A} ± 28.11	250.39 ^{A} ± 8.06
r-bar	0.52	0.48
Mean Basal Area Increment (cm^2/yr) Before	36.84^{Aa} ± 5.20	45.63^{Aa} ± 7.58
Mean Basal Area Increment (cm^2/yr) After	40.30^{Aa} ± 7.96	92.81^{Bb} ± 18.12
Mean Earlywood Density (g/cm^3) Before	0.68^{Aa} ± 0.009	0.72^{Aa} ± 0.02
Mean Earlywood Density (g/cm^3) After	0.69^{Aa} ± 0.01	0.71^{Aa} ± 0.02
Mean Middle wood Density (g/cm^3) Before	0.69^{Aa} ± 0.01	0.73^{Aa} ± 0.03
Mean Middle wood Density (g/cm^3) After	0.70^{Aa} ± 0.01	0.74^{Aa} ± 0.02
Mean Latewood Density (g/cm^3) Before	0.84^{Aa} ± 0.01	0.89^{Aa} ± 0.03
Mean Latewood Density (g/cm^3) After	0.86^{Aa} ± 0.01	0.88^{Aa} ± 0.02
Mean Ring $\delta^{13}C$ (‰) Before	-25.25^{Aa} ± 0.13	-25.31^{Aa} ± 0.20
Mean Ring $\delta^{13}C$ (‰) After	-25.60^{Ba} ± 0.13	-26.28^{Bb} ± 0.17
Mean Ring $\delta^{18}O$ (‰) Before	32.71^{Aa} ± 0.22	32.88^{Aa} ± 0.13
Mean Ring $\delta^{18}O$ (‰) After	32.43^{Aa} ± 0.31	32.55^{Aa} ± 0.13

differential pruning could be observed in the field. The canopy projection area (PA) was calculated based on the two measured perpendicular directions North-South ($D_{N–S}$) and East-West ($D_{E–W}$), according to Eq. 1:

$$PA \approx \pi \times (D_{N–S} \div 2) \times (D_{E–W} \div 2) \quad (1)$$

2.2. Tree-ring dating and chronology building

We polished the transversal surface of all samples using sandpapers with progressively finer grits (120–600 respectively) and cleaned the sample surface from wood powder using compressed air (Locosselli et al., 2019; 2020). The samples were then scanned (Epson Expression 12000XL) at 2400 dpi resolution. Tree rings were identified, marked, and measured for width using CooRecorder software (Maxwell and Larsson, 2021). We visually cross-dated them by analysing the year-to-year tree-ring width patterns (Stokes and Smiley, 1996). First, we evaluated common growth patterns from different radii of the same tree to check for false or missing rings. Next, we visually cross-dated radii from different trees within the same group (i.e., control or treatment) to assign the calendar year of each tree-ring formation. We calculated the mean tree-ring series using CDendro software (Maxwell and Larsson, 2021). Dating quality was checked using COFECHA software (Holmes, 1983). We further estimated the age of each tree, and used the method described by Hietz (2011) to estimate the age of samples without the pith.

We calculated the mean basal area increment (BAI) series using 'dplR' (Bunn, 2008), in R v.4.3.1 (R Core Team, 2023). To analyse the common growth signal, non-climatic trends were removed using a 12-year cubic smoothing spline, preserving only the high-frequency signal (Cook, 1987). We calculated the r-bar statistics – the average correlation between series (Briffa and Jones, 1990) – for the 12 studied years from 2011 to 2022, corresponding to six years before and six years after the start of irrigation in 2017.

2.3. Disturbance analyses and growth release detection

To statistically assess the impact of irrigation on tree growth, we conducted a Disturbance Analysis using the radial-growth averaging method (Nowacki and Abrams, 1997), chosen for its suitability with populations that are limited in sample size (Altman et al., 2014). Given the short length of the tree-ring series, the relative change of growth rate was calculated based on 15 years preceding (M_1) and 6 years after (M_2) the potential growth release, following Eq. 2:

$$\%GC = [(M_2 - M_1) \div M_1] \times 100 \quad (2)$$

where GC is the growth change, M_2 is the post-release period, and M_1 is the pre-release period (Nowacki and Abrams, 1997). We classified moderate growth release as ≥ 25 % ≤ 50 %, while major growth release was defined as > 50 % (Altman et al., 2014). The growth release is defined as the transition year after which a higher growth rate is kept sustained for at least six years. Thus, the target year to relate to irrigation is 2016/17. All analyses were performed using the package 'TRADER' (Altman et al., 2014) in R.

