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Responses of Local and Non-Local Tropical Plant Seedling Functional Traits to Simulated Drought

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Abstract: The increasing frequency and severity of drought, driven by global climate change, has emerged as a critical factor constraining the growth of landscaping trees in urban ecosystems. The local or non-local status of tree species is an important driver of plant function traits, which regulate plant performance. However, the differential impact of varying drought intensities on the functional traits of both non-local and local trees remains poorly understood. This study investigated the responses of leaf and root traits of seven typical tropical landscaping tree seedlings (three local species and four non-local species) to simulated drought conditions in a year-long greenhouse experiment. The results showed that drought significantly increased the specific leaf area, leaf thickness, and root exudate rate, while reducing root nitrogen content and leaf dry matter content, with differences observed between local and non-local species. The non-local species exhibited pronounced fluctuations in leaf and root traits between control and drought conditions. Local species tended to enhance the relationship between leaves and roots under drought, while non-local species showed a weakening of this relationship. Principal component analysis revealed that local species adopted a more conservative strategy under control conditions and a more acquisitive strategy under drought, while root strategies remained stable across conditions. The subordination function method in fuzzy mathematics identified *Terminalia neotaliala* (non-local) as the most drought-resistant species and *Artocarpus heterophyllus* (non-local) as the least drought-resistant species. Non-local species demonstrated greater drought resistance in leaf traits compared to local species, but the opposite was observed for root traits. These results underscore the importance of understanding the species-specific responses of local and non-local trees to drought stress. These findings provide a scientific basis for developing effective screening and management protocols for drought-resistant landscaping tree species.

Keywords: drought stress; leaf functional traits; root functional traits; local tree species; non-local species; landscaping trees

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1. Introduction

Climate change is expected to result in increased occurrences of more severe, prolonged droughts in the future, impacting ecosystem dynamics [1]. Understanding the mechanisms by which plants adapt to environmental changes is critical in the face of drought events. Plant functional traits—key characteristics that define a species' ability to respond to environmental stress—play a very pivotal role in mediating ecological processes and shaping ecosystem resilience [2]. Given the intensification of drought events, there is an urgent need to explore how plants adjust their functional traits to cope with these stressors [3,4].

Leaves and roots are key organs that perform the acquisition and storage of plant resources such as water, nutrients, and photosynthates [5–7]. Their functional traits, including morphological, biochemical, and physiological characteristics, are highly responsive to variations in water availability, making them essential indicators of ecosystem responses to drought [8–10]. In particular, the study of leaf and root traits provides critical insights into the adaptive strategies that plants employ under drought conditions, reflecting broader ecological processes both above and below ground [11,12]. Plants respond by modulating their leaf structures and physiological functions, such as closing stomata and altering photosynthetic rates, to conserve resources under water-deficient conditions [13,14]. Plants also change leaf morphological and biochemical traits in response to water scarcity. Thus, as precipitation decreases, leaf area and dry matter content of *Leymus chinensis* showed a decreasing trend, but specific leaf area and leaf nitrogen content significantly increased [14]. Additionally, fine roots, which directly absorb soil moisture, often exhibit adaptive strategies like increased specific root length and reduced diameter to optimize water uptake under drought stress [15–19]. Furthermore, drought can significantly influence root exudate production, with plants releasing more exudates to modulate soil microbial activities, aiding nutrient acquisition and enhancing stress tolerance [20]. However, some studies have indicated that the sensitivity of root traits to changes in precipitation is generally lower than that of leaf traits, with root trait adjustments often occurring when precipitation deviates significantly from the mean [20–22]. Therefore, the response of root traits to drought is still uncertain. The relationship between plant leaves and roots under drought conditions is complex and may vary between species, with some studies suggesting that these traits may shift from synergistic to trade-off relationships as drought intensifies [23]. Despite the importance of this distinction, much of the existing research has focused on the functional traits of individual plant organs (e.g., leaves or roots) in isolation, with limited integration of how these traits interact under drought conditions [24,25]. Therefore, quantifying the variation and coordination patterns of plant functional traits by species is crucial for gaining a deeper understanding of the mechanisms by which plants adapt to environmental changes [26,27].

In terrestrial ecosystems, urban ecosystems are particularly vulnerable to drought due to the combined pressures of climate change and increasing urbanization [28]. Landscaping trees play a vital role in these ecosystems, contributing not only to the aesthetic quality of urban spaces but also providing essential ecological services such as carbon sequestration, temperature regulation, and air purification [29,30]. The escalating effects of urbanization and global climate change have placed landscaping trees under increasing drought stress, with more frequent and prolonged drought events posing a significant threat [31]. Urban conditions such as altered hydrology, restricted root space, and infrastructural barriers further exacerbate this stress, underscoring the need for drought-tolerant tree species in sustainable urban planning [32,33]. Selecting species that can endure the harsh conditions of urban environments, including heat and drought stress, is a critical challenge as urban green spaces become increasingly limited [34,35]. Combining local and non-local tree species is a common approach in landscaping design and plant selection. Local species, having evolved in local environmental conditions, are often expected to be better adapted to regional climate and soil characteristics, with traits such as water-use efficiency, root depth, and leaf morphology [36]. On the other hand, non-local species, despite lacking these evolutionary adaptations, may employ alternative strategies to survive local stressors, in some cases outperforming local species under certain conditions [36]. Previous research has shown that the adaptability of introduced or invasive species to new environments often stems from differences in functional traits when compared to local species [33,37]. Therefore, understanding the functional traits of both local and non-local species is essential for assessing their respective drought tolerance mechanisms and informing species selection for urban landscapes [38,39]. This provides critical insights into the resource-use strategies and resilience of these species, helping to identify those best suited for the increasingly harsh conditions of urban ecosystems.

The seedling stage of plants is more sensitive to drought than the mature stage [40], making it crucial for further plants' existence and development. Therefore, studying seedlings is more relevant across all functional groups, not just trees [41,42]. By evaluating the response of seedling traits to drought, we can better understand how local and non-local species cope with drought conditions and aim to reveal the potential mechanisms behind the distribution patterns of tree species [43]. In this study, a short-term experiment simulating reduced rainfall was carried out with seven landscaping tree seedlings (local species: *Areca catechu*, *Livistona chinensis*, and *Artocarpus heterophyllus*; non-local species: *Spathodea campanulata*, *Samanea saman*, *Terminalia neotaliala*, and *Handroanthus chrysanthus*) (Figure 1), in a common greenhouse in Hainan Island. We investigated the morphological, biochemical, and physiological traits of leaves and roots under control and drought conditions, with a focus on understanding how these traits vary and coordinate in response to drought stress. We hypothesized that local and non-local tree species display distinct leaf and root responses to drought conditions, reflecting their adaptive strategies in response to varying environmental stressors. By elucidating the response patterns of functional leaf and fine root traits in common landscaping trees, this study aims to provide theoretical guidance for the selection, protection, and management of urban trees, contributing to the broader goal of enhancing urban ecosystem resilience in the face of global environmental change.

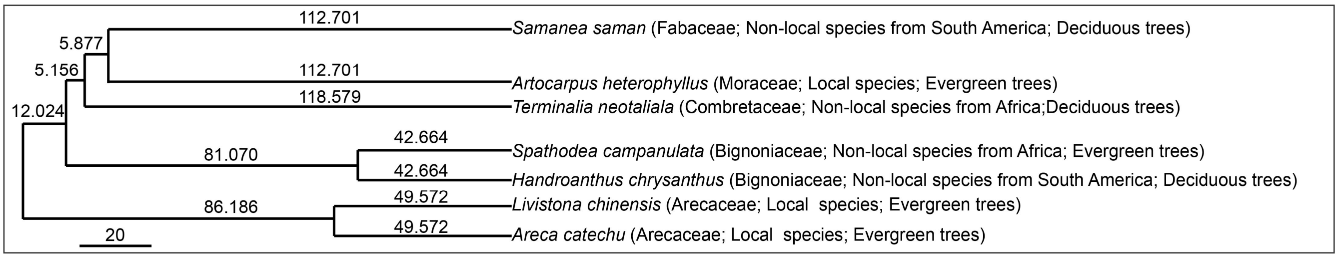

Figure 1. Evolutionary tree and characteristics of seven landscaping trees. The numbers on the branches of the evolutionary tree represent phylogenetic distances between species.

