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LEAF PHENOTYPIC PLASTICITY OF FOUR *ELEUTHEROCOCCUS* SPECIES GROWING IN THE URBAN ENVIRONMENT

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Background. Urban greening initiatives can significantly mitigate the challenges of climate change and urbanization. One of the innovative urban greening approaches involves the utilization of diverse tree and shrub varieties for urban landscaping. Species of *Eleutherococcus*, due to their exotic habitus and shade tolerance, stand out as attractive ornamental plants. It was previously demonstrated that adaptation of plants to a new environment is associated with phenotypic plasticity. The study aimed to establish the level of phenotypic plasticity for four *Eleutherococcus* species (*E. lasiogyne*, *E. senticosus*, *E. sessiliflorus*, *E. trifoliatus*) in an urbanized environment of Kyiv (Ukraine).

Materials and Methods. The indexes of phenotypic plasticity (PI) were established based on seven morphological and ten anatomical features of leaves developed in sun and shade conditions. Anatomical measurements were carried out and analyzed by light microscopy (Zeiss Axiocam MRc 5 digital camera, Carl Zeiss) using Axiovision AC software. The phenotypic plasticity index was calculated for each parameter and species. Student's *t*-test, one-Way ANOVA, Tukey's HSD *post hoc* test, and Principal component analysis (PCA) were performed, including all considered leaf morphological and anatomical variables, grouped per species. All statistical analyses were performed using R version 3.5.3 (R Core Team).

Results. The leaf traits of four *Eleutherococcus* species generally correspond to those of deciduous mesophyte trees, with LMA (the leaf dry mass per unit leaf area) ranging from 31 to 47 g m^{-2}. The species significantly differed from each other in the level of variability of morphological and anatomical parameters. Total PI rankings are as follows: *E. senticosus* (0.34) → *E. lasiogyne* (0,30) → *E. sessiliflorus* (0.22) → *E. trifoliatus* (0.20).

Conclusion. Our results contribute new insights into the phenotypic plasticity of trees and shrubs under new ecological and climatic conditions. *Eleutherococcus senticosus* exhibited the highest phenotypic plasticity among all investigated species, suggesting a high adaptive potential. The assessment of phenotypic plasticity can be useful for evaluating the adaptation potential of woody plants in urban greening.

Keywords: *Eleutherococcus,* phenotypic plasticity, leaf anatomy, functional traits, urban greening, botanical gardens

INTRODUCTION

Eleutherococcus Maxim. (Araliaceae Juss.) is a genus of shrubs or small trees primarily native to China, East Asia, and the Himalayan region (Flora of China, 2024). Some *Eleutherococcus* species are well-known in traditional Chinese medicine (Huang *et al*., 2011), and are recognized in the Western world for their predominantly adaptogen properties (Assessment Report…, 2013; Adamczyk *et al*., 2019). Medicinal substances have sparked interest in *Eleutherococcus* cultivation and propagation across Europe and North America (Li, 2001; Döring *et al*., 2003). Moreover, the appealing growth habit, decorative pinnate leaves, and shade tolerance make *Eleutherococcus* attractive for ornamental purposes. Recent reports have documented the successful cultivation of six *Eleutherococcus* species (*E. lasiogyne* (Harms) S. Y. Hu, *E. sessiliflorus* (Rupr. & Maxim.) S. Y.Hu, *E. divaricatus* (Siebold & Zucc.) S. Y. Hu, *E. sieboldianus* (Makino) Koidz., *E. trifoliatus* (L.) S. Y. Hu), *E. wardii* (W.W.Sm.) S. Y. Hu) in Ukraine, all of which have been recognized as suitable for urban greening (Morozko *et al.*, 2018).

According to the European Environment Agency report (Kazmierczak *et al*., 2020), climate change is one of the most significant challenges globally, having a particular impact on European cities. In this context, urban greening emerges as a crucial strategy for addressing the effects of climate change and urbanization. Furthermore, urbanization affects evolutionary processes, shapes genetic diversity, and facilitates species' adaptive responses (Johnson & Munshi-South, 2017), highlighting the critical importance of appropriate plant selection for urban greening initiatives.

