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# Population-Level Variability in the Morphology of *Acer pseudoplatanus* Samara

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## ABSTRACT

Population-specific variation in the sycamore maple (*Acer pseudoplatanus*) samara characteristics was examined to understand how geographic and environmental factors shape the samara's weight and morphology. Variability of samaras of six sycamore maple populations from different regions of Serbia, differing in elevation (from 1530 to 490 m.a.s.l.), mean annual precipitation and temperature, was analysed based on samara traits describing samara weight and length, and wing length and width. The significant differences between the populations' mean values for the analysed *A. pseudoplatanus* samara traits were determined using the post hoc Sheffé's test results. The samara weight was the highest in the Kopaonik population compared to Južni Kučaj, the population at the lowest elevation with the highest temperature and minimal precipitation throughout the year. The highest values for all samara traits were observed in the Kopaonik population. The wing length was smallest in the Golija population (1530 m.a.s.l., low temperature) and the Rogozna population (770 m.a.s.l., high temperature), with similar precipitation levels. The ANOVA results suggest that environmental and genetic factors influence samara weight and morphologya. According to the results of multivariate analyses, Principal Component Analysis (PCA) and Agglomerative Hierarchical Clustering (ACH), ecological factors such as elevation and mean annual precipitation significantly influence the variation in samara traits among *A. pseudoplatanus* populations, with distinct patterns observed in weight and morphology across different localities. The observed variation in samara weight and morphology reflects the adaptation of *A. pseudoplatanus* populations to local environmental conditions. Further research is needed to investigate the adaptive significance of these traits, particularly in relation to seed dispersal strategies and their influence on forest dynamics.

**Keywords:** samara traits; sycamore maple; variability; climatic factors; principal component analyses; cluster analysis

## INTRODUCTION

Plants, being sessile organisms restricted to their germination site, have evolved specialised mechanisms to rapidly respond to environmental changes and flexibly adjust their reproductive phase (Žádníková et al. 2015). Morphological characteristics of seeds, such as size, weight, and dispersal method, affect dispersion, growth of populations, and distribution range based on environmental conditions (Song et al. 2020). Seed dispersal is fundamental in shaping plant populations' spatial distribution and genetic structure (Howe and Smallwood 1982). In anemochorous species that rely on wind for seed dispersal, morphological characteristics of the diaspores, such as size, shape, and weight, are key determinants of dispersal distance and success (Greene and Johnson 1990). Among temperate tree species, samara-winged fruits adapted for wind dispersal exhibit considerable variation both within and between species (Nathan et al. 2002). Samara, a type of fruit that is present in 25 orders, 45 families, and 140 genera of angiosperms, is a single-seeded fruit with a leathery winged part adapted for wind dispersal. Species with this type of fruit have a wide distribution and inhabit different habitats like deserts, rainforests, and temperate and alpine regions (Du et al. 2022).

Samara aerodynamic traits among different *Acer* species (size, shape, wing area, and weight) have functional importance in seed dispersal and directly influence dispersal patterns (Schaeffer et al. 2024). Research on the *Hopea hainanensis* species revealed significant correlations between samara traits and stem height. Selection of genotypes with a specific samara morphology is the basis of selection that could improve the reproductive success and vigour of seedlings (Song et al. 2020). Understanding the genetic and environmental factors influencing samara morphology is crucial for forest management when planning breeding and conservation strategies (Cascante et al. 2022).

Sycamore maple (*Acer pseudoplatanus* L.) is a fast-growing species with high-quality wood, fulfilling numerous ecosystem functions (Vacek et al. 2018). In Europe, the sycamore maple is the most represented maple species, yet it constitutes only a small portion of the forest stock and is rarely found in pure stands (Heim et al. 2009, Cvjetićanin et al. 2016, Vacek et al. 2018). It is estimated that the number of sycamore maple trees will decrease in stands where ash is present and in places exposed to intense drought (Morecroft et al. 2008). Further research is essential to carefully select starting materials, facilitating seed collection and the production of reproductive material suited to diverse ecological conditions.