2. Materials and Methods

2.1. Study Site Information

Hainan Province is located at the southernmost edge of China, extending 18°09′–20°11′ N and 108°36′–111°03′ E. The study region belongs to a tropical monsoon humid climate, with an average annual precipitation of approximately 1600 mm (rainy season: 1300 mm; dry season: 300 mm). There is an obvious rainy season marked by frequent rainfall (from May to October) and a season during which rain is infrequent (from November to April of the following year). The average annual temperature is 23.29 °C. The typical soil in Hainan Province is lateritic soil. In typical garden construction, local and non-local tree species are used alike in landscaping to enhance the ability of gardens to resist plant mortality. Common local tree species include *L. chinensis*, *A. catechu*, *Terminalia catalpa*, and *Cocos nucifera* [44]. Common non-local tree species include *Pterocarpus indicus*, *Handroanthus chrysanthus*, *Spathodea campanulata*, *Khaya senegalensis*, and *Lagerstroemia speciosa*.

2.2. Experimental Design

In this study, three local landscaping tree species (*L. chinensis*, *A. catechu*, and *A. heterophyllus*) and four non-local landscaping tree species (*S. campanulata*, *Samanea saman*, *Terminalia neotaliala*, and *H. chrysanthus*) commonly seen in tropical areas were selected for seedling study (one-year old; growing well, without diseases, pests, nor damage) (Figures 1 and 2). Among the potted plants, a control group and a drought treatment group were set up, with 8 replicates for each treatment group. The experimental soil was taken from the upper 0–20 cm of forest land soil in the experimental area. After air drying and removing impurities, such as stones, through a 3 mm sieve, the seedlings were planted in the soil. An equal amount of soil was shoveled into each flowerpot (measuring 20 cm in diameter and 22 cm in height), and one seedling per pot was planted. April 2022, 112 seedlings, sprouted in March of last year, were potted in 112 pots, and the pots were randomly distributed throughout a greenhouse. To ensure that the seedlings would adapt to the soil environment and survive, all flowerpots were continuously watered with a normal amount of water (soil moisture contents at field capacity) for 6 weeks (three times a week) before the drought treatment began. In this experiment, the control groups were irrigated with water amounts that matched the long-term annual average precipitation observed in Hainan Province (1600 mm), while the drought groups received only two-thirds of this average. From May to October, pots were watered three times a week, with the control group receiving 1070 mL (approximately 360 mL/time) per week and the drought treatment group receiving 717 mL (approximately 240 mL/time) (Figure 2). From November to April of the following year, the control and drought groups received 247 mL (approximately 82 mL/time) and 165 mL (approximately 55 mL/time) of deionized water per week, respectively. The positions of potted plants were changed every week to avoid positioning effects. After one growth season (one year) of drought treatment, the functional leaf and root traits were collected and measured in the seven tree species.

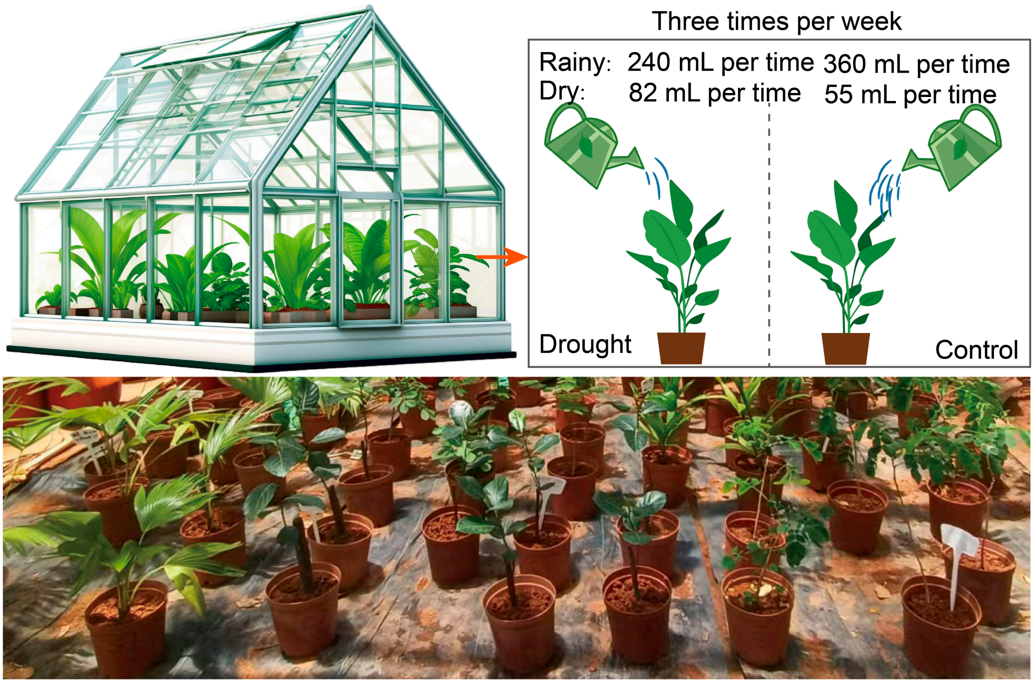

Figure 2. Experimental design and simulation of drought conditions.

2.3. Sample Collection and Determination

To evaluate the effects of the drought treatment on soil moisture, soil water content was measured before the start of the dry season using the ring knife method. This involved collecting soil samples with a cylindrical ring knife (Eijkelkamp, Giesbeek, The Netherlands) and immediately weighing them to determine the wet weight. According to gravimetric analysis method, the samples were then oven-dried at 105 °C for 72 h to achieve a constant dry weight. The soil water content was calculated as the difference between the wet and dry weights. After the drought treatment, all insect-free mature leaves were collected from each tree species sample, and the thicknesses (LT) of 3–5 leaves per plant were measured using a digital caliper with an accuracy of 0.01 mm, taking measurements at three different points (base, middle, and tip) of each leaf to ensure accuracy, and the average thickness was recorded for each plant. Subsequently, chlorophyll was extracted from fresh leaves by finely chopping them and immersing them in either acetone in the dark for twelve hours. The mixture was then filtered to obtain a clarified extract, which was analyzed spectrophotometrically at 665 nm for chlorophyll A and 649 nm for chlorophyll B, respectively. These measurements were then used to calculate the total chlorophyll content (TChl, mg kg^{-1}).

The fresh weight of leaves (g) was determined. We scanned the fresh leaves using a scanner and calculated the leaf area (LA, cm^2) using ImageJ software (version 1.54a). Leaves were then oven-dried (48 h, 65 °C), weighed (g), finely ground, and analyzed for leaf carbon content (LCC, mg g^{-1}) and nitrogen content (LNC, mg g^{-1}) using an elemental analyzer (Elemental vario MACRO cube, Elemental Analysensysteme GmbH, Hanau City, Germany). Specific leaf area (SLA, cm^2 g^{-1}) was calculated as the ratio of LA to dried weight of leaves. The leaf dry matter content (LDMC, mg g^{-1}) was calculated as the ratio of dried weight of leaves to fresh weight of leaves.

2.4. Collection of Root Exudates

After measuring the leaf characteristics, we carefully separated the root system of the entire plant from the soil, to minimize damage to the root system, and cleaned the soil with deionized water. Then, the roots were immersed in a container filled with carbon-free nutrient solution (0.1 mM KH_2PO_4, 0.2 mM K_2SO_4, 0.2 mM $MgSO_4$, 0.3 mM $CaCl_2$). To prevent the roots from drying and to avoid exposure to sunlight, we covered the container with aluminum foil and wrapped it in a black plastic bag. Then, we put the covered container back into the greenhouse for cultivation. After 24 h, the solution was collected from the container using a syringe and was then immediately filtered through a 0.22 μ m filter. The total organic carbon in the exudate was analyzed using a TOC analyzer (TOC-VCPH, Shimadzu, Japan). The root exudation rate (RE, mg g^{-1} h^{-1} L^{-1}) was calculated based on root mass, and the formula is as follows:

$$RE = \frac{REC\left(\mathrm{mg\ L^{-1}}\right)}{RDW(\mathrm{g}) \times Collection\ Time(\mathrm{h})} \tag{1}$$

RE is root exudation rate; REC is total carbon content of root exudates; RDW is root dry weight.