Phenotypic plasticity, the ability of a given genotype to express different phenotypes under diverse environmental conditions (Valladares *et al.*, 2007), has been identified as an aspect of the adaptation process (Gratani, 2014). Numerous studies have shown that the plasticity index for traits of angiosperm leaves ranges mainly from 0.20 to 0.60 (Gratani, 2014; Chelli *et al*., 2019).

While some morphostructural leaf traits of *Eleutherococcus* have been investigated, the phenotypic plasticity has not yet been studied. This study aimed to evaluate the level of phenotypic plasticity of four *Eleutherococcus* species growing in urban environments in Kyiv, using a comparative analysis of the leaf morphostructural characteristics.

MATERIALS AND METHODS

Plant material was obtained from Kyiv botanical gardens – O. V. Fomin Botanical Garden of Taras Shevchenko National University of Kyiv (FBG) and M. M. Gryshko National Botanical Garden of the National Academy of Sciences of Ukraine (GBG).

The adult plants were selected for four *Eleutherococcus* (Araliaceae Juss.) species: *E. lasiogyne* (grown in GBG), *E. senticosus* (Rupr. & Maxim.) Maxim. (grown in GBG), *E. sessiliflorus* (grown in GBG), and *E. trifoliatus* (L.) S.Y. Hu (grown in FBG). Species were recognized per the guidelines outlined in the Flora of China (Flora of China, 2024). The nomenclature was used according to the World Flora Online (POWO, 2022).

Fully expanded mature leaves were collected in late July – early August 2020. For each species, nine leaves were selected from the mid-to-upper part of the crown, from both sun-exposed and shaded conditions.

Study area and climate. The climate in Kyiv is a warm-summer humid continental. The mean minimum air temperature of the coldest months (January and February) varies from -3.2 to -2.3 °C, the mean maximum air temperature of the warmest months (July and August) varies from 21.3 to 20.4 °C and the mean annual air temperature is 9.0 °C. Total annual rainfall is 618 mm, most of which occurs in the summer period (Data from the Borys Sreznevsky Central Geophysical Observatory [http://cgo-sreznevskyi.kyiv.ua/en]).

Morphological leaf traits. Morphometric leaf parameters were determined with an accuracy of 1.0 mm using fresh material (three leaves from three plants in sun conditions, three leaves from three plants in shade conditions, n = 9 for each experimental variant). Six morphological variables were directly measured: leaf blade length, leaf blade width, petiole length, central segment (leaflet) length, central segment (leaflet) width, and number of leaf segments (leaflets).

Leaf area (LA, cm^2) was determined using leaves photocopy on scale-coordinate paper, and leaf dry mass (DM, g) was measured after the desiccation of lamina at 80 °C to constant mass. Leaf mass per unit of leaf area (LMA, g m^{-2}) was calculated by the ratio between DM and LA (Wright *et al.*, 2004).

Anatomical leaf traits. Anatomical measurements were carried out on the middle part of the central leaflet (three leaves from three plants in sun conditions, three leaves from three plants in shade conditions, n = 9 for each experimental variant) and analyzed by light microscopy (Zeiss Axiocam MRc 5 digital camera (Carl Zeiss) using an Image Analysis System (Axiovision AC software).

The epidermal features were evaluated on replicas obtained by applying acetate varnish to both surfaces of the leaf blade (three leaves from three plants in sun conditions, three leaves from three plants in shade conditions, n = 9 for each experimental variant), following the established protocol of obtaining epidermal impression (Sack *et al*., 2003). The parameters measured included adaxial epidermal cell length (µm), adaxial epidermal cell width (µm), stomata length and width (µm), and stomatal density (mm^{-2}), with nomenclature following P. J. Rudall *et al*. (2013).

The following parameters were determined in fresh transverse sections: total leaf thickness (µm), abaxial and adaxial epidermis thickness (µm), palisade and spongy mesophyll tissue thickness (µm).

Plasticity index. The index of phenotypic plasticity in the range from zero to one was calculated for each parameter and species as the difference between the minimum and maximum mean values divided by the maximum mean value, according to F. Valladares *et al*. (2000).

Data analysis. One-way ANOVA was carried out to assess the differences in the measured morphological and anatomical parameters of the species. Multiple comparisons were conducted using Tukey's HSD *post hoc* test. Principal component analysis (PCA) was performed, including all considered leaf morphological and anatomical variables, grouped per species. All statistical analyses were executed using the R Core Team (2023).

