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SHARED STRATEGIES FOR SURVIVAL: A COMPARATIVE ANALYSIS OF LEAF DRY MASS SUGGESTS SIMILAR DROUGHT TOLERANCE TRAITS WITHIN TAXODIACEAE SPECIES UNDER URBAN CONDITIONS

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Abstract

Urban environments expose trees to intense drought stress due to elevated temperatures and reduced soil moisture. Identifying woody, drought-resistant species is essential for sustainable landscaping. This study assessed leaf dry-matter content (LDMC) as an indicator of drought tolerance in three species from the former Taxodiaceae (now Cupressaceae) family - Metasequoia glyptostroboides, Taxodium distichum, and Sequoiadendron giganteum, growing in urban settings in the city of Sofia, Bulgaria. Leaf samples were collected from mature trees at different sites. Results did not show significant interspecific differences, although slight numerical variation in LDMC was observed among the species. These findings suggest that under the studied urban conditions, the species share similar physiological investment in leaf dry matter, indicating comparable levels of drought resistance. This may be due to shared adaptive strategies to urban stress or insufficient divergence in structural leaf traits under prevailing environmental conditions. Overall, LDMC proved to be a practical and reliable proxy for assessing drought resistance and could be used for proper coniferous species selection in urban areas.

Key words*: leaf dry-matter content, drought resistance, urban trees, Cupressaceae, Bulgaria.*

INTRODUCTION

Urbanization imposes multiple abiotic stress factors on trees such as elevated temperatures, reduced soil moisture, sealed and compacted soils, irregular precipitation patterns associated with urban heat islands (UHI), and pollution (Percival, 2023). Altogether, this increases evaporative demand and depicts a challenge for plants' water balance, which affects their vitality, resilience, and life expectancy, respectively (Tams et al., 2024). Understanding and identifying reliable and easy to measure functional traits that reflect woody species' drought responses and adaptation strategies is essential for sustainable landscape design and urban forest planning (Haase and Hellwig, 2022).

Under urban conditions, where environmental pressures are strong and consistent, different species may end up with similar trait values because only certain trait combinations can withstand repeated drought, heat, and soil alteration (Su et al., 2021). Studies across urban environments showed that leaf characteristics such as leaf dry-matter content (LDMC) and specific leaf area (SLA) could change in consistent directions as urban stress increases (Huang et al., 2020; Su et al, 2021). In this context, LDMC - the ratio between absolute dry leaf mass and fresh hydrated mass, is a widely used functional trait that integrates leaf structural investment and water content and often correlates with conservative water use strategies and drought tolerance in woody plants. LDMC is part of the leaf economics spectrum, as higher LDMC commonly indicates denser tissues, slower resource turnover, and greater tolerance of water deficit (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013; Tsvetkova & Anev, 2017).

The former family Taxodiaceae, now treated within Cupressaceae (Kusumi et al., 2000; Farjon, 2005), comprises conifers such as deciduous species *Metasequoia glyptostroboides* Hu & W.C. Cheng (dawn redwood), *Taxodium distichum* (L.) Rich. (bald cypress) and the evergreen species *Sequoiadendron giganteum* (Lindl.) J. Buchh. (giant sequoia).

The three species differ in life history and local habitat preferences in their native ranges (Farjon, 2008). They also differ in their adaptive strategies. *Taxodium distichum* tends toward structural adaptation under stress, with increased

wood density and reduced hydraulic vulnerability under stress. Its growth and hydraulic conductivity decline sharply under drought, which may compromise long-term performance in water-limited urban environments (Stiller, 2009). Physiological ecology studies on *M. glyptostroboides* (Vann, 2005) show moderate drought tolerance, but sensitivity during phenological growth stages, such as bud flush and shoot elongation. Species relative water-use efficiency and leaf traits may limit survival under episodic urban water deficits. *Sequoiadendron giganteum*, while capable of surviving multiyear droughts in favorable microsites, displays pronounced canopy stress and foliage dieback under extreme water limitation (Ray, 2017; Baeza et al., 2021). In Bulgaria, these species have been widely introduced and cultivated as ornamental trees, particularly in parks, arboreta, and historic landscapes (Tsavkov and Anisimova, 2013; Sokolov et al., 2016; Anisimova, 2018; Stoyanov and Anisimova, 2025). *Taxodium distichum* and *Sequoiadendron giganteum* have been present in the country for more than a century now (Ganchev and Prokopiev, 1959; Bonev, 1961, 1966, 1972), reflecting their long-standing horticultural value and adaptability to local conditions. Their application across diverse urban landscapes provides an important context for examining their functional traits under contemporary urban stressors.