Another reason for studying the sycamore maple samaras is that this species spreads invasively in introduced areas (Straigyte and Baliuckas 2015, Shouman et al. 2017). The contradictions between its endangered status in the natural part of its range and its intensive expansion in the introduced areas may lead to a drastic change in the distribution of this species in the future. Also, it is not always the case that different provenances of sycamore maple seedlings show differences in quality (Whittet et al. 2021). Therefore, selecting seeds with the desired characteristics is one of the basic mechanisms for eventually regulating sycamore maple stability. Additionally, understanding this species' fruit characteristics certainly represents the basis for mass production and regeneration of the sycamore maple trees.

Population analyses of samara morphology enable integrating the findings into forest breeding programs to improve seed dispersal efficiency, regeneration success, and overall forest management. The establishment and distribution of this species can be influenced by choosing the specific samara characteristics. This study aims to quantify and analyse the morphological diversity of samaras across different populations, investigating the potential influences of environmental and geographical factors on their dispersal capabilities. Research related to the morphological traits of sycamore maple samaras is quite rare, especially at the population level. The study of the morphological traits of sycamore maple samara from different parts of its natural range enables the assessment of variability between and within populations based on adaptation to a wide range of climatic conditions of the species' range. This variability in samara characteristics enables obtaining seed material from populations that are already adapted to specific environmental conditions and is the basis for future breeding programs.

The variability of *Acer pseudoplatanus* seeds is crucial for developing effective conservation and restoration strategies, as it directly influences the species' genetic diversity and adaptability. Incorporating this variability into management practices ensures the long-term resilience of forest ecosystems and supports biodiversity conservation efforts (Vranckx et al. 2012). Following all the above, this study aimed to examine the morphological traits of the sycamore maple samara collected from natural populations in Serbia. The expected contribution of the study include: I) assessesing variability of morphological characteristics of sycamore maple samaras within the population, II) analyizing the influence of climatic factors, temperature, and precipitation on the morphological characteristics of the samaras of the analyzed populations, III) evaluating the conditions necessary for obtaining seed material that would support sycamore maple breeding programs aimed at preserving the species in increasingly drier and warmer environments, as predicted by climate models.

## MATERIALS AND METHODS

Material for the analysis of variability of samara morphological traits in analysing morphological variability of sycamore maple populations was collected in six natural populations in Serbia (Figure 1). Each population is represented by 11 trees, and each tree by 30 healthy and undamaged samaras. Samaras were collected from regularly developed, isolated trees or trees on the forest's edge because, in those positions, their phenotype was fully expressed to show the recent state of the species without changes caused by cultivation measures (Zebec et al. 2010). A total of 1,980 samaras were collected and morphometrically processed. To prevent sampling genetically related trees, it was ensured that the sycamore maples were spaced at least 50 meters apart (Poljak et al. 2012). The tree's fruit, known as a samara, has a single seed with a flat, wing-like structure that helps it get carried by the wind. This design allows the seeds to travel over long distances. The colour and size of a samara can change depending on the local climate, such as temperature and humidity. Samaras for morphometric analysis were collected in October 2022. The analysed populations are located in the territory of Serbia at elevations ranging from 1530 to 490 m.a.s.l. Climatic factors like mean annual precipitation (MAP [mm]), mean annual temperature (MAT [˚C]), and their relationship were specific concerning the elevation of the locality (Figure 1).

The samara weight was measured using a precision balance with a 0.01 g accuracy, and the digital calliper with a 0.01 mm accuracy was used to take the dimension measurements. Eight samara traits of *A. pseudoplatanus* were measured: samara weight (F1) and following morphometric traits wing length including seed (F2), wing width (F3), wing length excluding seed (F4), wing length from the widest point of the wing (F5), length of the seed (F6), width of the seed (F7), thickness of the seed (F8) (Figure 2).