2.5. Collection and Measurement of Root Traits

After the collection of root exudates was complete, the roots were cut off from the plant to determine root morphological and biochemical properties. Root samples were scanned using a root scanner (Epson Perfection v850 Pro; Epson, ON, Canada), and the scanned images were analyzed using WinRHIZO Pro 2020a (Regent Instruments Inc., Quebec City, QC, Canada), which measures root diameter (RD, mm), root length (cm), root surface area (RSA, cm^2), and root volume (cm^3). After measurement, the root sample was dried in an oven at 65 °C to a constant weight to obtain root dry weight (RDW, g). Root tissue density (RTD, g cm^{-3}) is the ratio of root dry weight to root volume, and specific root length (SRL, cm g^{-1}) is the ratio of root length to root dry weight. The root carbon content (RCC, mg g^{-1}) and root nitrogen content (RNC, mg g^{-1}) were measured using an elemental analyzer (Elemental vario MACRO cube, Elemental Analysensysteme GmbH, Hanau City, Germany). Then, the root carbon to nitrogen ratio (RCC/RNC) could be calculated.

2.6. Statistical Analysis

Statistical analyses and figure illustrations were performed using R version 4.3.3 (https://www.r-project.org/ (accessed on 29 February 2024)) [45]. Before analysis, Kolmogorov–Smirnov and Levene's tests were used to check if the data met the normality and homogeneity of variance requirements. If it did not follow a normal distribution, square root or logarithmic transformation was performed. Two-way analysis of variance (ANOVA) was used to analyze the effects of drought and species on leaf and root traits. One-way ANOVA was used to analyze the differences in leaf and root morphological traits between different tree species. We also evaluated the effect of local and non-local tree species on these traits. Tukey's honey significant difference was used for multiple post hoc tests. Pearson correlation analysis was used to investigate the correlation between leaf and root morphological traits both under control and drought conditions, as well as the correlation between local and non-local tree species under drought conditions. This correlation analysis was used to identify how these traits interact and change in response to drought stress. The variation patterns of plant leaf and root traits both under control and drought conditions were analyzed using principal component analysis. Prior to the analysis, the data were standardized to ensure all traits had the same unit variance, preventing disproportionate influence from traits with larger variances. Additionally, highly correlated traits and ratio-composed traits were excluded to avoid inflation or over-representation effects in the analysis. T-tests were used to compare the differences in species distribution on the principal component axes under different treatments. In addition, phylogenetic trees and distance among seven species were obtained from the R ape package [46].

To evaluate how well seven different tree species resist drought, we used a method from fuzzy mathematics called the subordination function method [47]. All original test data were carried out through the standard transformation. The formula for calculating the subordination function value is as follows:

$$\mathrm{U}(X_{\mathrm{i}}) = \frac{(X_{\mathrm{i}} - X_{\mathrm{min}})}{(X_{\mathrm{max}} - X_{\mathrm{min}})} \tag{2}$$

$$\mathrm{U}(X_{\mathrm{i}}) = 1 - \frac{(X_{\mathrm{i}} - X_{\mathrm{min}})}{(X_{\mathrm{max}} - X_{\mathrm{min}})} (\mathbf{i} = 1, 2, 3 \ldots \boldsymbol{n}) \tag{3}$$

In the formula, X_{i} is the measured value of any parameter in seven species under drought treatment. Drought resistance was preliminarily assessed by measuring specific plant traits in seven species under drought stress. For each parameter (X_{i}), we determined whether a higher or lower value would indicate better drought resistance based on established physiological and ecological principles.

For each parameter, we identified the minimum (X_{min}) and maximum values (X_{max}) observed across all the tree species. For traits where higher values are indicative of better drought resistance (e.g., thicker RD), Formula (2) was applied. Conversely, for traits where lower values are beneficial for drought resistance (e.g., lower LA), Formula (3) was used. We repeated the calculation for all relevant traits (both leaf and root traits) for each tree species. Then, we grouped the leaf and root traits for each tree species and calculated the sum and average of all values, representing its overall drought resistance. The drought resistance value for each tree species was determined by calculating the average of all its plant traits. Comprehensive evaluation value (CEV) for local and non-local species were obtained by calculating the drought resistance values of all tree species within each group. Finally, we derived a standardized drought resistance score. A larger average value represents that a plant has a stronger resistance to drought and vice versa.

3. Results

3.1. Differences in Leaf and Root Traits of Landscaping Trees Under Drought

In this study, drought treatment significantly reduced soil water content (Figure 3; $p < 0.001$). Drought significantly increased SLA, LT, SRL, RE, and RCC/RNC and significantly reduced TChl, LDMC, RNC, and RSA (Table 1, $p < 0.05$). In addition, different species also had varying impacts on leaf and root traits (Figure 4, $p < 0.05$). Only LDMC and LT were affected by drought and species interactions ($p < 0.05$). Compared with the control group, drought increased the RE of local tree species (Figure 5, $p < 0.05$). The non-local tree species have higher SLA, TChl, LNC, LCC, and RE than local tree species but smaller LA and LT (Figure 5, $p < 0.05$).

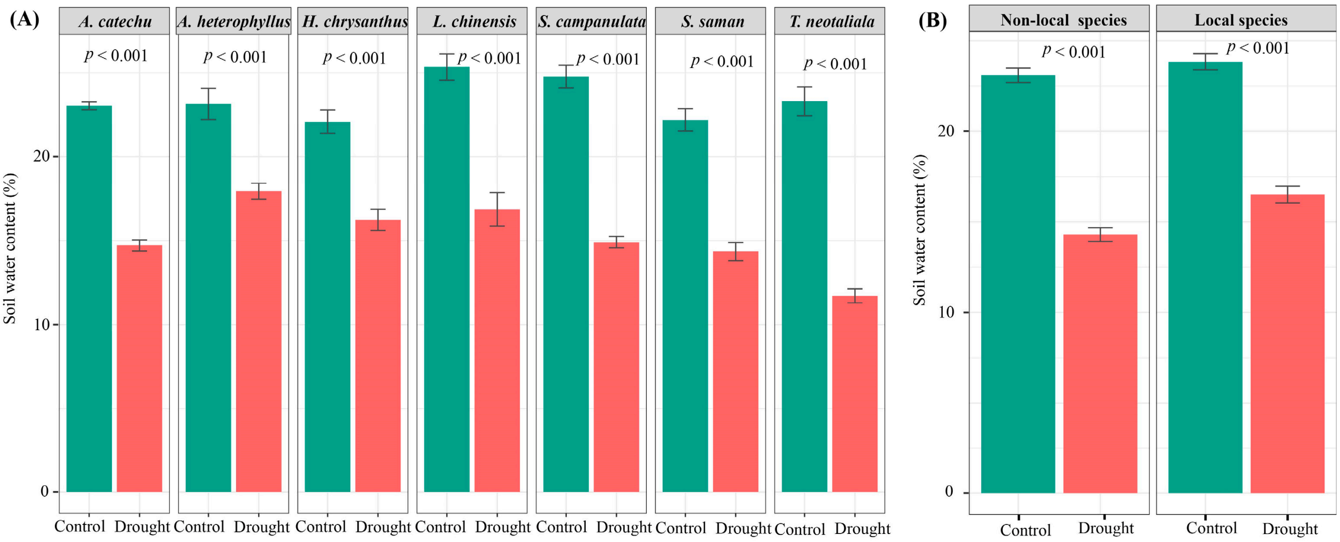

Figure 3. Soil water content between drought and control treatments ((**A**) tree species; (**B**) non-local and local species).

