

MORPHOLOGICAL, PHENOLOGICAL, AND BIOMASS TRAITS UNDERLYING THE INVASIVENESS OF *FALLOPIA* × *BOHEMICA*

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Abstract: *Fallopia × bohemica* (Bohemian knotweed), an invasive hybrid of *Fallopia japonica* and *Fallopia sachalinensis*, is one of the most aggressive invasive plant species in riparian and disturbed habitats across Europe. In this study, we examined morphological, phenological, and biomass-related traits that may underlie the invasive potential of the species. The external morphology of aboveground shoots, leaf traits, epidermal characteristics, stomatal parameters, pollen morphology, and flowering phenology were examined within a single population during the 2018 growing season. Substantial intra-population variability was observed in plant height (125–337 cm), aboveground biomass (17.31–431.79 g d.w.), branching pattern, and total leaf area (1,000–12,000 cm²), largely driven by spatial position within the stand. Biomass accumulation was strongly associated with stem diameter and total leaf area, while shoot length showed a weaker relationship with branching intensity. Zone-specific variation in leaf morphology and petiole length enhanced light interception and contributed to dense canopy formation and pronounced shading. Leaves exhibited mesophytic epidermal traits, including hypostomatic structure and dense non-glandular trichome coverage, which reduce cuticular transpiration. Flowering occurred continuously but asynchronously within the population and provided an important nectar source for pollinators, despite limited sexual reproduction. Based on these observations, vegetative spread via rhizomes was inferred to be the primary driver of population persistence and expansion. Overall, the invasive success of *Fallopia × bohemica* appears to be driven by rapid biomass production, flexible shoot architecture, effective light capture, and strong competitive shading rather than by reproductive output. These findings highlight the importance of structural and biomass-related traits in shaping the species' invasive performance.

Keywords: *Fallopia × bohemica*, Bohemian knotweed, invasive species, biomass allocation, shoot architecture, leaf morphology, phenology, stomatal index, trichomes, pollen morphology



INTRODUCTION

Species of the genus *Fallopia* are perennial plants native to East Asia and were introduced to Europe and North America in the 19th century as ornamental plants (Drazan *et al.* 2021; Kato-Noguchi 2022). Since then, it has spread rapidly and become established in many regions. Today, it is considered one of the world's 100 most problematic invasive species, *sensu lato*.

Fallopia × bohemica (syn. *Reynoutria × bohemica*) originated from the hybridization of *Fallopia japonica* and *Fallopia sachalinensis* in Central Europe during the 19th century (Bailey and Wisskirchen 2006). It has since spread widely across Europe and North America. The species serves as an ideal model for studying hybrid vigor and the ecological success of invasive taxa (Parepa *et al.* 2013).

The hybrid is now widespread throughout Europe, thriving in riparian zones, disturbed habitats, and anthropogenic landscapes (Bailey 2022). It primarily propagates through vegetative rhizome and stem fragments, often spread by human activities such as construction or soil movement (Bailey 2013). Seed-based reproduction is less common but can occur in mixed populations, contributing to genetic variability and adaptive potential (Tiébré *et al.* 2007).

The species displays high photosynthetic efficiency, rapid early-season growth, and substantial belowground biomass reserves (Rouifed *et al.* 2012). Its rhizomes contain large carbohydrate stores that enable regeneration after cutting or herbicide treatment. Studies have demonstrated tolerance to salt (Rouifed *et al.* 2012) and drought stress, thereby enhancing its colonization potential in roadside areas and saline soils. Hybrid vigor is evident in faster shoot elongation and greater biomass compared to parental taxa (Parepa *et al.* 2013). Allelopathic effects have been confirmed through activated carbon bioassays, suggesting secretion of phytotoxic compounds that inhibit native plant germination and alter soil microbial communities (Murrell *et al.* 2011; Kato-Noguchi 2022).

Dense monospecific stands of *F. × bohemica* displace native vegetation, reduce biodiversity, and modify nutrient cycling in invaded habitats (Beerling *et al.* 1994; Dassonville *et al.* 2008). The alteration of soil microbial assemblages and reduced arbuscular

mycorrhizal colonization further hinder the recovery of native species (Parepa *et al.* 2013; Kato-Noguchi 2022; Šoln *et al.* 2023). Experimental approaches in knotweed research include controlled greenhouse and field trials, rhizome regeneration assays, photosynthetic gas exchange measurements, and chlorophyll fluorescence analyses to assess physiological performance. Soil assays with activated carbon are used to evaluate allelopathic interactions (Murrell *et al.* 2011). Molecular methods such as AFLP and microsatellite analyses help quantify hybridization and genetic diversity (Tiébré *et al.* 2007).

In Central Europe, particularly in Hungary, *F. × bohemica* is probably the most widespread species of the genus and is considered a naturalized invasive plant that significantly transforms habitats. It is widespread along rivers (Danube, Tisza) and infrastructure corridors (railways, roadsides). It occurs mainly in semi-natural, degraded sites such as riverbanks, stream edges, and floodplains, but also appears in settlements and ruderal areas. It is common nationwide, especially in hilly regions, and shows morphological traits intermediate between its parent species.