The data analyses were conducted separately for each population based on the morphological traits of samaras to derive fundamental descriptive statistics, including mean values and standard errors (SE). Estimates of the statistical significance of different levels of phenotypic variability sources of samara traits were performed using analysis of variance (ANOVA procedure PROC GLM in SAS) (SAS Institute Inc. 2011).

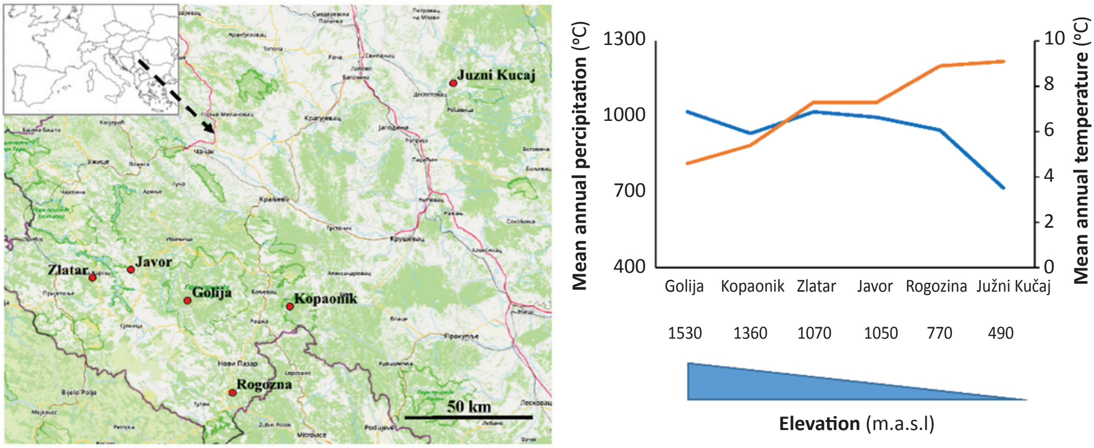


**Figure 1.** Map of *Acer pseudoplatanus* populations in Serbia with elevation, mean annual precipitation (mm), and temperature values (˚C).

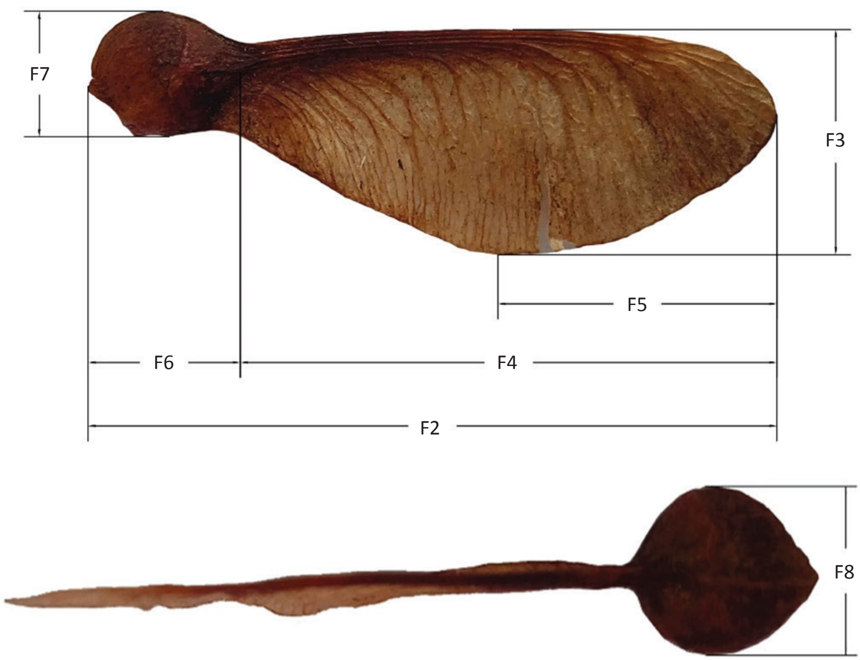


**Figure 2.** *Acer pseudoplatanus* samara. The image illustrates the sycamore maple (*Acer pseudoplatanus*) samara characteristics (two orientations).