In this context, the aim of this research is to analyse leaf dry-mass content (LDMC) as a functional trait linked to drought tolerance in the three conifer species: *Metasequoia glyptostroboides, Taxodium distichum,* and *Sequoiadendron giganteum.*

MATERIALS AND METHODS

Mature, healthy individuals of each species were sampled from different sites within Sofia's green infrastructure: Doctors' Garden, Sofia University Botanical Garden, the Bulgarian Academy of Sciences (BAS) Botanical Garden, Sofia Zoo, Sofia Tech Park, Borissova Garden, Knyazhevska Garden, Business Park Sofia, Garden "Algeer", Park "Pancharevo Lake", the BAS Scientific Laboratory Complex, "Frederich Joliot Curie" str., "Bulgaria" boulevard, the University of Forestry Arboretum, and South Park. Site distribution is shown on the map in Figure 1. These green areas represented a range of microclimatic and environmental conditions, differing in soil moisture availability, exposure to air pollution, different degrees of urban heat island influence, and different maintenance levels.

The field-based survey was carried out during the active growing season of 2025. To characterise the overall performance of the examined trees, the study included collecting data on the trees' height, diameter at breast height (DBH), and a phytosanitary status assessment. The latter was done using a five-grade scale adopted from Pencheva (2015), which classifies trees into the following categories: excellent condition (0), good condition (1), satisfactory condition (2), unsatisfactory condition (3), and poor condition or in a mortal state (4).

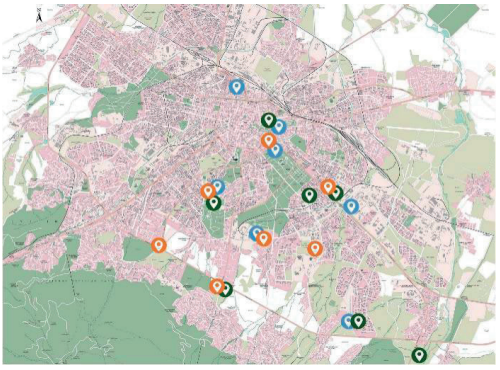

Figure 1. Map of the city of Sofia and site distribution Map underlay source: http://www.isofmap.bg/ (green – *Metasequoia glyptostroboides;* orange – *Sequoiadendron giganteum;* blue – *Taxodium distichum*)

To evaluate leaf dry-matter content, leaf material was collected from sun-exposed branches at mid-crown height to ensure comparability. Fresh leaf mass was measured immediately after sampling using a precision electronic balance. Samples were then oven-dried at 80°C to constant weight and weighed again to obtain dry mass. LDMC was calculated as the ratio of oven-dry mass to fresh mass for each individual and used as a proxy for tissue density and physiological investment in leaf structure. The gathered data were statistically tested for interspecific differences and site-related variation.

RESULTS AND DISCUSSIONS

A total of 21 individuals were examined, with 12 leaf samples collected from each specimen. Analysis of the specimen-level dataset provides additional context for interpreting LDMC patterns and drought-related performance (see Table 1.). The examined individuals were cultivated in a broad range of urban conditions, including pedestrian squares, street plantings, green areas adjacent to business and scientific complexes, and large urban parks in the city of Sofia.

According to Anisimova et al. (2025), Sofia's climate is characterized by pronounced temperature extremes, strong seasonal contrasts, and marked atmospheric drought during summer. Over the 10-year period from 2015 to 2024, daily maximum temperatures reached up to 48.1°C during late July and August, creating intense heat waves that contributed to early leaf discoloration and defoliation in sensitive tree species, particularly in non-irrigated urban areas. Relative humidity reached its lowest levels between June and September, frequently falling below 50%, and at times below 30%, indicating atmospheric drought conditions. Combined with limited irrigation and the urban heat island effect, these climatic stresses create challenging conditions for urban trees in Sofia.

The selected specimens also varied substantially in size and maturity: heights ranged from 8.2 to 21.7 m for *Metasequoia glyptostroboides*, 8.2 to 18.3 m for *Sequoiadendron giganteum*, and 12.4 to 16.4 m for *Taxodium distichum*, and DBH values reflecting similar variability. The phytosanitary status was generally good across all species, with most individuals classified in categories 0 and 1, although occasional specimens showed signs of decline, typically in street plantings or in sites exposed to pedestrian pressure. Site-specific characteristics include differing levels of shading, soil sealing, and management intensity. This highlighted pronounced differences in environmental stress: most street-planted individuals received no irrigation, semi-intensive maintenance prevailed in pedestrian squares, and only a subset of park specimens benefited from regular watering.