RESULTS AND DISCUSSION

Morphological leaf traits. All studied species had compound palmate leaves, comprising three (*E. trifoliatus*), five (*E. senticosus*), or three to five (*E. lasiogyne, E. sessiliflorus*) leaflets. The leaf blade area was the smallest in *E. trifoliatus* (31 cm^2) and did not significantly differ between the closely related species – *E. sessiliflorus* and *E. senticosus* (**Table 1**).

Table 1. **Morphological and anatomical parameters of *Eleutherococcus* species (mean value ± standard deviation)**

Parameter \ Species	*E. trifoliatus*	*E. lasiogyne*	*E. senticosus*	*E. sessiliflorus*
Morphological parameters				
Lamina length, cm	$7.54±0.82^{a}$	$11.62±2.88^{b}$	$17.72±4.8^{c}$	$16.29±16.29^{c}$
Lamina width, cm	$9.9±1.7^{a}$	$14.41±2.89^{ab}$	$20.77±6.58^{c}$	$18.73±4.02^{bc}$
Central leaflet length, cm	$6.41±0.53^{a}$	$9.38±1.79^{b}$	$13.33±3.34^{c}$	$12.97±1.62^{c}$
Central leaflet width, cm	$3.36±0.55^{a}$	$4.67±0.79^{b}$	$5.04±1.34^{b}$	$5.73±0.67^{bc}$
Number of leaflets, n	3	3–5	5	3–5
Petiole length, cm	$6.52±1.52^{a}$	$7.89±2.16^{a}$	$9.46±2.13^{b}$	$9.34±2.05^{bc}$
Leaf area, cm^2	$30.95±8.36^{a}$	$70.28±10.24^{b}$	$152.31±10.05^{c}$	$110.77±15.64^{bc}$
Leaf mass per unit of area, g m^{-2}	$32.36±3.56^{a}$	$42.57±8.34^{b}$	$31.12±2.98^{a}$	$47.10±3.82^{b}$
Anatomical parameters				
Epidermal features				
Adaxial cell length, μm	$49.06±7.60^{ns}$	$57.67±7.53^{ns}$	$57.03±8.90^{ns}$	$52.88±5.65^{ns}$
Adaxial cell width, μm	$33.95±5.25^{abc}$	$36.33±7.13^{bc}$	$32.66±5.77^{abc}$	$28.36±3.94^{a}$
Stomata length, μm	$26.20±3.65^{b}$	$23.59±3.08^{ab}$	$21.03±2.08^{a}$	$26.81±3.13^{b}$
Stomata width, μm	$17.61±2.23^{bc}$	$15.96±1.64^{b}$	$11.97±2.08^{a}$	$19.44±1.72^{c}$
Stomatal density (n mm^{-2})	$47.39±5.80^{a}$	$85.78±19.31^{b}$	$110.70±16.36^{c}$	$78.84±13.74^{b}$
Tissue thickness				
Total leaf, μm	$156.36±7.00^{c}$	$136.81±3.67^{b}$	$121.27±10.9^{a}$	$150.10±12.46^{cb}$
Adaxial epidermis, μm	$16.23±3.01^{b}$	$12.86±2.45^{a}$	$13.51±2.4^{ab}$	$14.48±2.6^{ab}$
Palisade mesophyll, μm	$29.87±3.26^{a}$	$34.52±10.32^{a}$	$28.95±5.92^{a}$	$47.24±4.9^{b}$
Spongy mesophyll, μm	$97.94±13.87^{b}$	$71.51±11.62^{a}$	$66.61±3.95^{a}$	$75.52±11.08^{a}$
Abaxial epidermis, μm	$14.42±2.99^{ns}$	$13.19±2,74^{ns}$	$11.32±2.74^{ns}$	$13.75±3.32^{ns}$

Note: different letters indicate significant differences between species, ns indicates no significant difference (One-way ANOVA, Tukey's HSD post hoc test, P-value ≤0.05)

The LMA of all examined species was within the range of 31-47 g m^{-2}, consistent with typical values for deciduous shrubs (Villar *et al*., 2013). Noteworthy is that the LMA was significantly different for two morphologically similar species – *E. sessiliflorus* and *E. senticosus* (47 and 31 g m^{-2}, respectively), potentially explained by variations in the anatomical structure of the leaf blades.