Table 1. Differences in leaf and root traits over seven tropical tree species under drought and control treatment. SLA, specific leaf area; LA, leaf area; LDMC, leaf dry matter content; LT, leaf thickness; TChl, total chlorophyll; LNC, leaf nitrogen content; LCC, leaf carbon content; SRL, specific root length; RD, root diameter; RTD, root tissue density; RSA, root surface area; RCC, root carbon content; RNC, root nitrogen content; RCC/RNC, root carbon/root nitrogen; RE, root exudate rate.

Trait	Control	Drought	*p* Value from *t*-Test
SLA (m^2 g^{-1})	20.09 ± 0.97	23.01 ± 1.06	0.044
TChl (mg kg^{-1})	15.48 ± 0.96	11.59 ± 0.84	0.003
LT (mm)	0.11 ± 0.01	0.12 ± 0.01	0.065
LCC (mg g^{-1})	456.95 ± 2.84	455.44 ± 3.27	0.727
LNC (mg g^{-1})	17.06 ± 0.97	17.21 ± 1.16	0.920
LDMC (mg g^{-1})	280.89 ± 9.34	260.86 ± 9.99	0.014
LA (cm^2)	206.03 ± 28.39	192.56 ± 29.24	0.025
SRL (m g^{-1})	65.77 ± 5.53	79.03 ± 8.28	0.018
RD (mm)	0.85 ± 0.04	0.81 ± 0.04	0.545
RTD (g cm^{-3})	0.34 ± 0.01	0.33 ± 0.01	0.578
RCC/RNC	35.54 ± 2.54	42.23 ± 3.27	0.017
RNC (mg g^{-1})	15.81 ± 1.61	13.51 ± 1.43	0.293
RCC (mg g^{-1})	417.26 ± 17.13	425.09 ± 14.50	0.730
RSA (cm^2)	344.74 ± 35.27	255.30 ± 28.75	0.047
RE (mg $g^{-1}h^{-1}L^{-1}$)	0.39 ± 0.04	0.48 ± 0.04	0.035

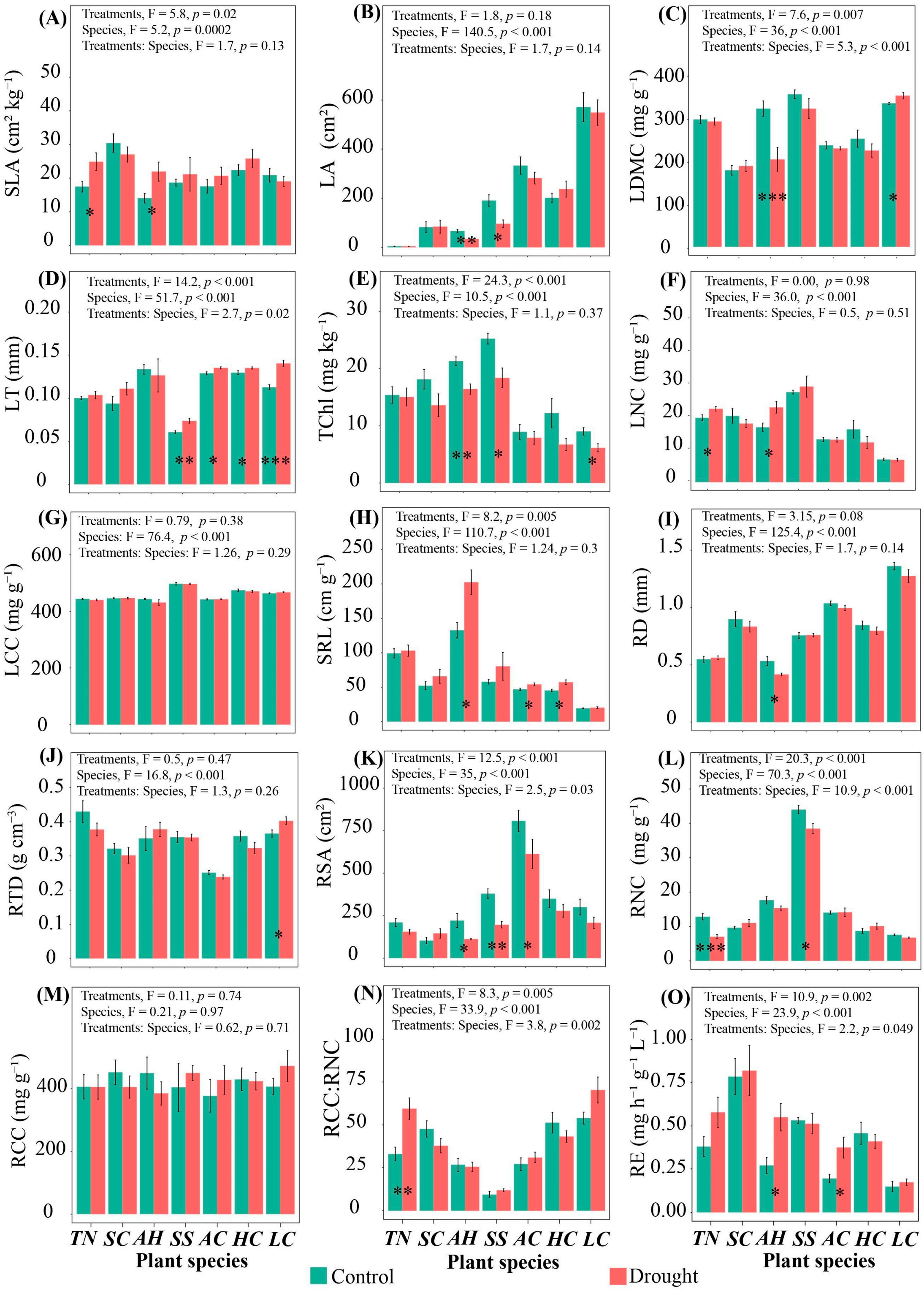

Figure 4. Changes in leaf and root traits of seven tree species under drought conditions. "*" indicates a significant difference between drought and control treatments; "*" $p < 0.05$; "**" $p < 0.01$; "***" $p < 0.001$. (**A**), SLA (specific leaf area); (**B**), LA, (leaf area); (**C**), LDMC (leaf dry matter content); (**D**), LT (leaf thickness); (**E**), TChl (total chlorophyll); (**F**), LNC (leaf nitrogen content); (**G**), LCC (leaf carbon content); (**H**), SRL (specific root length); (**I**), RD, (root diameter); (**J**), RTD (root tissue density); (**K**), RSA (root surface area); (**L**), RNC (root nitrogen content); (**M**), RCC (root carbon content); (**N**), RCC/RNC (root carbon/root nitrogen); (**O**), RE (root exudate rate). *TN*, *T. neotaliala*; *SC*, *S. campanulate*; *AH*, *A. heterophyllus*; *SS*, *S. saman*; *AC*, *A. catechu*; *HC*, *H. chrysanthus*; *LC*, *L. chinensis*.