In particular, individuals planted in intensively maintained park settings tended to exhibit better phytosanitary conditions and more favourable growth parameters, whereas those in highly sealed, non-irrigated street environments showed increased stress indicators. Overall, the microhabitat conditions and management regimes vary widely across Sofia's urban landscape, highlighting the importance of considering functional traits such as LDMC in identifying species capable of maintaining stable performance under diverse and drought-prone urban conditions.

Table 1. Characteristics of sampled specimens and their specific site conditions in Sofia's green infrastructure

№	Species	Specimen characteristics			Site	GI[1] element	Other site specifics		
		Height (m)	DBH (cm)	Phytosanitary condition			Irrigation	Maintanace level	Planting type
1	*Metasequoia glyptostroboides*	17	45	0	BAS Botanical Garden	Urban garden / park	Yes	Intensive	Group
2	*Metasequoia glyptostroboides*	15,60	65	1	BAS Scientific Laboratory Complex	Pedestrian square	No	Semi-intensive	Solitaire
3	*Metasequoia glyptostroboides*	15	52	1	Business Park Sofia	Pedestrian square	No	Intensive	Solitaire
4	*Metasequoia glyptostroboides*	14	38	2	"Frederich Joliot Curie" str.	Street plantings	No	Extensive	Solitaire
5	*Metasequoia glyptostroboides*	18.20	71	0	Park "Pancharevo Lake"	Urban garden / park	No	Semi-intensive	Group
6	*Metasequoia glyptostroboides*	21	67	0	Sofia University Botanical Garden	Urban garden / park	Yes	Intensive	Group
7	*Metasequoia glyptostroboides*	9	33	0	South Park	Urban garden / park	No	Extensive	Group
8	*Sequoiadendron giganteum*	17.40	108	0	BAS Botanical Garden	Urban garden / park	No	Intensive	Solitaire
9	*Sequoiadendron giganteum*	16.20	93	1	BAS Scientific Laboratory Complex	Pedestrian square	No	Semi-intensive	Group
10	*Sequoiadendron giganteum*	17.10	81.50	1	"Bulgaria" boulevard	Street plantings	No	Extensive	Group
11	*Sequoiadendron giganteum*	8.20	64	2	Knyazhevska Garden	Pedestrian square	No	Intensive	Solitaire

12	*Sequoiadendron giganteum*	18.30	106	0	Sofia Zoo	Urban garden / park	No	Intensive	Group
13	*Sequoiadendron giganteum*	13.60	45.50	1	South Park	Urban garden / park	No	Extensive	Group
14	*Sequoiadendron giganteum*	16	57	1	The University of Forestry Arboretum	Urban garden / park	No	Semi-intensive	Group
15	*Taxodium distichum*	16	41	2	Borissova Garden	Urban garden / park	No	Semi-intensive	Solitaire
16	*Taxodium distichum*	12.40	38	1	Business Park Sofia	Street plantings	Yes	Intensive	Solitaire
17	*Taxodium distichum*	14.70	44	1	Doctors' Garden	Pedestrian square	No	Semi-intensive	Solitaire
18	*Taxodium distichum*	13.80	52	0	Garden "Algeer"	Pedestrian square	No	Semi-intensive	Solitaire
19	*Taxodium distichum*	7	16	0	Sofia Tech Park	Urban garden / park	Yes	Intensive	Solitaire
20	*Taxodium distichum*	12.60	36	1	Sofia Zoo	Urban garden / park	No	Intensive	Group
21	*Taxodium distichum*	13.60	39	1	South Park	Urban garden / park	No	Extensive	Group

[1]GI – Green Infrastructure

The LDMC raw dataset (n = 21) showed moderate variation both among species and across sites. The LDMC raw dataset (n = 21) showed moderate variation both among species and across sites. Summary descriptive statistics (Figure 2.) indicated that *M. glyptostroboides* exhibited the lowest median LDMC (0.3153), *T. distichum* the highest (0.3587), and *S. giganteum* showed an intermediate value.

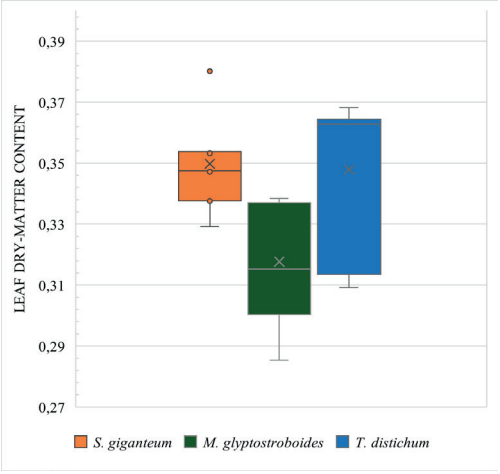

Figure 2. Distribution of leaf dry-matter content (LDMC) for *S. giganteum, M. glyptostroboides,* and *T. distichum*