The plant typically reaches 2.5–3.5 m in height, with a hollow stem. Leaf shape varies along the stem: lower leaves have a cordate base, whereas upper leaves are straight or obtusely cuneate at the base. Leaves are 10–23 × 9–20 cm, with an intermediate texture. The lower surface is slightly hairy, with hairs restricted to the veins. The inflorescences are clustered panicles. Male flowers are erect and may have branched lateral axes, while female flowers can be slightly arching. Each cluster contains 3–5 flowers. Flowering lasts from July to October. The fruit is a bronze-shining achene enclosed by narrow ovate perianth segments, measuring 2–4 mm (Balogh 2004, 2008). The hybrid knotweed exhibits a highly heterogeneous gene pool, determined by the specific parental species or cultivars involved in hybridization, thereby generating substantial genetic diversity (Hollingsworth *et al.* 1998). Post-hybridization, resultant genotypes may display pronounced morphological divergence from preceding generations, reflecting differential expression of parental traits. This elevated genetic variability is considered a key factor underlying the hybrid's ecological success and invasive potential.

Its expansion has been documented by the Hungarian Ministry of Agriculture and the Institute for Soil Science. Mechanical eradication remains challenging due to rhizome regeneration. Combination

strategies involving repeated mowing, chemical control (glyphosate-based applications), and restoration with competitive native species are most effective (Jones *et al.* 2018; Skinner *et al.* 2012; Clements *et al.* 2016; Hocking *et al.* 2023). Recent Hungarian studies emphasize the need for long-term monitoring and soil microbiome rehabilitation following removal (Balogh 2004; Békésiné Kallenberger *et al.* 2016).

Our objective was to investigate the morphological, phenological, and biomass-related traits of *Fallopia × bohemica* in order to assess how these characteristics contribute to the species' invasive potential. As a general objective, a deeper understanding of invasive species can provide valuable insights for developing effective control and management strategies against them.

We hypothesized that the invasive success of *Fallopia × bohemica* is primarily driven by a combination of morphological, phenological, and biomass-related traits that enhance light acquisition, rapid biomass accumulation, and competitive dominance over native vegetation.

MATERIALS AND METHODS

Sampling site and Plant material

The sampling site in Gyöngyös (47°46'04.5"N 19°54'47.2"E) is located along a highly disturbed stream section surrounded by human infrastructure (*Figure 1*). Although regular mowing is conducted in the surrounding area, the focal knotweed population remained unaffected by these management activities. From this *Fallopia × bohemica* population, eight individuals were randomly selected for various measurements. Selection was based on growth form categories, comprising two small individuals with few branches and leaves, four medium-sized individuals with moderate branching and foliage, and two large individuals exhibiting extensive branching and dense leaf cover.

The study area has a moderately warm, moderately dry temperate climate, characterized by slight cooling and increased precipitation, influenced by the nearby Mátra Mountains. The Gyöngyös stream's microclimatic effects further shape local conditions. Monthly precipitation averages 30–70 mm, peaking in May, which supports rapid spring growth of knotweed, and reaching its minimum in September, facilitating flowering and seed

maturation. Despite seasonal variability, precipitation is unlikely to constitute a limiting factor, given the perennial nature of streamflow sustained by rainfall and groundwater-fed springs in the Mátra region.

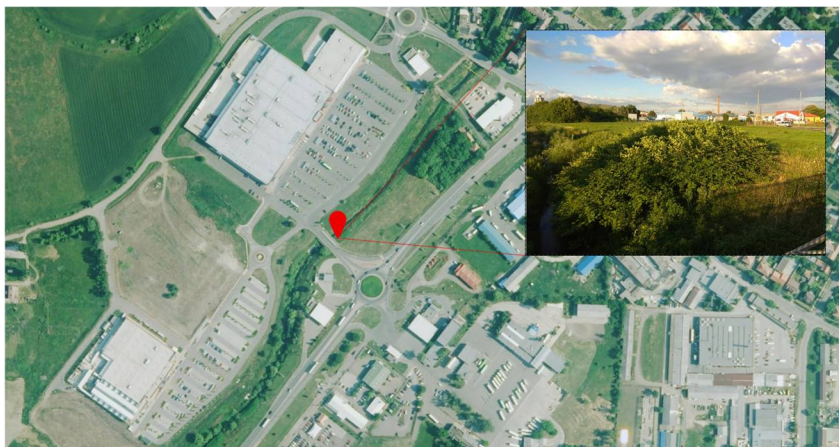


Figure 1. The sampling site (47°46'04.5"N 19°54'47.2"E) is located next to the Gyöngyös stream, within the town of Gyöngyös. Photograph of the sampled *Fallopia × bohemica* population. Source of map: E-közműtérkép. Photo: Krisztina Csákné Nemoda.