According to this hierarchical three-way model, populations were treated as fixed factors, with trees nested within populations and samara nested within trees. The results of this analysis describe the statistical significance of phenotypic variability between and variability within population. The post hoc test, Scheffe's test, was used to compare the mean values of samara traits between populations.

Principal Component Analysis (PCA) was conducted to analyse the multivariate dependence of samara morphological traits and climatic variables. PCA is a dimensionality reduction technique that uses the variance of all original variables, captured in a covariance or correlation matrix, to create new uncorrelated variables (principal components) that represent the most informative directions in the data.

The principal components that are used to present the relationship among populations and among examined variables are selected according to Keiser's role, by which selected principal components must be greater than 1. The plot shows the relationship between all variables, and each variable is represented as a vector. The length and direction of a vector indicate the strength and correlation of a variable's dependence on a specific climatic factor. The strength and sign of the relationship between the two examined traits were evaluated regarding the position of their vectors. To visualise the grouping patterns within the data, the scores of the first two principal components were plotted in a biplot or scatter plot. Agglomerative Hierarchical Clustering (AHC) was performed to assess the clustering of examined populations based on examined samara morphological traits. The distance matrix was calculated using Euclidean distance, and agglomeration was carried out using Ward's method. The resulting dendrogram was visualised to examine the relationships between clusters.

Statistical data analysis was conducted using the appropriate procedures from the SAS 9.1.3 software package (SAS Institute Inc. 2011). Graphical representations of the results were created using the XLSTAT add-in for Microsoft Excel.

## RESULTS

The mean values of *A. pseudoplatanus* samara weight (F1) and morphological traits (F6, F7, and F8) in the Kopaonik population were significantly higher than those in the Južni Kučaj population. The length of the samaras' wings with and without seed (F2 and F4) was the smallest for the Golija and Rogozna populations. The wing width (F3) was highest for the Golija, Južni Kučaj, and Kopaonik populations. The smallest mean values for wing length from the widest point of the wing (F5) were recorded for the Kopaonik, Golija, and Južni Kučaj populations compared to the Zlatar and Javor populations. The results of the post hoc Sheffé test (based on hierarchical analysis of variance) confirmed significant differences between the population's means for the analysed samara traits (Figure 3).

The three-way hierarchical analysis of variance was performed to assess effect of examined sources of phenotypic variability of the samara traits: the effects of population (P), trees nested within populations (T) and samaras nested within trees. The analysis revealed that population (P) significantly influenced both samara weight and samara morphology traits (F1-F8), suggesting that environmental factors at the population level play a significant role in these traits (all $p < 0.05$). Trees within the population (T) had a considerable effect on all analysed samara traits, indicating considerable genetic variability among trees within the population (for all morphological traits: $p < 0.05$). No significant effects were found for samara-level variability (for all morphological traits: $p > 0.05$). These results suggest that besides environmental and genetic factors, too influence samara weight and morphology between and within the examined *A. pseudoplatanus* populations (Table 1).

The first two principal components explained 55.58% (PCA1) and 21.92% (PCA2) of the total variance, capturing the majority (77.49%) of the variability in the dataset (Figure 4). Climatic factors, such as elevation and mean annual precipitation (MAP), significantly influenced samara weight (F1) and seed morphological traits F7 and F8. The correlation values are statistically significant, with the highest correlation coefficients observed between weight and seed traits F6, F7, and F8 ($r > 0.8$, $p < 0.05$), as well as between samara weight and traits F7 and F8 with the elevation and MAP ($r > 0.8$, $p < 0.05$). According to PCA1, the populations of Golija and Rogozna are separated from the others, as they have similar precipitation values, but Rogozna has higher MAT values, while according to PCA2, the Južni Kučaj population, with the highest MAT and the lowest MAP, is separated from the other populations. The separation of the Kopaonik and Zlatar populations is mainly driven by the traits of samara length and wing length (F2 and F4, $r > 0.98$, $p < 0.05$), for both of which the mean values were statistically significantly higher compared to other populations. The traits F1, F6, F7, and F8 are morphological traits with the strongest relation with the examined climate parameters, elevation and MAP. These results indicate that elevation and precipitation conditions drive the observed differences in the mean values of samara traits among the various populations (Figure 4).