2.4. X-ray micro densitometry

We selected one radius from all trees for the micro-density analysis based on the strength of the common growth signal. We used a circular saw (Proxxon KS 230) to obtain thin transverse sections (~2 mm thickness), which were conditioned under controlled conditions (20 °C and 50 % relative humidity) until reaching 12 % moisture content (Ferreira and Tomazello-Filho, 2009). High-resolution wood density measurements were performed using an X-Ray densitometry chamber (Faxitron X-Ray) with a cellulose acetate wedge of known density (1.274 g/cm^3) to create a standard curve for density calibration. We analysed the digital radiographs using WinDendro Density 2017a software (Regent Instruments Inc.) to determine high-resolution wood density profiles (Pompa-García et al., 2024). We used local regression (LOESS) to characterize the wood density profiles. Then, we compared the radial density profiles, as well as the mean wood density in the earlywood (intra-annual position 0–25 %), middle (26–75 %), and latewood (76–100 %), between control and treatment trees, and the periods before and after the onset of irrigation. Density plots were used to assess the distribution of wood density data. The non-parametric Wilcoxon Signed-Rank test (Woolson, 2005) was applied to evaluate differences between periods in the same group, and the non-parametric Kolmorogov-Smirnov test (Berger and Zhou, 2014) to determine differences between the same period in different groups.

2.5. Cellulose extraction and stable carbon and oxygen isotopes analyses

We performed cellulose extraction adapted from Kagawa et al. (2015), and subsequently, analysed the stable carbon and oxygen isotopes for the 12 sampled trees for every year between 2011 and 2022. Each transversal section sample was placed inside supports made with perforated Teflon sheets, and submerged twice in 5 % NaOH solution within glass beakers, each immersion lasting 2 h, in a water bath at 70 °C. Then, we washed the samples with distilled water. Subsequently, we treated them four times with a 7.5 % $NaClO_2$ solution (pH 4 – 5), each treatment lasting 9 h. Finally, we washed the samples in distilled water at 60 °C. We froze the samples and freeze-dried them for 72 h.

We individualized the tree rings using a razor blade under a stereomicroscope and stored each tree-ring cellulose sample in one 2 mL microtube with 1 mL of deionized water, for homogenization in a Geno-Grinder for 10 min at 1200 RPM. We freeze-dried the homogenized samples, then weighted between 95 µg and 105 µg of cellulose and packed it inside tin capsules for $\delta^{13}C$ and silver capsules for $\delta^{18}O$, comprising a total of 288 samples. For $\delta^{13}C$ analysis the samples were combusted at 1020 °C, and pyrolyzed at 1350 °C for $\delta^{18}O$, both over glassy carbon in an EA-IRMS system, composed of a Delta V Advantage (ThermoScientific) Isotope Ration Mass Spectrometer (IRMS) coupled with a ConFlo IV and Element Analyser (EA; ThermoScientific).

We performed Principal Component Analyses (PCA), using

FactoMineR package in R (Husson et al., 2016) to evaluate the association between the tree-ring parameters in each group of trees. We calculated the 95 % confidence ellipses to test for differences between the two studied periods for each group of trees. We compared the behaviour of trees before and after 2017 for both control and treatment trees to ensure that any observed difference is due to irrigation only, and not any other factor such as climate.

3. Results

3.1. Growth patterns

The mean estimated ages, tree height, crown base height, and canopy area between control and treatment trees were not statistically different (Table 1). Control and treatment trees also share clear common long-term ontogenetic patterns in BAI series, displaying a growth decline between 1980 and 2000 related to the age-size trend (Fig. 2A). The r-bar, between the individual tree-ring width series was of 0.52 and 0.48 for control and treatment trees, respectively (Table 1). The correlation between de-trended control and treatment average tree-ring series was