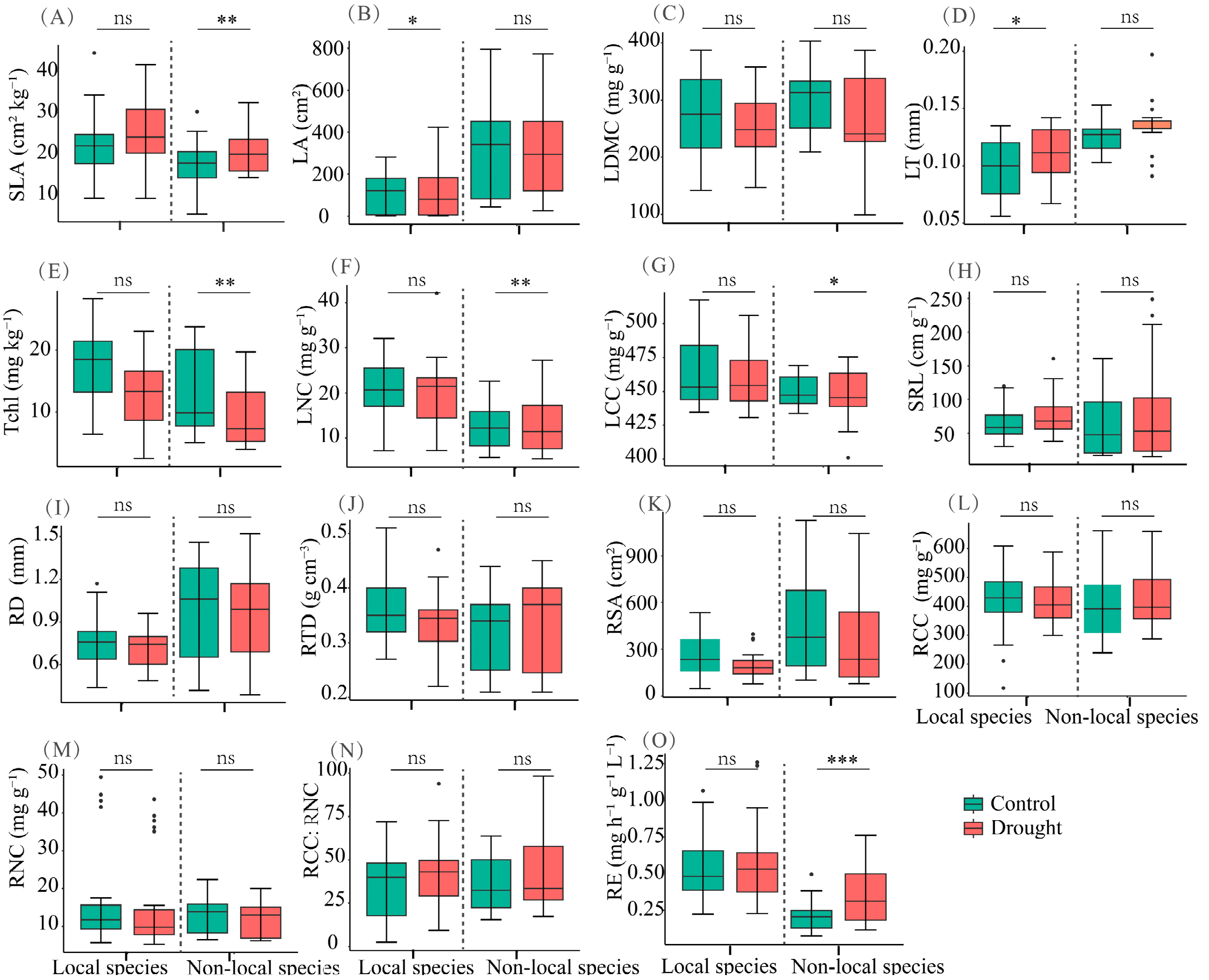

Figure 5. Changes in leaf and root traits of local and non-local tree species under drought and control treatments. Significance levels indicate as follows: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns, no significant. (**A**), SLA (specific leaf area); (**B**), LA, (leaf area); (**C**), LDMC (leaf dry matter content); (**D**), LT (leaf thickness); (**E**), TChl (total chlorophyll); (**F**), LNC (leaf nitrogen content); (**G**), LCC (leaf carbon content); (**H**), SRL (specific root length); (**I**), RD, (root diameter); (**J**), RTD (root tissue density); (**K**), RSA (root surface area); (**L**), RNC (root nitrogen content); (**M**), RCC (root carbon content); (**N**), RCC/RNC (root carbon/root nitrogen); (**O**), RE (root exudate rate).

3.2. Correlation Analysis of Garden Plant Traits Under Drought Conditions

Compared to the control, drought resulted in a negative correlation between LA and LT ($p < 0.001$, Figure 6A,B). Under drought conditions, the correlations between LCC and LT, LNC and LCC were not significant ($p > 0.05$). In root traits, drought significantly enhanced the negative correlation between RE and RCC/RNC ($p < 0.05$). Additionally, drought strengthened the relationship between leaf and root traits (Figure 6B), with LCC and LT showing significant positive correlations with RD ($p < 0.05$), and LCC was significantly negatively correlated with SRL ($p < 0.05$). LDMC exhibited significant negative correlations with both RE ($p < 0.01$) and SRL ($p < 0.05$). Notably, drought significantly enhanced the leaf and root traits of local tree species and their interrelationships, while it weakened these correlations for non-local species (Figure 6C–F).

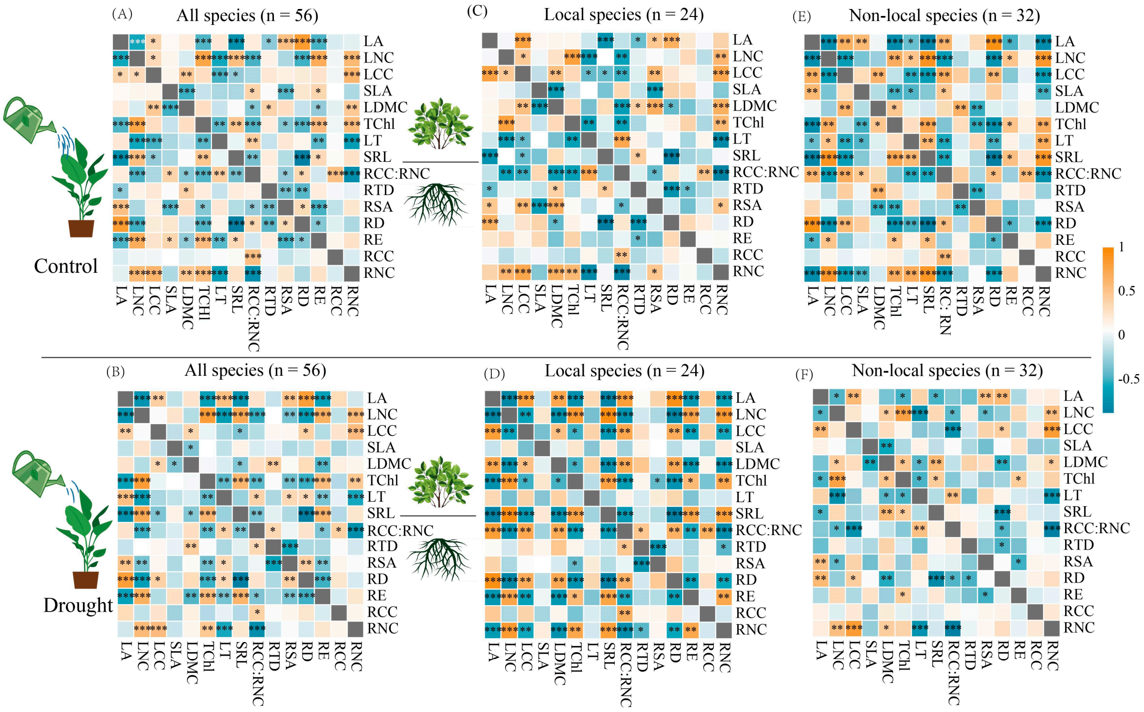

Figure 6. Correlation between leaf and root traits of all tree species (**A**,**B**), local tree species (**C**,**D**), and non-local tree species (**E**,**F**) under control (**A**,**C**,**E**) and drought conditions (**B**,**D**,**F**). SLA, specific leaf area; LA, leaf area; LDMC, leaf dry matter content; LT, leaf thickness; TChl, total chlorophyll; LNC, leaf nitrogen content; LCC, leaf carbon content; SRL, specific root length; RD, root diameter; RTD, root tissue density; RSA, root surface area; RCC, root carbon content; RNC, root nitrogen content; RCC/RNC, root carbon/root nitrogen; RE, root exudate rate. "*" $p < 0.05$; "**" $p < 0.01$; "***" $p < 0.001$.