**Table 1.** Results of three-way hierarchical analysis of variance for samara weight and samara morphology traits between *Acer pseudoplatanus* populations (P), trees (T) within population and samaras within trees (P T). For acronyms, see the Materials and Methods section.

| | | Seed Mass | | F2 | | F3 | | F4 | |
|---|---|---|---|---|---|---|---|---|---|
| **Source of Variation** | **df** | **MS** | **F Value** | **MS** | **F Value** | **MS** | **F Value** | **MS** | **F Value** |
| Population | 5 | 0.11 | 139.60**** | 596.70 | 62.96**** | 84.95 | 50.10**** | 384.76 | 50.14**** |
| Tree (P) | 30 | 0.01 | 19.35**** | 584.16 | 61.68**** | 144.58 | 85.27**** | 491.12 | 64.00**** |
| Seed (P T) | 319 | 0.27 | 1.10 | 9.46 | 1.00 | 1.81 | 1.07 | 7.34 | 0.96 |
| Error | 1595 | 0.00 | | 9.47 | | 1.70 | | 7.67 | |
| | | F5 | | F6 | | F7 | | F8 | |
| **Source of Variation** | **df** | **MS** | **F Value** | **MS** | **F Value** | **MS** | **F Value** | **MS** | **F Value** |
| Population | 5 | 174.88 | 39.95**** | 42.84 | 95.08**** | 46.71 | 218.33**** | 81.77 | 258.44**** |
| Tree (P) | 30 | 172.54 | 39.42**** | 22.47 | 49.86**** | 9.80 | 45.81**** | 7.16 | 22.62**** |
| Seed (P T) | 319 | 3.99 | 0.91 | 0.45 | 0.99 | 0.22 | 1.02 | 0.31 | 0.99 |
| Error | 1595 | 4.38 | | 0.45 | | 0.21 | | 0.32 | |