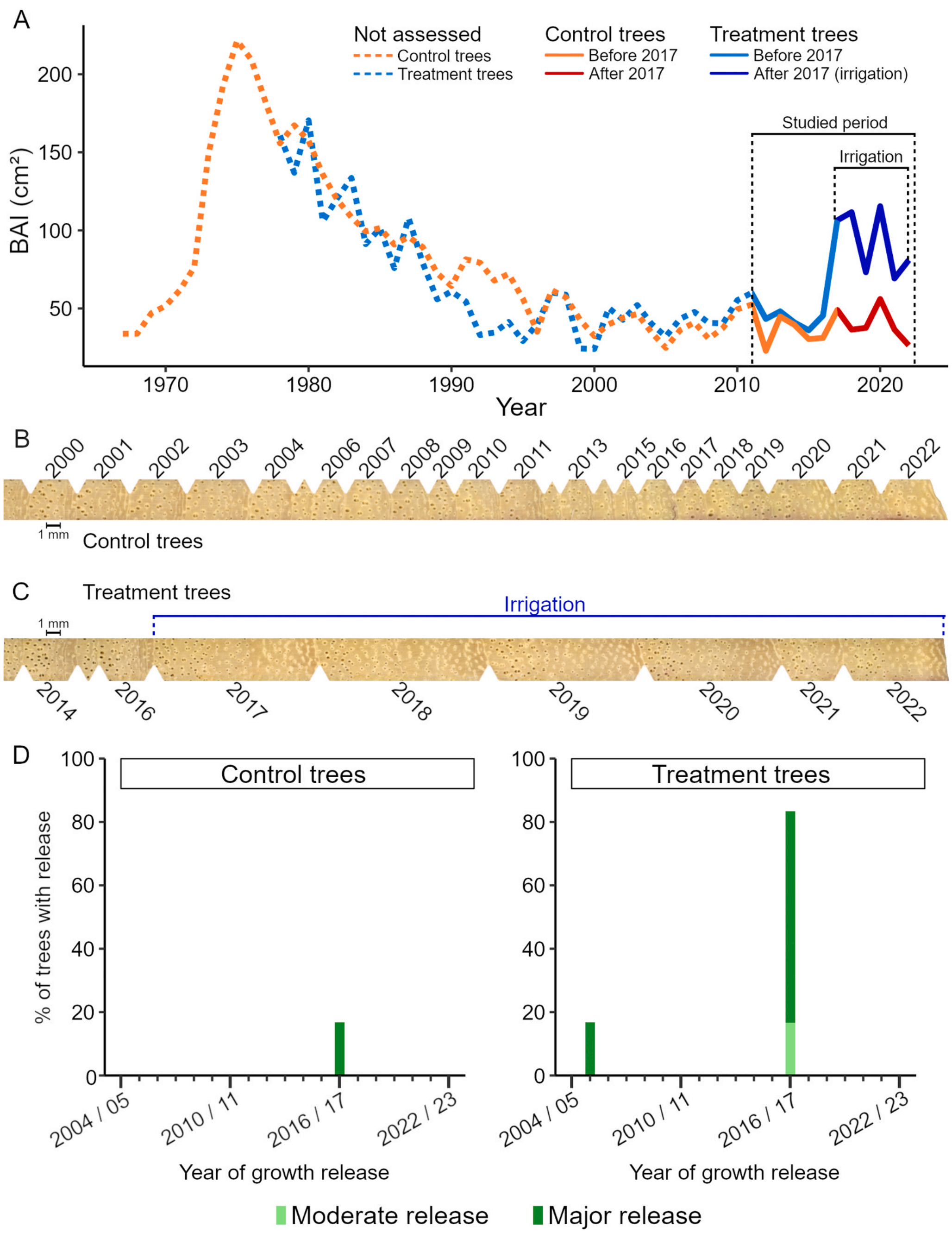

Fig. 2. A) Average basal area increment (BAI) values of the two studied groups of *Tipuana tipu* trees, illustrating the influence of the irrigation system on the treatment trees since its implementation in 2017. The dotted lines represent the period not assessed in this study, only used to reconstruct the BAI series and estimate the age of the trees. B, C) Examples of scanned images of two increment cores, from the control and treatment trees. D) The percentage of control and treatment trees with growth release by year. Light green bars represent moderate release (≥25 %≤50 % of sustained growth increase), and dark green bars represent major release (sustained growth increase >50 %).

also significant (r = 0.67, $p = 0.02$).