Anatomical leaf traits. Both sciomorphic (hypostomatic leaves, protruding above the epidermal surface stomata, and a substantial volume of intercellular spaces in the mesophyll) and heliomorphic (significant development of the adaxial epidermis thickness, massive cuticular striae, particularly noticeable in *E. lasiogyne*), and mesophyll differentiation) anatomical features were observed (**Table 1**, **Fig. 1**).

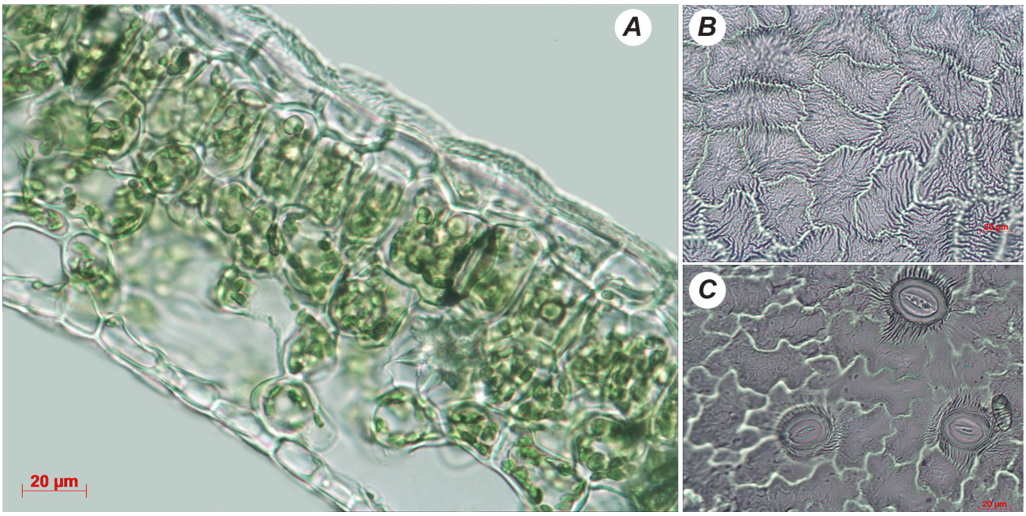

Fig. 1. Anatomical features of *Eleutherococcus* leaves: (***A***) cross leaf section of *E. senticosus* leaf; (***B***) adaxial epiderma of *E. lasiogyne* leaf; (***C***) abaxial epiderma of *E. lasiogyne* leaf

The total leaf thickness exhibited significant variation among all studied species. *E. senticosus* demonstrated the thinnest leaf blades (121 μm), corresponding to the lowest LMA (31 g m^{-2}). The positive correlation between leaf thickness and LMA has been proven for a large number of plant species and life forms (Poorter *et al*., 2009; Villar *et al*., 2013). However, in our experiment, *E. trifoliatus* exhibited the maximum leaf blade thickness (156 μm), with the same LMA as *E. senticosus* (32 and 31 g m^{-2}, respectively). This deviation can be explained by the large thickness of the spongy parenchyma in *E. trifoliatus* leaves (98 μm), and, consequently, a higher volume of intercellular space fraction. This parameter negatively correlates with LMA (Poorter *et al.*, 2009; Villar *et al*., 2013) and reflects the mesophilic nature of *E. trifoliatus*.

Figs. 2 and **3** illustrate the morphological and anatomical traits variability among all studied species under different light conditions. Differences between light and shade leaves were pronounced for all species, both for morphological and anatomical features. For example, the leaf area of *E. senticosus* in the shade was 60% larger than in the sun (**Fig. 2**), whereas this parameter was not significantly different for *E. trifoliatus.* The most labile anatomical indicator was the stomatal density, which increased more than twice in the sun in *E. lasiogyne*.