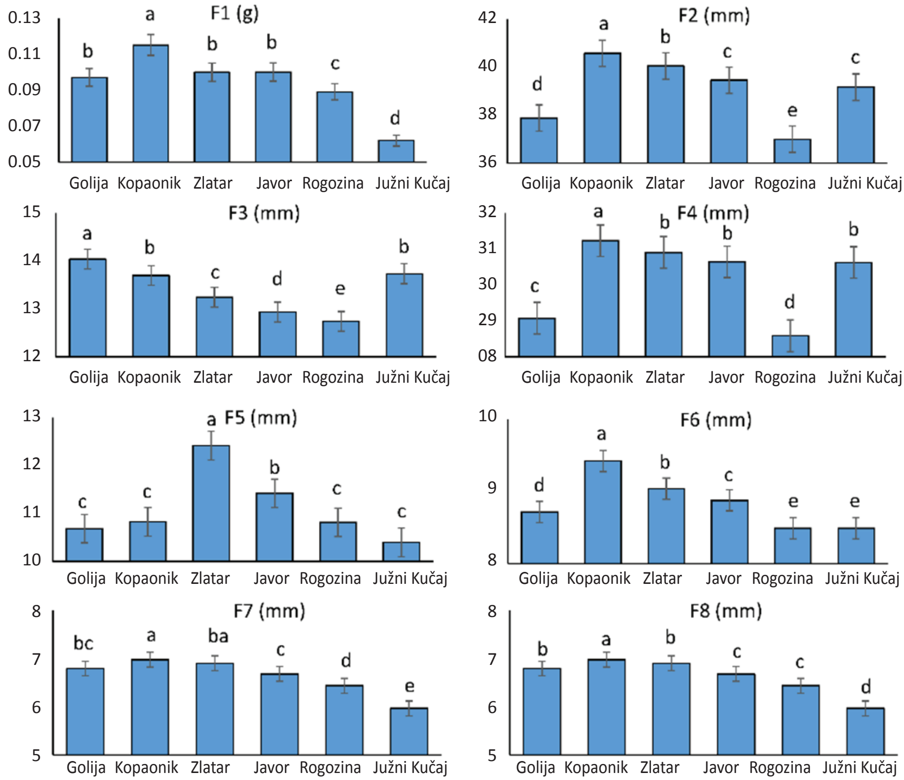


**Figure 3.** Histograms displaying the mean values of *Acer pseudoplatanus* samara traits for six populations. The bars represent the mean values of the morphological traits (F1-F8), with error bars indicating the standard error. Statistical significance between populations is indicated by p values below the threshold of 0.05, according to the results of the post hoc Scheffé's test (different lowercase letters indicate significant differences between populations for the analysed traits of samaras). For acronyms, see the Materials and Methods section.

The agglomerative hierarchical clustering (AHC) analysis revealed distinct clusters based on samara traits and environmental conditions. The dendrogram illustrates that populations are grouped (at a distance threshold of 2.77) into three clusters based on their similarity. The Južni Kučaj population formed one cluster, Kopaonik, Javor, and Zlatar formed the second, and Golija and Rogozna formed the third (Figure 5). The highest MAT values, the lowest elevation, and MAP in the Južni Kučaj population resulted in samaras with the lowest samara weight and lowest values of other samara traits, as well as small wing length. The second cluster (Kopaonik, Javor, and Zlatar populations) had similar MAP and MAT values and exhibited similar values of samara weight, wing length, samara length, and samara width. The populations in the third cluster have a low samara length (F2) and wing length without seeds (F4). The average characteristics of the Golija and Rogozna sites differ (elevation 1530 m vs. 770 m a.s.l.; MAT 4.6°C vs. 8.9°C, respectively), while the MAP values were similar, which probably led to similar samara morphological traits in populations on these sites.

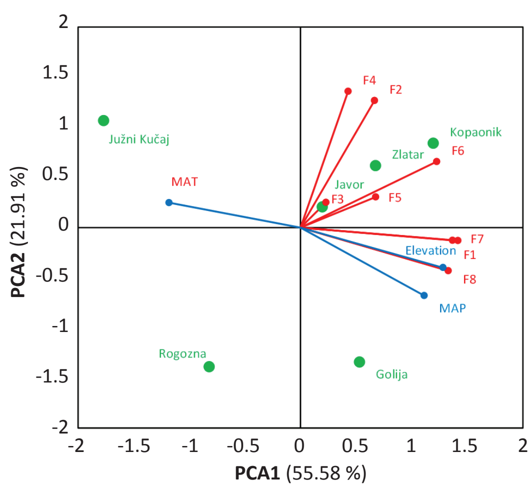


**Figure 4.** The scatterplot of Principal Component Analysis (PCA), the multivariate analyses of morphological traits (F1-F8) and climatic factors (Elevation, MAP, and MAT) of *Acer pseudoplatanus* samara populations. For acronyms, see the Materials and Methods section.

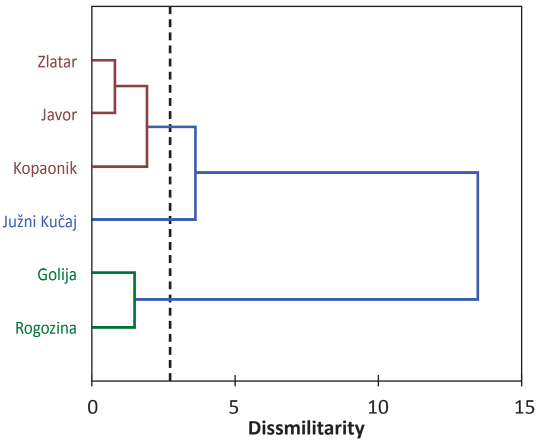


**Figure 5.** Agglomerative Hierarchical Clustering (AHC) dendrogram of morphological traits (F1-F8) and climatic factors (Elevation, MAP, and MAT) of *Acer pseudoplatanus* samara populations. For acronyms, see the Materials and Methods section.