During the irrigation period, from 2017 to 2022, the average Basal Area Increment (BAI) of treatment trees was 130.3 % higher than that of control trees (92.81 cm^2/yr compared to 40.30 cm^2/yr, respectively). Also, treatment trees showed 103 % increase in the average BAI when comparing the periods before (45.63 cm^2/yr) and after 2017 (92.81 cm^2/yr) (Table 1; Fig. 2A). Not only did trees exhibited a higher growth rate, but it was sustained over the years of irrigation. The disturbance analysis identified a major growth release event experience by 80 % of the treatment trees in the transition between 2016 and 2017 (Fig. 2E), only shared by 20 % of the control trees (Figure D). This sustained release in the transition between 2016 and 2017 onwards, following irrigation, was the strongest for the studied period. No other growth release events in the studied tree-ring time series reached a comparable magnitude or involved such a high percentage of individuals.

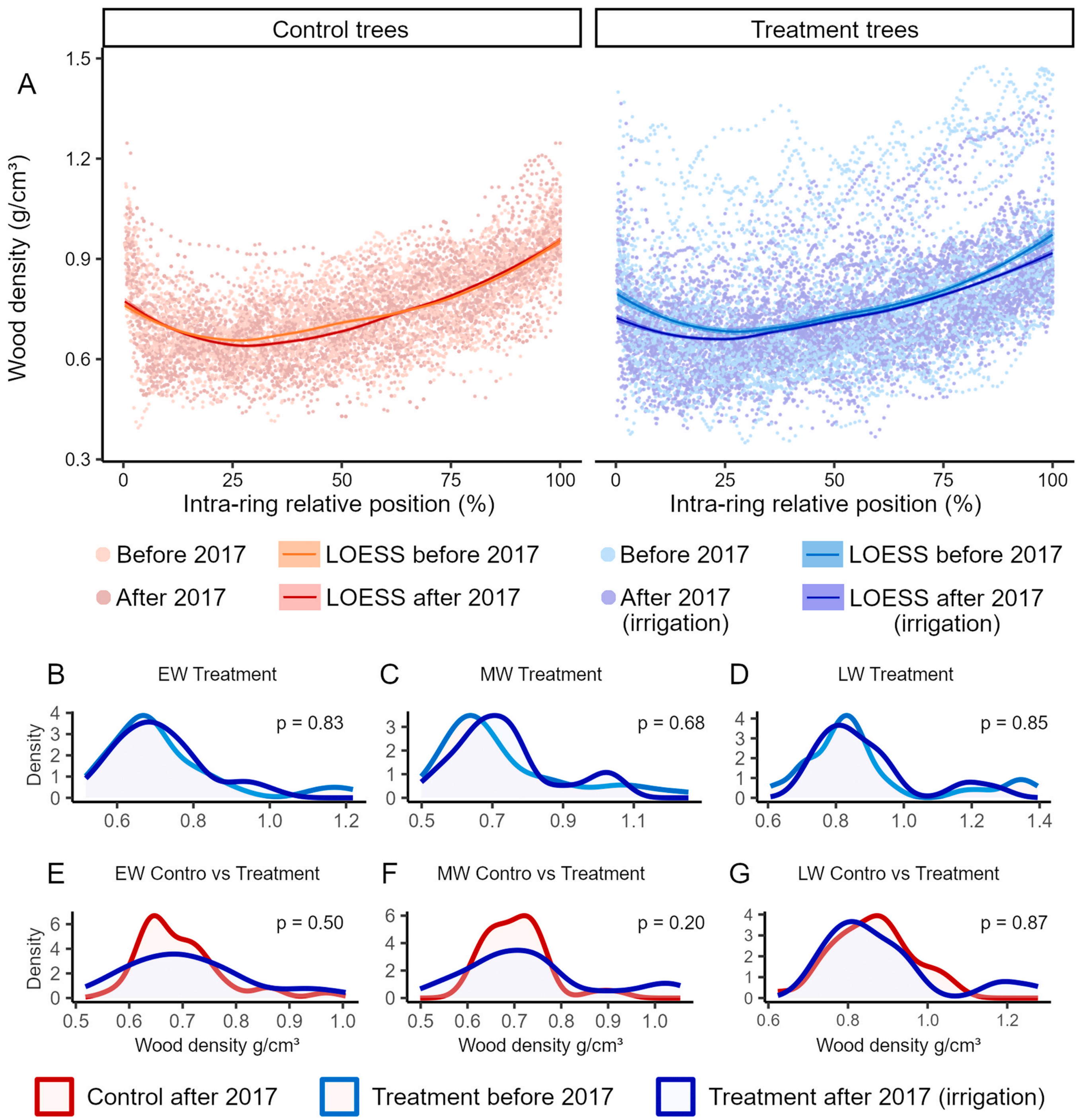

Fig. 3. Wood density profiles for the period before and after the onset of irrigation. (A) High-resolution wood density of each sample and the LOESS smoothed curves of the periods before and after 2017, the start of irrigation. (B to C) The Wilcoxon Signed-Rank test was used to detect the significance of density variations between the periods within the same group, before and after the onset of irrigation in 2017 in the treatment trees. (E to G) the Kolmogorov Smirnov test for variations between the control and treatment groups comparing the wood density after 2017. EW: earlywood; MW: middle; LW: latewood. Refer to Tables S4 and S5 in Supplementary Material for the effect size (r).