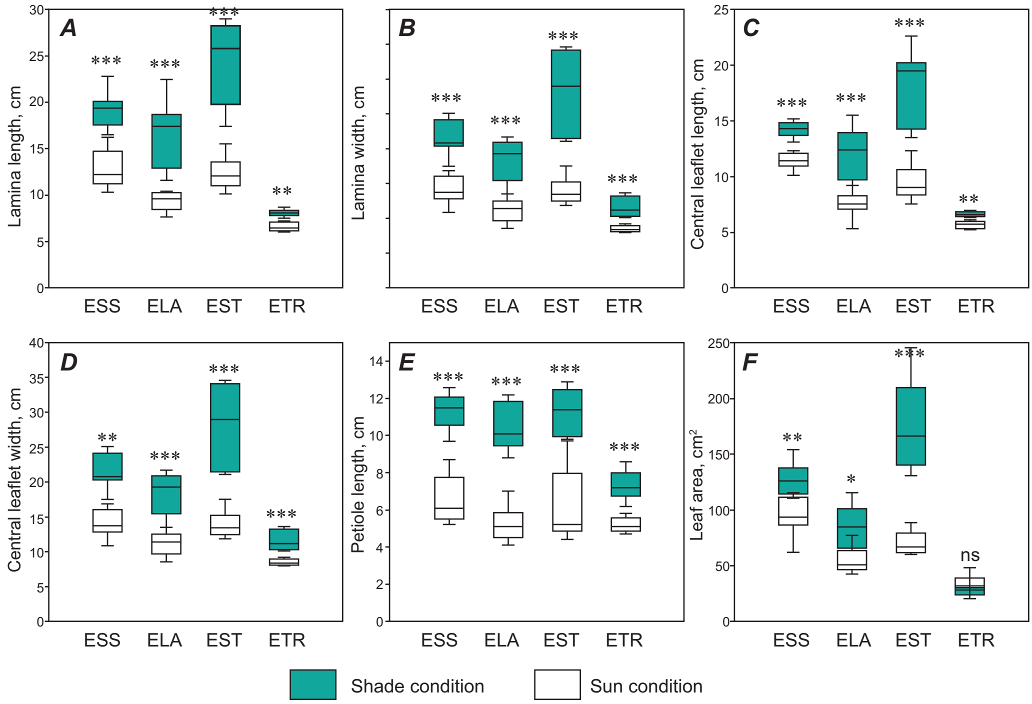

Fig. 2. Boxplot for the morphological parameters of *Eleutherococcus* sun and shade leaves: ESS – *E. sessiliflorus*; ELA – *E. lasiogyne*; EST – *E. senticosus*; ETR – *E. trifoliatus* (*t*-test, the asterisks indicate the significance levels, i.e. *p <0.05; **p <0.01; ***p <0.001)

Overall, all species tended to form larger leaf blades with reduced thickness in shade. Sunlight exposure stimulated the formation of a thicker layer of the epidermis and the waxy layer (especially adaxial), decreasing epidermal cell size and increasing stomatal density.

The phenotypic plasticity. To distinguish the species by plasticity, the phenotypic plasticity index (PI) was calculated (**Table 2**). Regarding morphological features (PI_{morf}), species can be ranked in order from *E. senticosus* (0,46) to *E. trifoliatus* (0.23). According to anatomical plasticity (PI_{an}), the ranking was changed from *E. lasiogyne* (0.24) to *E. sessiliflorus* (0.16). The total PI rankings were as follows: *E. senticosus* (0.34) → *E. lasiogyne* (0.30) → *E. sessiliflorus* (0.22) → *E. trifoliatus* (0.20). Therefore, we consider *E. senticosus* the most plastic compared to the other studied species.

Principal component analysis (PCA) was performed on 18 morphological and anatomical characteristics measured in this study (**Fig. 4**). This method allowed us to evaluate the contribution of each parameter in the scope of the dispersion, and therefore highlight the differences between the studied species. The principal components are new artificially created variables that are not correlated and consist of all the studied variables, each of which has its own weight. The PCA demonstrated that two main components collectively accounted for over 90 % of the variability in all traits (PC1 (component 1) – 79.41 %; PC2 (component 2) – 11.61 %). Moreover, the PCA indicated a high degree of overlap in the multivariate space occupied by different species, indicating a close relationship between species of the same genus.