3.3. The Impact of Drought on the Acquisition Strategies of Leaf and Root Trait Resources in Landscaping Trees

Principal component analysis showed that plant leaf traits were mainly explained by three principal components, contributing 39.1%, 26.5%, and 16.9% of the variation, respectively (Figure 7, Table 2). The first principal component was mainly influenced by LA, LT, TChl, and LNC, reflecting the relationship between different traits. The second principal component was influenced by SLA, LDMC, and LCC, demonstrating a trade-off between SLA and LDMC. The distribution of drought and control treatment samples was consistent on PC1, but there was a significant difference on PC2 ($p = 0.04$, Table 2). Under drought conditions, plant SLA increased and LDMC decreased, indicating a shift in plant leaf trait resource utilization strategies from slow and conservative to rapid acquisition under drought conditions.

Leaf traits differed significantly between local and non-local tree species under drought treatment on PC1 (Figure 7C, Table 2), thereby indicating that local tree species responded to drought by increasing LA and LT, while non-local tree species responded to drought by increasing LNC and TChl. This indicates that under drought conditions, the leaf traits of rural tree species adopt a slow and conservative strategy, while the leaf traits of non-local tree species adopt a rapid acquisition strategy.

The root traits of plants were mainly explained by three principal components, with explanatory rates of 31.8%, 25.2%, and 13.6%, respectively (Figure 7B, Table 2). The first principal component (PC1) was mainly explained by the morphological traits RD and SRL. RD was located at the positive end of the first axis, while SRL was located at the negative end, suggesting a trade-off between RD and SRL. The second principal component (PC2) was explained by RSA, RTD, RNC, and RCC/RNC, with a trade-off between RNC and RTD, while the third principal component (PC3) was explained by RCC and RE. The sample points of the drought and control treatments were evenly distributed on PC1 and PC2, with no significant difference (Table 3, $p > 0.05$). This indicates that the impact of drought on plant root resource acquisition strategies is not significant and that their resource acquisition strategies are influenced by tree species. In the control treatment, there was a significant difference in PC1 between local tree species and non-local tree species (Table 3, $p = 0.004$), indicating that local tree species obtain water through large RD and small SRL, while non-local tree species do so in the opposite direction. Under drought conditions, both the local and non-local tree species were distributed along PC1 ($p = 0.056$).

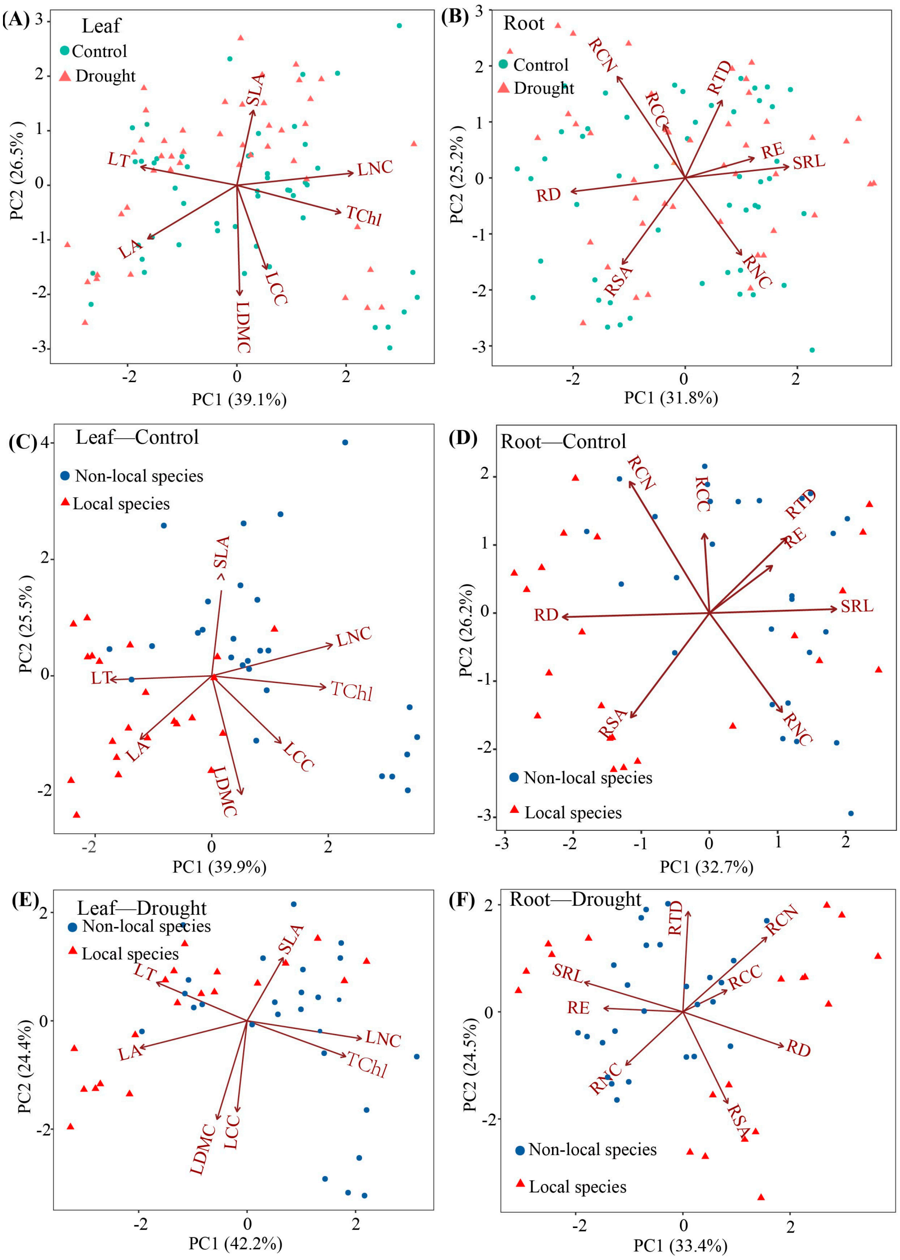

Figure 7. Principal component analysis of leaf and root traits of all species. (**A**) Leaf traits; (**B**) root traits; (**C**) leaf traits under control conditions; (**D**) root traits under control conditions; (**E**) leaf traits under drought conditions; (**F**) root traits under drought conditions. SLA, specific leaf area; LA, leaf area; LDMC, leaf dry matter content; LT, leaf thickness; TChl, total chlorophyll; LNC, leaf nitrogen content; LCC, leaf carbon content; SRL, specific root length; RD, root diameter; RTD, root tissue density; RSA, root surface area; RCC, root carbon content; RNC, root nitrogen content; RCC/RNC, root carbon/root nitrogen; RE, root exudate rate.

Table 2. Loadings of principal component analysis for leaf and root traits of all species. SLA, specific leaf area; LA, leaf area; LDMC, leaf dry matter content; LT, leaf thickness; TChl, total chlorophyll; LNC, leaf nitrogen content; LCC, leaf carbon content; SRL, specific root length; RD, root diameter; RTD, root tissue density; RSA, root surface area; RCC, root carbon content; RNC, root nitrogen content; RCC/RNC, root carbon content/root nitrogen content; RE, root exudate rate.

Leaf				**Root**			
Trait	**PC1**	**PC2**	**PC3**	**Traits**	**PC1**	**PC2**	**PC3**
LA	–0.71	0.43	0.42	RSA	0.49	–0.67	0.01
TChl	0.83	0.22	–0.28	RD	0.89	–0.11	0.03
LT	–0.76	0.15	–0.34	RCC	0.17	0.41	0.67
LNC	0.93	–0.09	0.06	RNC	–0.44	–0.60	0.18
LCC	0.24	0.67	0.56	RE	–0.54	0.15	0.57
SLA	0.13	–0.61	0.69	RCC/RNC	0.53	0.79	0.09
LDMC	0.02	0.88	–0.14	RTD	–0.29	0.60	–0.52
				SRL	0.81	0.09	–0.06
Eigenvalue	2.73	1.86	1.18		2.54	2.01	1.08
Percentage of variance	39.10%	26.50%	16.90%		31.80%	25.20%	13.60%
Cumulative percentage of variance	39.10	65.59%	82.51%		31.78%	56.99%	70.58%

Table 3. *T*-test analysis of PC1 and PC2 for leaf and root traits of all species, local tree species, and non-local tree species under drought and control watering conditions.