3.2. Wood density patterns

The high-resolution wood density series (Fig. 3A) illustrates the tree-ring wood density profile for control and treatment trees. The LOESS curves display the intra-annual patterns in wood density for both periods, before and after 2017, for each group of trees. All assessed tree rings exhibit a common increasing wood density pattern from the beginning to the end of the ring. The Wilcoxon Signed-Rank tests (Fig. 3B to D) and Kolmorogov-Smirnov tests (Fig. 3E to G) results for earlywood, middle, and latewood exhibited no significant differences in wood density before and after the irrigation in 2017, and neither between control and treatment trees.

3.3. $\delta^{13}C$ and $\delta^{18}O$ patterns

The average stable isotopic values for each ring from 2011 to 2022 for six control and six treatment trees are shown in Fig. 4. The $\delta^{13}C$ values of treatment trees substantially decreased after 2017. In contrast, no change in the range of values was observed after 2017 in the $\delta^{18}O$ signatures, showing similarities between control and treatment populations before the onset of irrigation.

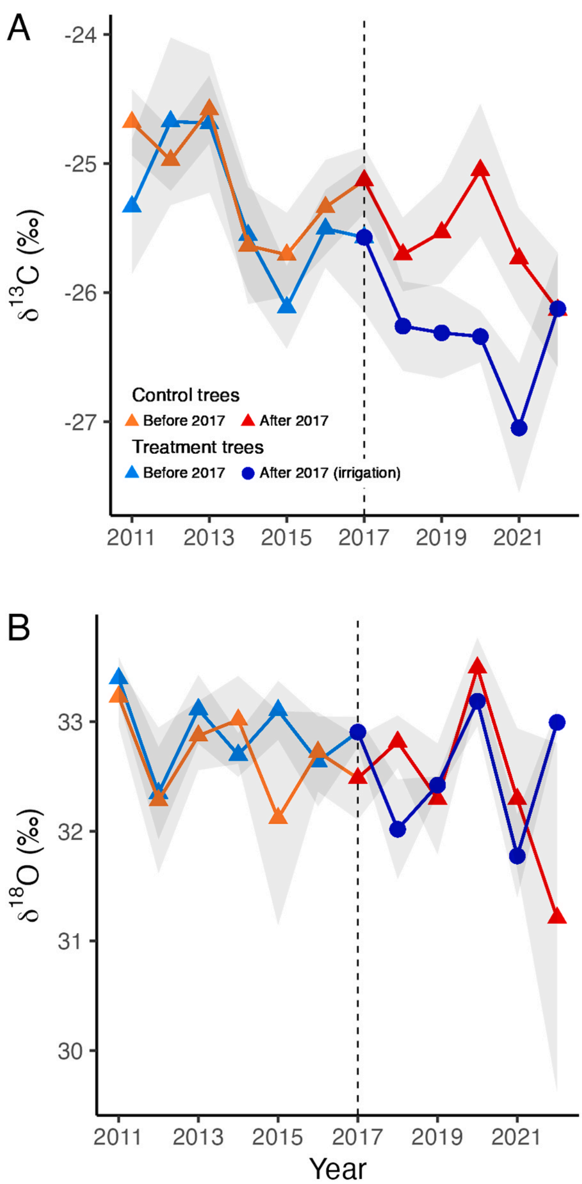

Fig. 4. Mean stable isotope series for control trees and treatment trees. The dotted black vertical line indicates the implementation of the irrigation system in 2017. The shaded area displays the 95 % confidence interval. (A) Stable carbon isotope signatures ($\delta^{13}C$) and (B) Stable oxygen isotope signatures ($\delta^{18}O$) of the studied trees.