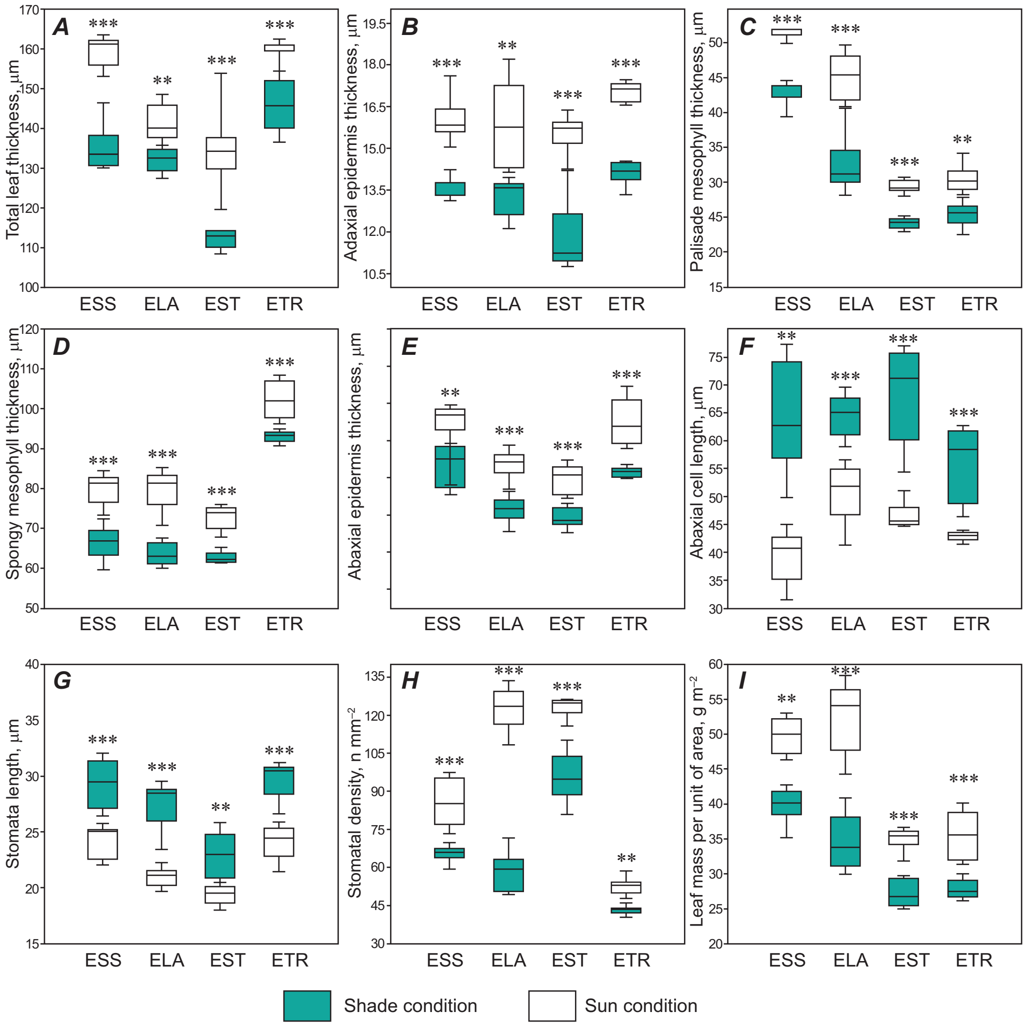

Fig. 3. Boxplot for the anatomical parameters of *Eleutherococcus* sun and shade leaves: ESS – *E. sessiliflorus*; ELA – *E. lasiogyne*; EST – *E. senticosus*; ETR – *E. trifoliatus* (*t*-test, the asterisks indicate the significance levels, i.e. *p <0.05; **p <0.01; ***p <0.001)

Phenotypic plasticity at physiological, morphological, and anatomical levels plays a crucial role in plant adaptation to environmental conditions. Each level can be differently involved in the formation of adaptive reactions. The plasticity allows plants to grow and reproduce in an environment undergoing constant change, and where new stress factors are introduced (Gratani, 2014). The PI was first established for *Eleutherococcus* species, ranging from 0.20 to 0.34, which falls within the average range for deciduous shrub species (Wang *et al*., 2021). Interestingly, morphologically similar species (*E. sessiliflorus* and *E. senticosus*) showcased differences in their PI, despite their coexistence in temperate forests of northern China (Wang *et al.*, 2016). Our findings demonstrated a 7 % higher PI for *E. senticosus* than the previous species. Interestingly, a considerably higher level of genetic variation is demonstrated for the native population of *E. senticosus* in comparison to *E. sessiliflorus* (Wang *et al*., 2016). Genetic diversity allows *E. senticosus* to withstand a wider range of changes in environmental factors, in particular, temperature fluctuations, enabling it to expand its range and increase its altitude by 300 m, compared with *E. sessiliflorus* (Wang *et al.*, 2016).