Aboveground shoot assessment

Eight individuals in the plant population were selected for the aboveground shoot measurements. Shoot length was measured from the soil surface to the apical growing point of each plant. Stem diameter was determined at 10 cm above the soil surface using a caliper.

Petiole length was measured in upper, middle, and lower leaf zones along the stem. Leaf blade length was determined from the base of the lamina (at the point where the blade begins) to the apex along the midrib (*Figure 2*). Leaf blade width was defined as the maximum width of the lamina and was measured using a caliper.

Determination of total leaf number

The total leaf number was determined by counting all leaves present on each shoot of the eight individual plants.

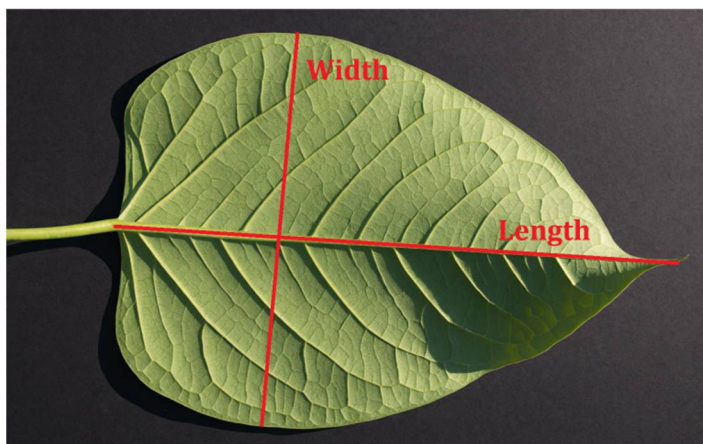


Figure 2. Measurement scheme for leaf blade length and width in knotweed (*Fallopia × bohémica*).

Biomass determination (total shoot, branches, and leaves)

Plant biomass was determined by oven-drying all sampled individuals at 105°C until constant weight was achieved. Following drying, the plant material was separated and weighed according to different morphological components. Biomass measurements were conducted for branches with leaves, stems with leaves, branches alone, stems alone, and leaves alone. This approach allowed biomass estimation both at the branch level and for the entire plant, providing separate values for stem biomass, leaf biomass, and their combined total.

Determination of total leaf area

Leaf area was measured individually for each leaf, and total leaf area per plant was calculated as the sum of all measured leaf areas. Leaves, branches, and stems were precisely numbered to ensure accurate identification and data consistency throughout the measurements.

Investigation of flower number and flowering phenology

Flower number was assessed in five individuals of the studied knotweed population. The number of flower clusters was recorded

for each branch, and flowering phenology was monitored by documenting the precise onset and total duration of the flowering period.

Light microscopic plant anatomical analyses

To examine the abaxial epidermis of the leaves, epidermal peels were prepared from the upper, middle, and lower leaf zones of the examined plant individuals. Stomatal density (number of stomata per mm²) and stomatal index (stomatal number / number of epidermal cells per mm²) were determined. The morphology of trichomes was also examined.

Pollen samples were collected from flowers, and pollen morphological analyses were conducted following fuchsin staining.

Statistical analysis

Statistical analyses were performed using SigmaPlot version 16.0 (Grafiti LLC, Palo Alto, CA, USA). Differences among treatments were evaluated using one-way analysis of variance (ANOVA), followed by the Holm–Šidák post hoc test to detect significant pairwise differences. Where applicable, probability values were derived from the ANOVA results. Errors are presented as standard deviations.

Measurements were performed using three independent biological replicates (n=3), with three replicates analyzed per treatment. Replicates consisted of separate, non-homogenized samples, each representing a single branch. No data transformation was required before statistical analysis.

RESULTS AND DISCUSSION

Morphology of the aboveground shoot

Based on shoot length measurements, plants ranging in height from 125 to 337.4 cm were recorded within the same phenological phase between 26 June and 5 July 2018 (*Figure 3*).

The assessment of total aboveground shoot biomass involved determining the dry mass of shoots (stems and leaves) after drying to constant weight. Data for stems, branches, and leaves were recorded separately (*Figures 3, 4*). Total biomass per plant ranged from 17.31 to 431.79 g. Individual plants bore between 0 and 15

branches (Figure 10). The total number of leaves ranged from 10 to 166 per plant. Based on these traits, two individuals were classified as small, with few branches and leaves; three individuals as medium-sized, with a moderate number of branches and leaves; and two individuals as large, with numerous branches and dense foliage (Figure 4). The two tallest plants (plants 2 and 3) exhibited exceptionally high biomass values compared to the others (Figures 3, 4). These data were analyzed from multiple perspectives. A comparison of shoot length and biomass (Figure 3) showed that shorter plants had lower biomass; however, taller plants could be divided into two groups: tall plants with lower biomass and tall plants with higher biomass. Analysis of the stem-to-leaf biomass ratio revealed that in the two tallest plants (plants 2 and 3), shoot mass accounted for approximately 70% of the total biomass, whereas in the other two tall plants (plants 4 and 7) this proportion was 60% and 80%, respectively. In plants shorter than 221 cm, this ratio ranged between 40% and 55%, indicating that in smaller plants, stem and leaf biomass contributed nearly equally to total biomass (Figure 5).