Based on the Principal Component Analyses (PCA – Fig. 5), no significant difference was observed before and after 2017 in the control trees regarding BAI, wood density, $\delta^{13}C$, and $\delta^{18}O$, as revealed by the 95 % confidence superimposed ellipses. The first and second components explain together 81 % of data variability, and the vectors indicate a significant positive association between the two stable isotopes ($r = 0.58$, $p < 0.04$), and between growth and $\delta^{18}O$ ($r = 0.74$, $p < 0.01$, Tables S12, Figure S2). For treatment trees, the first and second components of the PCA explain 64.7 % of the data variability, revealing a markedly different pattern of association among tree-ring parameters. A significant difference is evident between tree rings before and after 2017, revealed by the 95 % confidence non-superimposed ellipses. Under irrigation, trees exhibit higher BAI and lower $\delta^{13}C$ and $\delta^{18}O$, while wood density remains orthogonal to the axis of average tree-ring variability.

4. Discussion

Comparable growing conditions across different management regimes are essential to isolate the effect of real-world irrigation on mature street trees (Madrigal-González et al., 2025). The studied trees have similar ages, average DBH, and are exposed to the same environmental conditions (Fig. 1) confirmed by the strong common ontogenetic growth trends between the control and treatment trees before 2017 (Fig. 2). This careful selection of the study site, combined with the multi-proxy approach, likely compensates for the limited sample size in this dendroecological study (Leavitt, 2010; Miyahara et al., 2022), yielding robust results on the impacts of irrigation on *Tipuana tipu* trees.

The benefits of irrigation have been largely reported for young specimens transplanted from nurseries to the streets, a critical moment for trees to establish a rooting system for anchorage and self-sustained water uptake (Koeser et al., 2014, Pearson et al., 2014). Early irrigation has proven benefits in terms of leaf water potential, growth and survival of young trees, which tend to show an initial strong positive impact on growth only during the initial years of irrigation (e.g. Thom et al., 2022). In contrast, evidence for mature trees is scarcer. Studies tend to agree that mature trees also benefit from irrigation, displaying significant growth increases up to two-fold, like in *T. tipu* trees in Lisbon and *Cedrus* spp. also growing under the Mediterranean climate in Spain (Madrigal-González et al., 2025). This increase in growth rate cannot be explained by any factor other than irrigation and thus corroborates our first hypothesis. Not only do mature trees grow faster, but they are also able to sustain that higher growth rate for six years of more (Madrigal-González et al., 2025). Although growth responses are clear, this observation questions the role of the often-limited irrigation system coverage compared to the distribution of the root system of mature trees that spreads for several meters around their trunk (dos Santos et al., 2025). Still, the literature shows that trees respond to irrigation by adapting their rooting systems (Mohamadzade et al., 2021), and the irrigation supports additional moisture depth reaching active roots for prolonged periods (Luketich et al., 2019), particularly if trees are growing in wide tree lawns, as in the Duque de Saldanha Square.

While the growth increase is well-supported by the above literature, the absence of a significant reduction in wood density due to irrigation contradicts our second hypothesis. At both the interspecific and intraspecific levels, high grow rates are often linked to thin-walled and wide conductive cells, a strategy eventually linked to reduced wood density (e.g. Rathgeber, 2017; Zobel and Van Buijtenen, 2012). Water availability strongly influences this trade-off in urban and natural environments, allowing specimens to adjust to environmental changes (Wimmer and Downes, 2003). Changes in wood density often reflect variations in the latewood-to-earlywood ratio, with drought affecting tree-ring