## DISCUSSION AND CONCLUSIONS

This study examined for the first time the morphological variability of sycamore maple samaras in natural populations situated at different elevations, with a characteristic relationship between precipitation and temperature. The weight of sycamore maple samaras was the smallest in the population of Južni Kučaj, which is at the lowest elevation and experiences the least precipitation and the highest temperature. Trees originating from the Kopaonik population had the highest values of samara weight and all other samara morphological traits (except for F3 and F5). The wing length and width were similar for both the Juzni Kucaj and Kopaonik populations, and these values were higher compared to the same traits in the Rogozna population, which has climate conditions more similar to those in Južni Kučaj. It is known that environmental factors at different elevations affect morphological, chemical, and physiological variability while not affecting sycamore maple seed germination (Carón et al., 2014). Sycamore maple is a potentially adaptable species to climate change, indicating a need for its more intensive use in European plantations (Iliev et al. 2022). The findings in our study indicate considerable variability of the analysed samara traits within and between populations. Specific environmental factors at each location impacted the observed variability in the morphological traits of the samaras, reflecting the species' adaptability to these conditions. Also, the variability of sycamore maple samara within populations was confirmed, which leads to the conclusion that selecting the starting material with suitable characteristics is possible. This selection could enable the extension of the species' distribution area. Seeds originating from populations with arid and warm climates (Južni Kučaj and Rogozna) can be the starting material for species breeding programs.

Variations in samara traits within and between populations are important evolutionary and ecological premises that indicate that seeds' hereditary traits are subjected to ecological and evolutionary selection to adapt to spatial and temporal environmental changes (Song et al. 2020).

The spread of the species depends on the morphological traits of the samara. By analysing the influence of the genus *Acer* samara characteristics on the spreading, it was found that the samara angle has the most significant influence on the settlement velocity and the horizontal dispersal distance, and the smallest on the seed width. The settlement velocity of samara was positively correlated with seed and wing length, solely wing length, wing width, seed length to width ratio, seed length to wing length ratio, and negatively correlated with samara angle and seed width. Horizontal distance was positively correlated with seed width and negatively correlated with samara angle, seed and wing length, wing width, seed length to width ratio, and seed length to wing length ratio. Both the samara angle and the ratio of seed length to wing length can be used as important factors for the classification of the genus *Acer* (Hong et al. 2021).

Other species within the genus *Acer*, such as the Norway maple (*Acer platanoides*), demonstrate a greater potential for adaptation to changing climate conditions. This adaptability is particularly evident in their reproductive success and early growth stages under altered environmental factors. Research by Carón et al. (2015) indicates that *A. platanoides* exhibits higher germination rates and larger seedlings compared to *A. pseudoplatanus* when exposed to warming and drought conditions. These traits may provide a competitive advantage, allowing *A. platanoides* to better cope with the impacts of climate change. One of the aspects of studying morphological traits is the relationship between samara size and fungal infections. This practically means that samaras of different dimensions can be affected by pathogens to varying degrees that reduce their vigour or germination, which is why the need to use samaras adapted to specific ecological conditions is highlighted. Another aspect refers to pathogens specialized primarily on species from the genus *Acer* (Ellis and Ellis 1985, Ginetti et al. 2014, Brglez et al. 2020, Kowalski et al. 2021, Bußkamp et al. 2024), which can cause significant damage after seed germination, especially in combination with unfavorable habitat conditions. Therefore, knowledge of the morphological characteristics of sycamore maple samaras is of great importance in forest protection. Although some studies state that there is no connection between the surface of the fruit and the diversity of fungi that appear on it (Tang et al. 2003), a large number of fungal species colonise damaged samaras or those that are in unfavourable conditions (Perera et al. 2020). Also, the fungal communities that colonize fallen seeds primarily depend on the tree species and less on forest characteristics, soil type, or time spent on the soil (Sarmiento et al. 2017).