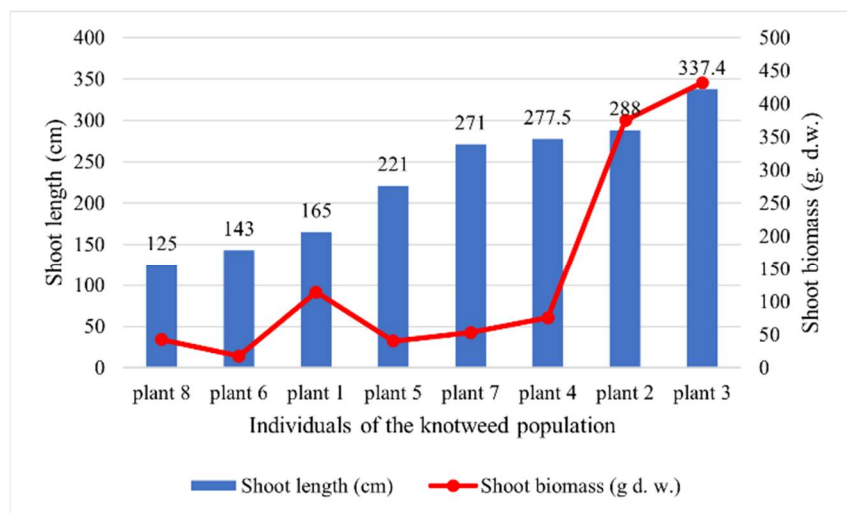


Figure 3. Relationship between shoot biomass (g d.w.) and shoot length (cm) in individuals of the studied population. Shoot length increases from left to right for the studied plant individuals.

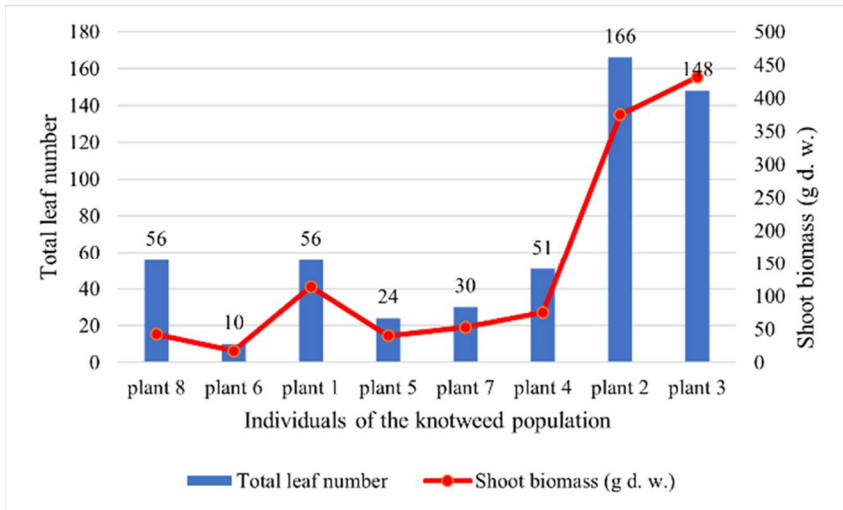


Figure 4. Relationship between shoot biomass (g d.w.) and total leaf number in individuals of the studied population. Shoot length increases from left to right for the studied plant individuals.

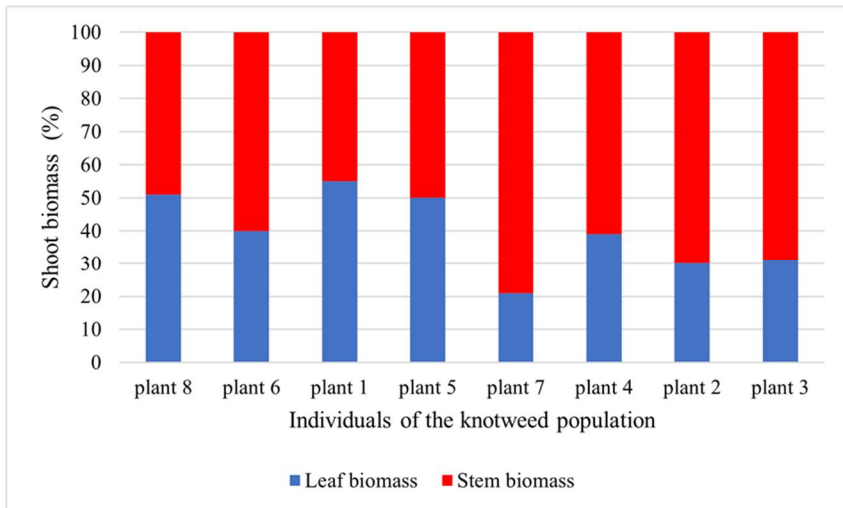


Figure 5. Proportional distribution of shoot biomass as a percentage of stem and leaf biomass. Shoot length increases from left to right for the studied plant individuals.