		All Species			**Local Species**			**Non-Local Species**		
		Control	**Drought**	***p***	**Control**	**Drought**	***p***	**Control**	**Drought**	***p***
Leaf	PC1	0.12 ± 0.14	–0.13 ± 0.15	0.22	–0.69 ± 0.13	0.57 ± 0.17	0.001	–0.62 ± 0.27	0.45 ± 0.15	0.003
	PC2	0.20 ± 0.14	–0.22 ± 0.15	0.04	–0.38 ± 0.16	0.31 ± 0.21	0.010	–0.11 ± 0.19	0.08 ± 0.22	0.510
Root	PC1	0.08 ± 0.14	–0.08 ± 0.15	0.44	–0.46 ± 0.24	0.38 ± 0.13	0.004	0.37 ± 0.30	–0.27 ± 0.11	0.056
	PC2	–0.17 ± 0.15	0.19 ± 0.14	0.08	–0.28 ± 0.20	0.23 ± 0.19	0.070	–0.17 ± 0.27	0.13 ± 0.15	0.360

3.4. Drought Resistance of Leaf and Root Traits of Landscaping Trees Under Drought Conditions

A comprehensive evaluation of changes in plant traits for seven species of seedlings under drought stress was conducted using the subordination function method in fuzzy mathematics. The species ranked in order of leaf trait drought resistance, from highest to lowest, are as follows: *T. neotaliala* (0.71) > *L. chinensis* (0.63) > *S. campanulata* (0.57) > *S. saman* (0.47) > *H. chrysanthus* (0.43) > *A. catechu* (0.29) > *A. heterophyllus* (0.29) (Table 4); local tree species had significantly lower leaf trait drought resistance (0.40) compared to non-local tree species (0.55) (Table 4).

In order from most to least root trait drought resistance, the species were as follows: *A. catechu* (0.86) > *T. neotaliala* (0.57) > *A. heterophyllus* (0.53) > *L. chinensis* (0.50) > *S. saman* (0.47) > *S. campanulate* (0.41) > *H. chrysanthus* (0.35) (Table 4); local tree species had greater root trait drought resistance (0.63) than non-local tree species (0.45) (Table 4). Ranked by overall drought resistance from highest to lowest, the species are as follows: *T. neotaliala* (0.67), *L. chinensis* (0.57), *A. catechu* (0.53), *S. campanulata* (0.50), *S. saman* (0.50), and *A. heterophyllus* (0.38) (Table 4).

Table 4. The subordination function values of leaf and root traits of seedlings of seven tree species (including local and non-local tree species) under drought stress. SLA, specific leaf area; LA, leaf area; LDMC, leaf dry matter content; LT, leaf thickness; TChl, total chlorophyll; LNC, leaf nitrogen content; SRL, specific root length; RTD, root tissue density; RSA, root surface area; RCC, root carbon content; RNC, root nitrogen content; RCC/RNC, root carbon content/root nitrogen content; RE, root exudate rate. *TN*, *T. neotaliala*; *SC*, *S. campanulate*; *AH*, *A. heterophyllus*; *SS*, *S. saman*; *AC*, *A. catechu*; *HC*, *H. chrysanthus*; *LC*, *L. chinensis*. CEV, comprehensive evaluation value; DTR, drought resistance ranking.

		Local Species			**Non-Local Species**			
	Trait	***AH***	***AC***	***LC***	***HC***	***SS***	***SC***	***TN***
Leaf	TChl	0.00	0.00	0.31	0.00	0.00	0.00	1.00
	LT	0.00	1.00	1.00	0.36	1.00	1.00	1.00
	LDMC	0.00	0.00	0.99	0.61	0.64	1.00	0.00
	LA	0.00	0.00	0.68	1.00	0.00	1.00	1.00
	SLA	1.00	0.00	0.04	0.39	0.36	0.00	1.00
	LNC	1.00	0.00	0.38	0.00	0.37	0.00	1.00
	RCC/RNC	0.00	1.00	1.00	0.68	0.92	1.00	0.00
	Mean value	0.29	0.29	0.63	0.43	0.47	0.57	0.71
	CEV	0.40			0.55			
Root	RSA	0.00	1.00	0.20	0.32	0.01	1.00	1.00
	RCC	0.00	1.00	1.00	0.47	0.93	0.14	0.00
	RNC	0.70	1.00	0.56	1.00	0.55	1.00	0.00
	RE	1.00	1.00	0.24	0.00	0.00	0.00	1.00
	RCC/RNC	0.00	0.00	0.51	0.05	0.47	0.00	1.00
	RTD	1.00	1.00	1.00	0.12	0.60	0.31	0.00
	SRL	1.00	1.00	0.01	0.46	0.72	0.44	1.00
	Mean value	0.53	0.86	0.50	0.35	0.47	0.41	0.57
	CEV	0.63			0.45			
All	Mean value	0.38	0.53	0.57	0.41	0.50	0.50	0.67
	DTR	7	3	2	6	5	4	1

4. Discussion

4.1. The Impact of Drought on the Functional Traits of Landscaping Trees

We found that drought significantly impacted some leaf and root traits (Table 1). In general, leaf and root characteristics are sensitive to changes in the external environment. When precipitation decreases, plants make a series of adjustments to adapt [48]. However, these changes are not consistent among species (Figure 4). For example, to cope with water scarcity situations, the leaves of *S. saman*, *H. chrysanthus*, *A. catechu*, and *L. chinensis* will reduce transpiration and increase water storage by adjusting leaf thickness and fence tissue thickness [49,50]. In this study, drought treatment significantly increased SLA and decreased LDMC across all species. This finding contrasts with previous research, which reported a decrease in SLA and an increase in LDMC under drought conditions [51,52]. The reason for this difference may be attributed to the low soil moisture availability under drought conditions, which leads plants to close their leaf stomata and reduce photosynthesis, thereby limiting the water lost via transpiration [53,54]. LDMC is affected by leaf moisture content, and when leaf moisture is high, LDMC will decrease [23,55]. In this study, drought had a minimal impact on LA, but a decrease in LDMC resulted in an increase in SLA (Figure 4). This further indicates that plant leaves can adapt to drought by increasing SLA and LT. This finding may be attributed to the geographical origin of the species examined. Local and non-local species often possess distinct evolutionary adaptations to cope with environmental stresses [38]. Tree species from regions with frequent droughts may exhibit higher SLA as a strategy to enhance light capture and resource acquisition during water-limited conditions. On the other hand, species from more stable environments may maintain lower SLA to conserve resources. Thus, the geographical context of these species could shape their physiological responses to drought. Obviously, to withstand the prolonged water shortage, plants undergo various physiological and morphological changes. Further research is encouraged to explore the underlying mechanisms and genetic factors driving these adaptive responses.

Plants adapted to drought by increasing SRL under drought conditions (Figure 4). SRL is an important trait that indicates a plant's ability to absorb water and nutrients; the longer the SRL, the lower the biomass input, thus resulting in higher resource acquisition efficiency [56]. Compared with the control group, RNC was significantly reduced under drought conditions (Table 1). This may be due to water scarcity, during which the root system prioritizes more nitrogen for the acquisition of water resources and their nutrients, thereby alleviating the adverse effects of drought on plant photosynthesis [57]. A recent meta-analysis indicates that, under climate change, woody plants obtain more nutrients by releasing more root acid phosphatase [58]. Under drought conditions, plants increase the proportion of total biomass they allocate to underground organs to optimize soil resource absorption, increase root metabolic substrates, and enhance life activities, thereby consuming RNC [59]. The results of this study also showed that RE increased significantly (Table 1) and that metabolic activities required more nitrogen participation under drought, which may have led to the significant decrease in RNC. For local species, except for LA and LT, no leaf and root traits changed significantly under drought conditions; for non-local species, SLA, TChl, LNC, and RE showed significant correlation under drought and control treatment (Figure 5). This observation highlights the differential responses of local and non-local tree species to drought, where local species often exhibit adaptive resilience by maintaining stability in their leaf and root traits. In contrast, non-local tree species show significant trait plasticity, allowing them to adjust to environmental changes. Under drought conditions, non-local tree species have demonstrated remarkable advantages, including enhanced tolerance to high temperatures, elevated photosynthetic rates, and improved water-use efficiency [47]. This may be attributed to the relatively greater influence of individual tree species on the response of plant functional traits to drought [30]. Future research should continue to explore the intricacies of these trait relationships across a broader range of species and environmental conditions to further elucidate the dynamics of plant responses to drought.