Table 2. **Plasticity index of four *Eleutherococcus* species based on morphological, anatomical traits, and LMA**

Parameter	*E. trifoliatus*	*E. lasiogyne*	*E. senticosus*	*E. sessiliflorus*
Lamina length, cm	0.19	0.42	0.49	0.33
Lamina width, cm	0.28	0.40	0.52	0.35
Central leaflet length, cm	0.15	0.37	0.47	0.20
Central leaflet width, cm	0.26	0.43	0.47	0.18
Petiole length, cm	0.28	0.49	0.44	0.41
Leaf area, cm^2	0.27	0.04	0.44	0.13
Leaf mass per unit of area, g m^{-2}	0.17	0.36	0.61	0.25
Morphological traits plasticity index	**0.23**	**0.36**	**0.46**	**0.26**
Adaxial cell length, μm	0.23	0.22	0.32	0.39
Adaxial cell width, μm	0.18	0.31	0.30	0.18
Stomata length, μm	0.19	0.24	0.16	0.17
Stomata width, μm	0.17	0.16	0.30	0.17
Stomatal density, n mm^{-2}	0.17	0.52	0.23	0.24
Total leaf thickness, μm	0.09	0.06	0.17	0.15
Adaxial epidermis thickness, μm	0.17	0.16	0.24	0.15
Palisade mesophyll thickness, μm	0.16	0.28	0.18	0.16
Spongy mesophyll thickness, μm	0.09	0.20	0.14	0.17
Abaxial epidermis thickness, μm	0.18	0.19	0.18	0.15
Anatomical traits plasticity index	**0.16**	**0.24**	**0.22**	**0.19**
Total plasticity index	**0.20**	**0.30**	**0.34**	**0.22**

The distribution of *E. lasiogyne* (PI = 0.30) covers the regions of Tibet, which, due to the mountainous conditions, require significant adaptive responses from plants (Li *et al.*, 2022). *Eleutherococcus trifoliatus* exhibited the lowest plasticity index (PI = 0.20) among the studied species. While *E. trifoliatus* has a broader geographic range than *E. lasiogyne*, it mainly inhabits southern coastal areas, characterized by more stable monsoon climatic conditions (Flora of China, 2024; WFO, 2022). Thus, we can assert that a species with a higher PI is able to live in a wider range of environmental factors.

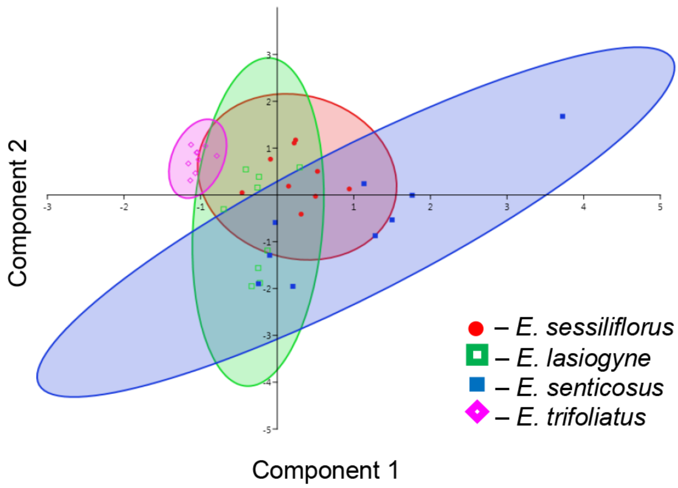

Fig. 4. Principal component analysis of the morphological and anatomical parameters of the *Eleutherococcus* species (*E. sessiliflorus* (dots), *E. lasiogyne* (open squares), *E. senticosus* (empty squares), *E. trifoliatus* (diamonds)

Although substantial evidence suggests that climatic variability is positively associated with plant phenotypic plasticity (Valladares *et al*., 2014; Vázquez *et al*., 2017), a positive correlation of plasticity in morphological and physiological parameters of leaves has been observed only with mean annual temperature globally (Stotz *et al*., 2021). Our research demonstrates the possibility of using botanical gardens' plant collections as alternative data sources to expand global trait frameworks, which is necessary for understanding global plant functional diversity (Puglielli, 2024).