The study of samara characteristics is a valuable indicator of ecosystem resistance to drought (Luo et al. 2022). The same authors state that due to adaptation to drought, there is a shortening of samara length and an increase in the thickness of the samara and the thickness of the samara's coat. In this sense, samaras of shorter length and greater thickness have a greater potential to adapt to drought-affected regions due to climate change. Also, samaras that form earlier have a greater potential to avoid frost damage (Bianchi et al. 2019). The selected starting material enables the creation of future stability of sycamore maple stands in this part of the distribution area through greater adaptability to the harmful effects of various external factors.

The special importance of the selected populations is reflected in knowing the connection between the geographical distribution of the different populations and the characteristics of the samaras produced on the sycamore maple trees. The need to study variability within a population, which represents evolutionary potential, has been highlighted recently due to global changes (Des Roches et al. 2018). The variability within the population regarding the following traits: samara weight, wing width, wing length, wing length to widest part, samara length, samara width, and samara thickness may indicate the influence of tree genotype and environmental characteristics affecting the population. Also, variability within a population enables adaptation to changes in the habitat (Mitchell et al. 2016). In this study, the variability within the population, namely, the genetic variability of the morphological characteristics of samara within sycamore maple populations, was confirmed. The characteristics of samara weight, as well as its length and width, are most correlated with elevation and precipitation. The Kopaonik and Golija populations are at the highest elevations, but the Golija population has lower temperatures and more precipitation. High temperatures separate the Južni Kučaj and Rogozna populations from other populations. The cluster analysis results, which include morphological characteristics of the sycamore maple samara and climatic characteristics, indicate closeness between Zlatar, Javor, and Kopanik populations, as well as between Rogozna and Golija populations. At the same time, South Kučaj is a separate population with climatic factors that are closest to the predictions of climate scenarios, and this influenced the fact that the smaras are smaller compared to the other analysed populations. These results are of great theoretical and practical importance for further research and field work on improving the condition and restoration of sycamore maple stands in this part of the distribution area.

Finally, it is necessary to point out that selecting a specific trait related to the locality and the predicted stress factor represents one of the challenges in ecology (Harrison and LaForgia 2019). First of all, the effects of drought are more harmful to larger trees (Bennet et al. 2015). The selected material for young sycamore maple seedlings provides a realistic basis for successful adaptation and survival, primarily due to the small need for care measures for young sycamore maple in specific mixed stands (Collet et al. 2008). In this way, through the production or natural regeneration of seedlings with targeted characteristics and their regular care measures in the later stages of development, continuity is achieved in creating adaptable populations to certain stress factors. Incorporating variability in forest management practices enhances ecosystem resilience by allowing forests to better adapt to environmental changes and disturbances (Lindenmayer et al. 2006). This approach also supports biodiversity conservation by maintaining habitat heterogeneity, which is crucial for sustaining diverse species populations (Franklin et al. 2002).

Southeast Europe represents a part of the sycamore maple distribution area with still unexamined populations based on different morphological parameters. This study determined the variability of sycamore maple samara dimensions within and between selected populations in Serbia. The Zlatar, Javor, and Kopaonik populations are similar in samara characteristics, as well as the Rogozna and Golija populations, while the Južni Kučaj population stood out. Based on the presented data, it is possible to further work on selecting starting materials for producing samaras with targeted characteristics that will correspond to specific needs in the field, primarily due to global climate change. The findings in this study represent the basis for further research or practical work related to producing reproductive material of sycamore maple from this distribution area.

## Author Contributions

VP and DM conceived the idea and designed the study. VP, SJ, AL, and LJR conducted fieldwork. DM and AV performed statistical analyses, data curation, and visualization of results. VP, DM, and BF wrote the manuscript.

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## Conflicts of Interest

The authors declare no conflict of interest.

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