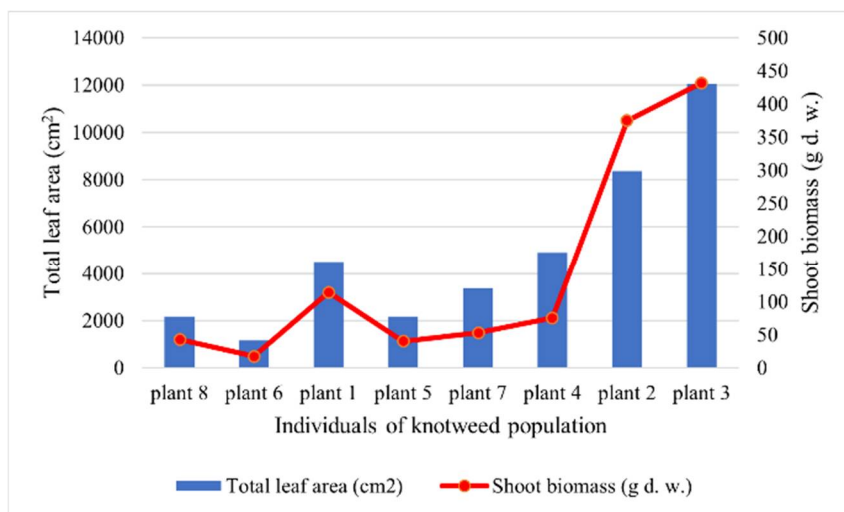


Figure 6. Relationship between shoot biomass (g d.w.) and total leaf area in individuals of the studied population. Shoot length increases from left to right for the studied plant individuals.

A linear regression relationship was observed between stem diameter and shoot biomass ($R^2 = 0.8347$) (Figure 7). The relationship between shoot diameter and shoot length yielded an R^2 value of 0.697 (Figure 8). In contrast, shoot length and branch number did not show a strong correlation ($R^2 = 0.3295$) (Figure 9).

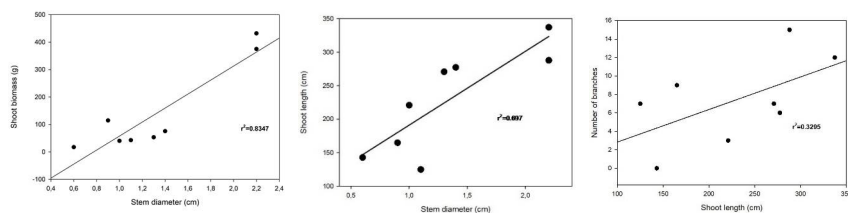


Figure 7. (left) Relationship between stem diameter (cm) and shoot biomass (g d.w.) in individuals of the studied knotweed population. ($r^2=0.8347$). **Figure 8.** (middle) Relationship between stem diameter (cm) and shoot length (cm) in individuals of the studied knotweed population. ($r^2=0.697$). **Figure 9.** (right) Relationship between shoot length (cm) and number of branches in individuals of the studied knotweed population. ($r^2=0.3295$).

Spatial position within the population also had a significant influence on biomass development. In taller individuals, biomass

was more strongly affected by positional factors. Plants located at the edge of the stand had greater space availability, enabling the development of more complex shoot systems and denser foliage. In contrast, individuals situated away from the population margin were forced to grow upward in competition for light, resulting in greater height but fewer branches and, consequently, reduced leaf area. Shoot biomass was most strongly influenced by leaf number. Total leaf area in the examined plants ranged from 1,000 to 12,000 cm² (Figure 6).

The previously described shoot architecture and extensive total leaf area enable the plant to cast heavy shade over large areas along stream banks, thereby displacing native, and in some cases protected, riparian vegetation. This competitive ability is further enhanced by its dense stem production per square meter. In long-established stands, the species is capable of overgrowing and enveloping neighboring plants. These observations are in agreement with earlier studies demonstrating that invasive *Fallopia* taxa form dense monospecific stands that reduce native plant diversity and substantially alter community structure and ecosystem functioning through shading and space monopolization (Beerling *et al.* 1994; Dassonville *et al.* 2008; Parepa *et al.* 2013). In addition to physical shading, allelopathic interactions may further intensify the exclusion of native species, as *Fallopia* taxa are known to release phytotoxic compounds that inhibit germination and growth of competing plants (Murrell *et al.* 2011; Kato-Noguchi 2022). Stem diameter ranged from 0.6 cm in the smallest individuals to 2.2 cm in the largest (Figure 7). A direct proportional relationship was consistently observed between plant height and stem diameter (Figure 8). The stem exhibited a hollow internal structure.