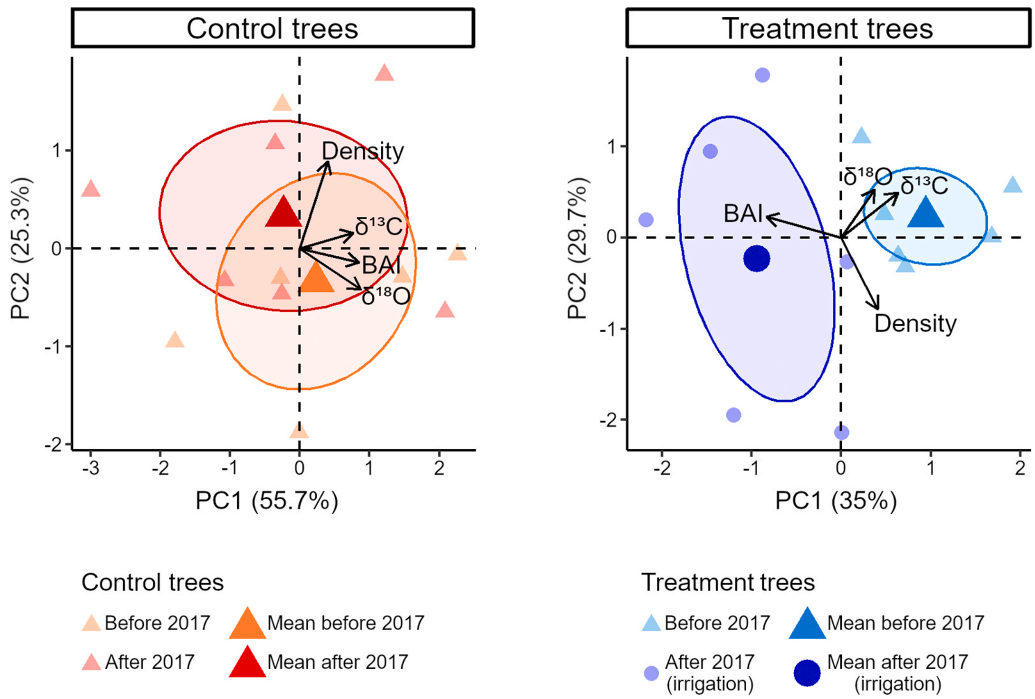

Fig. 5. Principal Component Analysis (PCA) showing the influence of dendrochronological parameters (black vectors) on the proportion of six tree rings formed before and six after the onset of the irrigation system, for both control and treatment trees. Refer to the Supplementary Materials for the PCA score matrix, eigenvalues, eigenvectors, and correlation matrix (Tables S8 – S13).

growth patterns depending on its timing and intensity during the growing season (Torresan et al., 2024). Increased growth rates and the consequent reduction in wood density can risk structural integrity of the trunk and pathogen infection (Larjavaara and Muller-Landau, 2010; Niklas and Spatz, 2010; Rathgeber, 2017). Yet, we found no evidence of sustained wood density despite the irrigation in *T. tipu* trees.

A key question remains: how do *T. tipu* trees coordinate xylogenesis with leaf-level physiological responses to irrigation? This is an essential question for understanding how trees integrate structural and functional responses to changes in water availability. The correlation between δ^{13}C and δ^{18}O suggests that trees are growing under limited stomatal conductance (Rodriguez-Caton et al., 2021), and likely the strong positive association between growth rate and δ^{18}O in the control trees suggests a high atmospheric demand during growth (Cintra et al., 2019). This observation contrasts the positive association between growth and δ^{13}C observed in the same species, but growing in the subtropical climate of the city of São Paulo, Brazil, pointing to a photosynthetic limitation during the wet summer (Locosselli et al., 2024). But this relationship can be reconciled by the fact that the studied trees in Lisbon are likely growing during the Mediterranean dry summer.

Similarly in another study in a Mediterranean climate city, Los Angeles in the United States, Ibsen et al. (2023) found that *T. tipu* has a relatively high leaf water potential compared to other drought-tolerant species like *Quercus agrifolia* and *Fraxinus uhdei*, also implying a fine stomatal control to cope with water limitations during the dry summer. Stomatal control in combination with the relatively high wood density compared to other 29 studied species in Los Angeles (Ibsen et al., 2023) likely confers the known drought tolerance of *T. tipu*. Conversely, treatment trees shifted from a positive to a negative association between growth and both δ^{13}C and δ^{18}O in the PCA (Fig. 5), indicating a higher growth rate supported by high stomatal conductance and gas exchange. This is further supported by the decrease in δ^{13}C values (Fig. 4A) and increase in BAI (Fig. 2A) from 2017 onwards.