CONCLUSION

This study contributes new insights into the phenotypic plasticity of trees and shrubs under new ecological and climatic conditions. Among all investigated species (*E. lasiogyne, E. senticosus, E. sessiliflorus, E. trifoliatus*), *E. senticosus* exhibited the highest phenotypic plasticity, suggesting a high adaptive potential. The assessment of phenotypic plasticity can be useful for evaluating the adaptation potential of woody plants in urban greening.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of 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.

AUTHOR CONTRIBUTIONS

Conceptualization [O.V.; R.P.; N.D.]; methodology [O.V.; V.K.]; data analysis [O.V.; V.K.]; investigation [O.V.; V.K.]; resources [O.V.; R.P.; N.D.]; writing – original draft preparation [O.V.]; writing – review and editing [O.V.; R.P.; N.D.]; visualization [O.V.; V.K.].

All authors have read and agreed to the published version of the manuscript.

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ФЕНОТИПІЧНА ПЛАСТИЧНІСТЬ ЛИСТКІВ ЧОТИРЬОХ ВИДІВ *ELEUTHEROCOCCUS*, ЩО ЗРОСТАЮТЬ В УРБАНІЗОВАНИХ УМОВАХ

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Вступ. Міські зелені зони можуть значно пом'якшити виклики, що постають унаслідок змін клімату й урбанізації. Інноваційні підходи до озеленення міст передбачають використання видового та сортового різноманіття дерев і кущів. Представники роду Елеутерокок, завдяки своєму екзотичному габітусу і тіньовитривалості, є перспективними декоративними рослинами. Раніше було продемонстровано, що адаптація рослин до нового середовища пов'язана з фенотипічною пластичністю. Метою дослідження було встановити рівень фенотипічної пластичності для чотирьох видів *Eleutherococcus* (*E. lasiogyne*, *E. senticosus*, *E. sessiliflorus* і *E. trifoliatus*), що зростали в урбанізованому середовищі м. Києва.

Матеріали та методи. Індекс фенотипічної пластичності (PI) встановлювали за сімома морфологічними та десятьма анатомічними ознаками листків, що утворювалися на сонці та в тіні. Анатомічні вимірювання проводили й аналізували за допомогою світлової мікроскопії (Zeiss Axiocam MRc 5, Carl Zeiss) з використанням програмного забезпечення Axiovision AC. Індекс фенотипічної пластичності встановлено для кожного параметра та виду. Дані проаналізовано з використанням *t*-критерію Стьюдента, дисперсійного аналізу, тесту Тьюкі та методу головних компонент, який включав усі розглянуті морфологічні й анатомічні параметри листків, згруповані за видами. Статистичний аналіз проведено в програмному середовищі R.

Результати. Морфологічні й анатомічні характеристики листків чотирьох видів *Eleutherococcus* загалом відповідали таким для листопадних мезофітних дерев, з LMA в діапазоні від 31 до 47 г м$^{-2}$. Види істотно відрізнялися один від одного рівнем мінливості морфолого-анатомічних показників. Загальний індекс пластичності знижувався в ряду: *E. senticosus* (0,34) → *E. lasiogyne* (0,30) → *E. sessiliflorus* (0,22) → *E. trifoliatus* (0,20).

Висновки. Результати розширюють уявлення про фенотипічну пластичність дерев та кущів у нових екологічних і кліматичних умовах. *E. senticosus* виявив найвищу фенотипічну пластичність серед усіх досліджених видів, що свідчить про високий адаптивний потенціал. Аналіз фенотипічної пластичності може бути корисним для оцінки адаптаційного потенціалу деревних рослин у міському озелененні.

Ключові слова: *Eleutherococcus,* фенотипічна пластичність, анатомія листка, функціональні ознаки, міське озеленення, ботанічні сади

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