4.2. Correlation Between Landscaping Plant Functional Traits Under Drought Conditions

For leaf morphological traits, there was a significant positive correlation between LT and LA under drought (Figure 6A,B) and a significant negative correlation between SLA and LDMC (Figure 6A,B). There were no correlations between biochemical traits. Different leaf traits usually do not act independently but rather tend to have close trade-off or synergistic relationships with each other, demonstrating that there is a universal correlation between leaf morphological traits due to long-term adaptation to environmental change [60]. Root traits also exhibited the same correlation. Under drought conditions, plants enhance correlations between leaf and root traits to adapt to drought, and this relationship also exists in local tree species, in particular. The correlation between leaf and root traits weakened among non-local tree species (Figure 6), indicating that there was a trade-off between the leaf and root traits of non-local tree species under drought conditions. This aligns with the result that plant leaf and root traits adopt a synergistic or balanced approach to cope with climate change during the growth process [28]. Some studies indicate that deciduous tree species are at one end of the acquisition strategy in the leaf economic spectrum [31,61]. Deciduous tree species adjust their aboveground and underground biomass redistribution, enabling them to quickly acquire survival resources in a short period of time [26]. In this study, the leaf and root traits of deciduous and evergreen species exhibited significant differences in response to drought (Figures S2 and S3), reflecting their distinct adaptive strategies. Deciduous species often exhibit increased leaf thickness and root elongation under drought, optimizing water uptake and minimizing loss, while evergreen species maintain a more conservative approach by enhancing water-use efficiency and sustaining physiological functions with their relatively stable leaf traits. In summary, the correlation between leaf and root traits was weakened to help the non-local plants adapt to drought. Furthermore, a broader range of species would provide a more comprehensive understanding of how plant functional traits respond to drought across different ecological strategies. Additionally, the influence of factors such as phenology (e.g., leaf lifespan) and life history traits (e.g., fast-growing vs. slow-growing species) was not extensively explored and could add further depth to the analysis.

4.3. Resource Acquisition Strategies for Landscaping Trees' Functional Traits Under Drought Conditions

The results of principal component analysis showed that plant leaf traits changed from a conservative resource strategy to a rapid acquisition strategy under drought (Figure 7, Table 3). Previous studies have shown that plant leaf traits tend to adopt conservative strategies under drought, but when the degree of stress is low, plants will adopt an acquisition strategy instead [15]. Plants respond to drought by increasing SLA, reducing LDMC, improving their light harvesting ability and photosynthetic capacity by increasing height or SLA, and adopting faster nutrient cycling strategies to adapt to the environment [62]. The plants exhibited high LDMC and low SLA under drought conditions, indicating a resource acquisition strategy adapted to their environment [63] that was in line with the balance of leaf economic spectrum. PC1, however, also indicated that the sample points were evenly distributed on PC, and both drought and control plants may have had high LNC and LT, likely due to the influence of tree species. In terms of root traits, both the control group and the tree species under drought conditions were distributed on both sides of PC1 and PC2 (Figure 7), which indicates that there was no significant difference in the scores of different species on the PC1 and PC2 axes. Compared with leaf traits, the morphological traits of underground roots were influenced by the annual precipitation threshold and were not sensitive to changes in precipitation. Changes can only occur when a certain threshold is exceeded [22]. Therefore, these species' resource acquisition strategies have not changed.

Others have demonstrated that there is a trade-off in the investment and utilization of resources by plants. In other words, as one resource usage falls, another rises. Thus, an increase in investment in a certain trait will inevitably lead to a decrease in investment in other trait resources [51,64]. The research results here indicate that the correlation between garden plant leaf functional traits in arid environments and the economic spectrum of the leaf are basically the same. This indicates that the economic trade-off between leaf traits also exists in arid environments and generally tends towards the fast investment return end of the spectrum. There is also a trade-off between plant traits in the root system, but drought does not affect these root resource strategies. Future research could broaden its scope to examine whole-plant trait responses to drought, encompassing not only leaf and root traits but also stem characteristics, reproductive strategies, and phenological changes. The findings highlight the need for research that considers interactions between different stressors to better understand plant stress tolerance mechanisms [65]. This integrative approach would offer a more comprehensive understanding of how plants allocate resources and adapt to dry conditions.

The local and non-local tree species demonstrated distinct strategies in response to drought conditions (Figure 7). Local species typically employed a conservative strategy characterized by slow resource acquisition, which minimizes risk in unpredictable environments. In contrast, non-local species adopted a rapid acquisition strategy, allowing them to capitalize on available resources quickly and thrive in less stable, human-altered environments. These contrasting strategies reflect the broader evolutionary adaptations of these species to their native environments. Many tree species are widely non-local in the urban ecosystems based on their rapid growth and resilience. While non-local species offer valuable ecosystem services in urban landscapes, such as carbon sequestration and temperature regulation, their aggressive resource acquisition strategies can pose risks to local ecosystems [66]. These species may disrupt native biodiversity and ecological balance, especially when they outcompete local species for resources [67]. While the rapid acquisition strategy allows non-local species to compete more aggressively, the slow, conservative approach of local species ensures resilience in the face of long-term stress, contributing to ecosystem stability and sustainability. Thus, broader ecological impacts of non-local tree species must be carefully managed. Understanding the adaptive strategies that enable their environmental tolerance is essential for developing management practices that mitigate their potential risks to local ecosystems. Future research should focus on quantifying the long-term effects of non-local species on soil health, native biodiversity, and ecosystem resilience, especially under shifting climate conditions. This knowledge will guide the development of management practices aimed at balancing the benefits and risks of using non-local species in urban ecosystems. While the status of being "local" or "non-local" offers insights into their adaptive strategies, the leaf lifespan behavior (deciduous vs. evergreen) likely plays an equally important role in explaining the differential drought responses observed in this study. Future research should integrate more factors to provide a more comprehensive understanding of the species' drought resilience.

5. Conclusions

Drought significantly increases the specific leaf area, leaf thickness, and root exudate rate while reducing root nitrogen content and leaf dry matter content in common landscaping trees. The observed differences in leaf and root functional traits across species indicate that landscaping trees employ distinct adaptive strategies to cope with drought stress. Local species tend to adopt a more conservative strategy, optimizing long-term survival through efficient resource use, while non-local species often exhibit a more acquisitive strategy, favoring rapid resource uptake in response to drought. However, these contrasting strategies may be influenced by their leaf lifespan behavior (evergreen vs. deciduous), which plays a significant role in shaping their adaptive responses to drought. As climate change drives more frequent and prolonged droughts, it is expected that leaf traits in landscaping trees will continue shifting from conservative to acquisitive strategies, although root traits may remain relatively stable. Principal component analysis reveals that traits such as LNC, TChl, and LT play critical roles in drought adaptation. Among the species studied, *T. neotaliala* and *L. chinensis* demonstrated the highest drought resistance, while *A. heterophyllus* was the least drought resistant. Interestingly, local and non-local tree species exhibited opposite patterns in their leaf and root trait responses, with non-local species showing enhanced leaf drought resistance but weaker root drought tolerance compared to local species. These findings suggest that, to optimize resource use, minimize maintenance costs, and promote sustainable urban landscaping, species with strong drought resistance, such as *T. neotaliala* and *L. chinensis*, should be prioritized in production, seedling cultivation, and tree selection. Understanding the functional trait differences between local and non-local species will provide critical guidance for selecting trees that can thrive under future arid conditions, ensuring both ecological sustainability and the long-term resilience of urban landscapes.

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