The lower, middle, and upper leaf zones were defined based on leaf morphology and their position along the stem (Figure 14). We examined the effect of leaf position on petiole length and found that petioles were longest at the lower part of the stem, particularly at the 1st–3rd nodes, reaching approximately 5 cm (Figure 13). Moving upward along the stem, petiole length decreased in the middle zone to around 3 cm and further declined in the upper zone to approximately 2.5 cm. This trait facilitates the ability of the knotweed to reposition leaf blades located at the lower nodes in a manner that maximizes light interception.

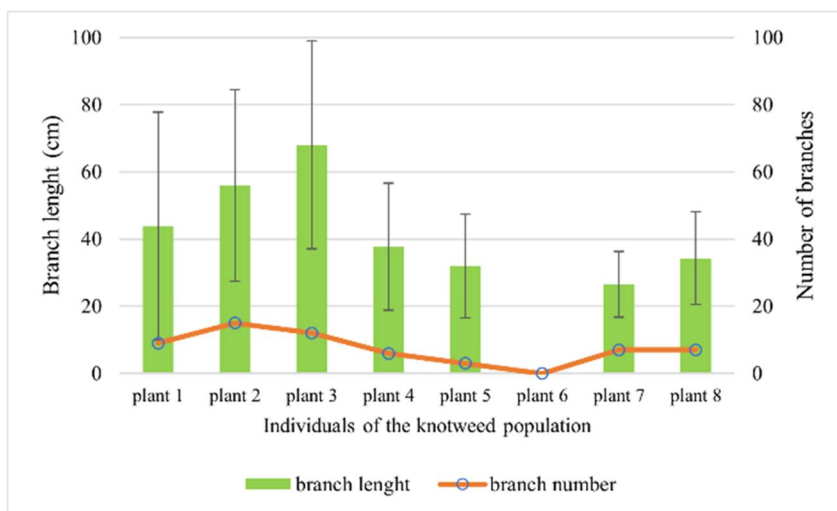


Figure 10. Variation in branch length and branch number in the individuals of the studied knotweed population.

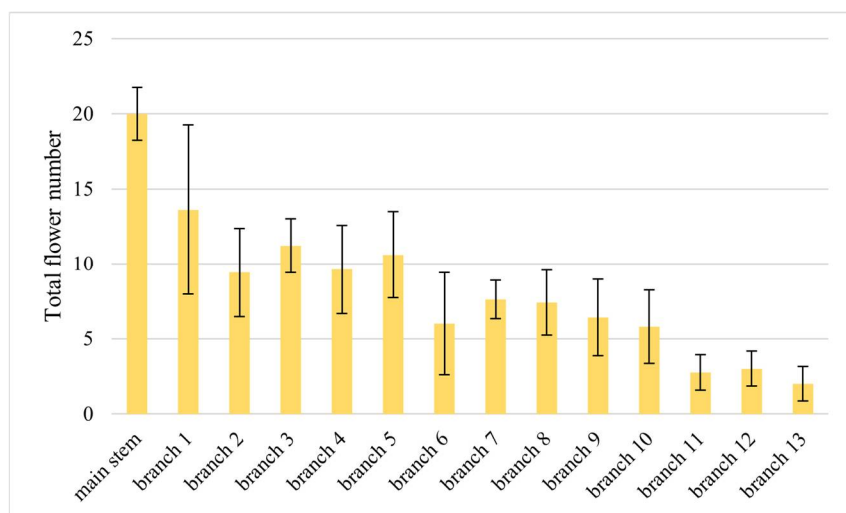


Figure 11. Total flower number on the main shoot and branches in 5 individuals of *Fallopia × bohémica* plants (n=5).

The greatest similarity in leaf blade length was observed in the lower leaf zone, which was also characterized by the lowest variation (Figure 15). The most pronounced morphological variation occurred in the upper zone, where both smaller leaves and leaves with markedly elongated apices were present. In contrast, the

greatest variation in leaf blade width was characteristic of the lower leaf zone (*Figure 15*).

Interestingly, in cases where narrower leaves occurred in the lower leaf zone of individual plants, greater leaf blade widths were observed in the other two zones (*Figure 14*).

These results indicate pronounced intra-population variability driven primarily by spatial position and shoot architecture. Based on qualitative observations not supported by quantitative measurements, individuals located at the margin of the plant group were smaller in size and possessed fewer branches, as they represented newly emerged shoots; this warrants further investigation.