Higher stomatal conductance and transpiration rates are a must-needed strategy to cope with the observed carbon demands (Liang et al., 2023) during the xylogenesis under irrigation. It is largely known that trees must rely on higher transpiration rates to support enhanced assimilation, unless trees lose less water per assimilated carbon by increasing water-use efficiency (McCarroll and Loader, 2004). According to the δ^{13}C results, *Tipuana tipu* trees relied on increased gas exchange to support assimilation. These leaf-level adjustments may not be enough for *T. tipu* trees to cope with the carbon demands under irrigation. Trees may also rely on larger crown and number of leaves. Although crown area does not differ significantly between groups, likely due to the small sample size, *T. tipu* treatment trees have on average 36 % wider crowns, consistent with other studies (e.g. Torres et al., 2024). Irrigation can also support a prolonged growing season, allowing trees to assimilate carbon longer to meet the xylogenesis demands (Bühler et al., 2006).

Therefore, continuous irrigation using an automatic system proved beneficial and effective for drought-tolerant *T. tipu* trees. The observed change in tree functioning under irrigation implies a greater contribution of these trees to the city and its inhabitants through enhanced ecosystem services. For instance, although not directly measured, the higher carbon assimilation and allocation in woody tissues can also result in a higher potential of tree carbon sequestration that contributes to offsetting urban carbon emissions (Zhang et al., 2022). In addition, higher transpiration rates lead to enhanced evaporative cooling and a local-scale temperature reduction potential of 0.67 °C (Haupt et al., 2025). As such, these trees will provide ecosystem services without the risk of decreased wood density and related mechanical failures or susceptibility to pathogens that will negatively affect tree growth and risk failure (Cavalari et al., 2024); factors that subsequently decrease the supply of tree benefits (Roman et al., 2013; Lafortezza and Chen, 2016). Altogether, these co-benefits can compensate for the financial and water costs of the irrigation system for *T. tipu* trees in Lisbon.

5. Conclusion

This multi-proxy tree-ring analysis approach advanced our understanding of how urban trees respond to site characteristics, management and maintenance practices such as the automatic irrigation system, highlighting the integrated physiological and structural responses to increased water availability. By focusing on *Tipuana tipu*, a key drought-tolerant tree species that is increasingly being used for urban landscapes worldwide and one of the most abundant in Lisbon, we demonstrated that a full-season automatic irrigation regime modulates tree physiology by enhancing stomatal conductance. Consequently, biomass production increased, supporting higher radial growth without any evidence of compromising wood density These findings question the assumption of the trade-off between growth and wood density in irrigated trees, showing that this species maintains wood density while benefiting from additional water resources. Normally, tree irrigation is a costly management tool in water-scarce cities. However, our results provide science-based evidence for urban planners and decision-makers to adopt automated irrigation systems as a reliable and water-use effective strategy even for drought-tolerant species. Thus, increased tree growth via efficient irrigation systems can make for an efficient method to enhance ecosystem service provision – including carbon sequestration, shade, and air cooling– without necessarily increasing risks associated with structural instability or reduced wood durability.

CRediT authorship contribution statement

Laia Andreu-Hayles: Writing – review & editing, Formal analysis, Conceptualization. **Souto Giulia Nunes de Aguir:** Writing – review & editing, Methodology. **Francisco William da Cruz:** Writing – review & editing, Resources, Methodology. **Francisco J Escobedo:** Writing – review & editing, Conceptualization. **Ana Paula Ramos:** Writing – review & editing, Methodology, Conceptualization. **Locosselli Giuliano:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Funding acquisition, Formal analysis, Conceptualization. **Augusto Akio Lucchezi Miyahara:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Milena Godoy-Veiga:** Writing – original draft, Supervision. **Tomazello Filho Mario:** Writing – review & editing, Resources, Methodology. **Filipa Maia:** Writing – review & editing, Conceptualization. **Ana Julia Francisco:** Writing – review & editing, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ufug.2026.129341.

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