These patterns were reflected across sampling locations. *S. giganteum* exhibited its highest LDMC at South Park (0.3802), *M. glyptostroboides* - its lowest at "Frederich Joliot Curie" Street (0.2853), while *T. distichum* showed comparatively consistent LDMC values across sites (0.3092-0.3682). Given the right-skewed distribution of the data and unequal sample sizes, a Kruskal-Wallis test was applied to test for interspecific differences in LDMC. The results ($x^2 = 2.375$, df = 2, $p = 0.305 > 0.05$) indicated no statistically significant differences among the three species. Mean ranks followed the trend *T. distichum* (13.17) > *S. giganteum* (11.88) > *M. glyptostroboides* (8.14), but these differences were not statistically meaningful. High within-species variation, likely driven by microenvironmental heterogeneity, appears to overshadow differences attributable to species' identity.

Despite the lack of significant interspecific differences, the overall LDMC patterns support its use as a proxy for identifying drought-resistant trees. The convergence toward similar LDMC values suggests that all three taxa adopt comparable water-conserving leaf architectures when exposed to Sofia's harsh urban microclimate. Such functional convergence is consistent with environmental filtering, where only certain trait configurations particularly support survival under combined heat, drought, and pollution stress. This interpretation aligns with the "leaf economics spectrum" (LES) described by Wright et al. (2004), in which LDMC is inversely related to growth rate and nutrient turnover, and is associated with conservative resource-use strategies.

These findings are further supported by broader empirical evidence. Münchinger et al. (2023) demonstrated in a comparative study that drought-tolerant conifers typically possess thicker and more rigid leaves, lower specific leaf area (SLA), and greater tissue density, all traits closely aligned with higher LDMC and increased resistance to drought stress. Likewise, global analyses confirm that LDMC responds not only to phylogenetic constraints but also to

environmental pressures such as aridity and climatic stress (Dai et al., 2025).

In the present study, LDMC values did not consistently correlate with site-specific environmental variables (soil moisture, pollution proxies, or microclimate conditions), suggesting that within Sofia's urban context, both species identity and local site variation exert limited influence on leaf structural investment. Pooled values across species and sites fall within the lower-to-moderate LDMC range typical of evergreen conifers in temperate and urban settings, which range from approximately 0.25 to 0.40 g g^{-1} (Tsvetkova & Anev, 2017), further reinforcing the idea that LDMC serves as an effective comparative indicator of drought resilience under urban stress conditions. The reduced spread of LDMC across the dataset also suggests that urban conditions constrain trait expression, narrowing the variation these species would otherwise display along the LES. However, LDMC represents only one dimension of drought tolerance. While it is a powerful and easily measured proxy for identifying species with more conservative water-use strategies, it does not directly capture hydraulic properties such as xylem vulnerability, stomatal behavior, rooting depth, phenology, or whole-plant water dynamics (Sterck et al., 2024). Studies of drought-induced conifer mortality further show that leaf traits alone cannot fully predict survival, as whole-plant hydraulic resilience and growth legacies often drive mortality risk under prolonged or repeated stress (Song et al., 2022). Similarly, weak coordination has been observed between LDMC and direct physiological indicators of drought tolerance, such as the turgor loss point or stomatal regulation thresholds (Vásquez, 2025).

CONCLUSIONS

Taken together, these findings highlight both the value and the limitations of LDMC as a functional trait proxy. The three studied species - *Metasequoia glyptostroboides, Taxodium distichum,* and *Sequoiadendron giganteum,* exhibited similar LDMC values. This indicates that they share a broadly convergent leaf structural investment, suited to drought-prone urban environments, and potentially similar drought-related strategies.

However, because LDMC reflects only one aspect of plant water-use strategy, these outcomes should be regarded as preliminary. A more comprehensive assessment of drought tolerance would require the investigation of additional functional traits and whole-plant hydraulic metrics.

As a pilot study, this research underscores the importance of trait-based approaches in guiding species selection for planning urban GI plantings. Importantly, the observed LDMC ranges align with established ecological strategies documented in the literature, demonstrating that even in the absence of statistical differences, functional traits offer meaningful insight into urban tree resilience and management needs. Even so, LDMC remains a practical indicator for identifying resilient woody species for urban landscaping under climate change, capable of withstanding prolonged heat, frequent drought events, and reduced moisture availability. The long-term survival and performance of the studied Taxodiaceae species in urban plantings in Sofia depend on careful micro-site selection and management.

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