At the study site, mean monthly temperatures range from –2 to +28°C, while average values during cold winter nights may reach –10°C and peak summer days may exceed +38°C. This temperature amplitude of more than 50°C is tolerated by the plant through effective seasonal strategies. Harmful winter frosts are overcome by utilizing nutrient reserves stored in the rhizome during the growing season, which enable the rapid development of a new shoot system in spring. The accumulation of substantial carbohydrate reserves in the rhizome is a well-documented survival strategy in invasive knotweed species and plays a key role in their rapid regeneration following mechanical disturbance or control attempts (Bailey 2013, 2022). Tolerance to summer heat is facilitated by the species' preferred habitats – although it is not restricted exclusively to flowing or standing waters – as well as by its large leaf area, which allows continuous transpiration supported by stream water even during periods of severe drought. Similar physiological advantages, including enhanced tolerance to abiotic stress and high growth performance, have been reported for invasive knotweed taxa, particularly for hybrid forms exhibiting heterosis, which contributes significantly to their invasive success (Rouified *et al.* 2012; Parepa *et al.* 2013). The extensive foliage has a pronounced shading effect (*Figures 4, 5*), resulting in lower leaves being shielded from excessive radiation. This trait not only protects the plant itself but also contributes to the displacement of other organisms within the habitat. By heavily shading stream banks, slower-growing and lower-stature vegetation receives insufficient light and is consequently excluded from the site. In the hybrid species *Fallopia × bohemica*, it has also been observed that when plants grow away

from water bodies, for example, in drier environments such as abandoned gardens, they develop shorter stems and smaller leaves. In 2018, flowering was delayed compared to the usual phenological pattern and occurred continuously but asynchronously within the population, first appearing on the eastern side of the stand. Flowering phenology was monitored in the (untreated) plant population between 15 August and 30 October 2018. *Fallopia × bohémica* is an entomophilous species, pollinated by honey bees and other bee species. During August, the number and spatial distribution of flowers on individual plants were recorded (Figure 11). The paniculate inflorescences are arranged in glomerules located at the base of the petioles (Figure 12). The highest number of glomerules was observed on the main stem, while the first-order branch exhibited the highest flower abundance.

By investigating floral traits and flowering phenology, we provide data that contribute to studies aiming to elucidate the causes of the drastic decline in domestic bee populations, as the species is regarded as a melliferous plant. *Fallopia × bohémica* produces a three-winged achene; however, seed production does not represent its primary mode of reproduction. Nevertheless, occasional sexual reproduction and hybridization events may contribute to considerable genetic variability within populations, thereby enhancing adaptive potential and long-term invasion success (Hollingsworth *et al.* 1998; Tiébré *et al.* 2007). Due to sexual dimorphism and the presence of hermaphroditic individuals, not all populations are capable of producing viable fruits.

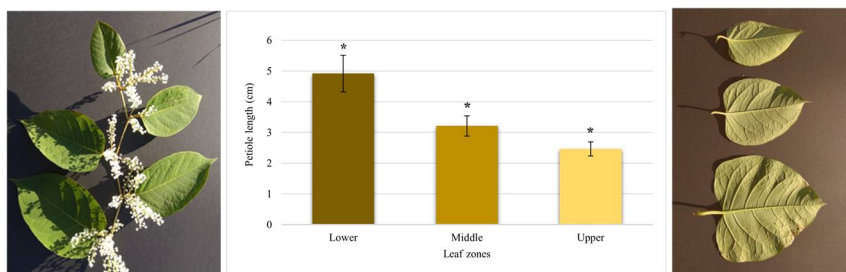


Figure 12. (left) Inflorescences are located at the base of the petiole in *Fallopia × bohémica* leaves (n=5). Photo: Krisztina Csákné Nemoda. **Figure 13.** (middle) Petiole length in lower, middle and upper leaf zones in *Fallopia × bohémica*. *= Statistically significant ($p < 0.05$). Error bars are STDs, where n=24. **Figure 14.** (right) Leaf blades with petioles of *Fallopia × bohémica* originating from three different shoot zones (Photo: Krisztina Csákné Nemoda).

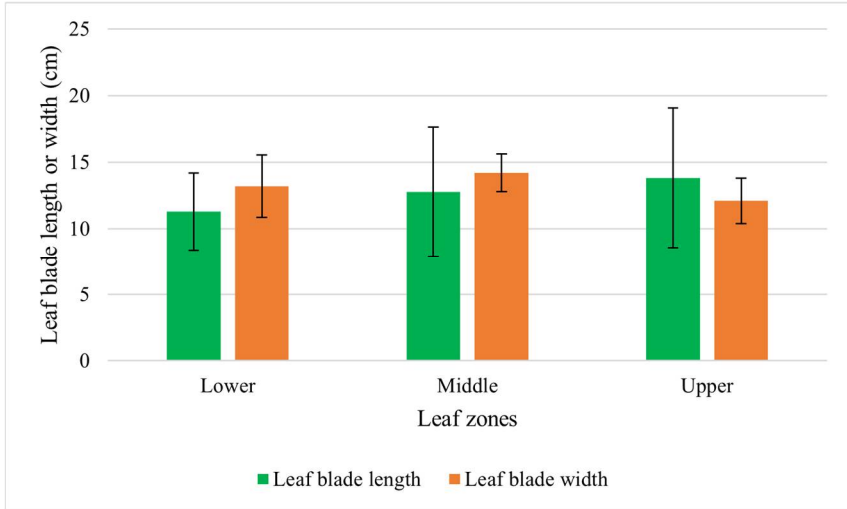


Figure 15. Leaf blade length and width in lower, middle and upper leaf zones in *Fallopia x bohemica*. Error bars are STDs, where n=24.

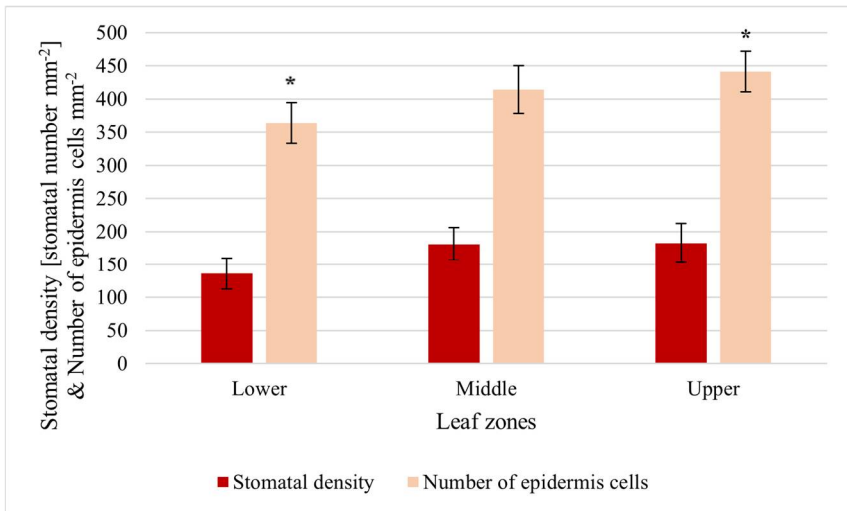


Figure 16. Stomatal density and number of epidermis cells mm⁻² in lower, middle, and upper leaf zones in *Fallopia x bohemica*. * = Statistically significant (p<0.05). Error bars are STDs, where n=24.

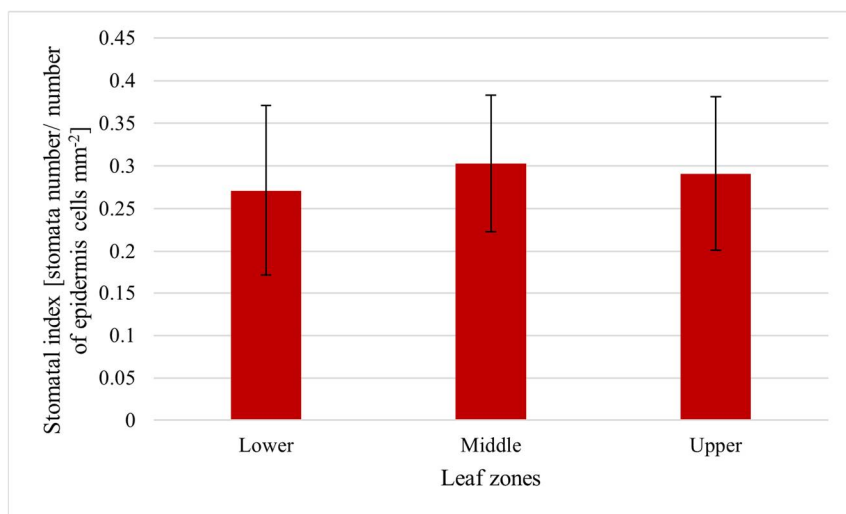


Figure 17. Stomatal index (stomata number/ number of epidermis cells · mm⁻² in lower, middle, and upper leaf zones in *Fallopia × bohémica*. Error bars are STDs, where n=24.

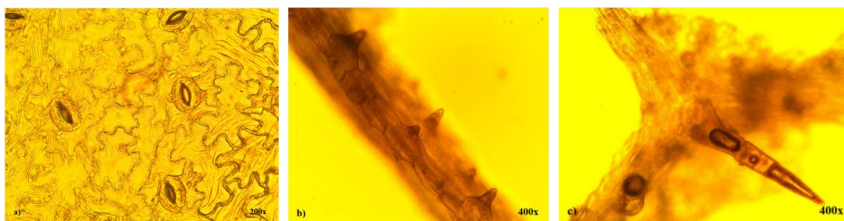


Figure 18. Light micrographs of the epidermis of *Fallopia × bohémica*: **a)** the undulating-walled epidermal cells with stomata at 200× magnification; **b)** unicellular **c)** and tricellular trichomes at 400× magnification. Photos: Krisztina Csákné Nemoda.

Leaves were sampled from the lower, middle, and upper leaf zones of the plants for epidermal and stomatal analyses. As the species possesses hypostomatic leaves, peels of the abaxial epidermis were examined. The stomatal density ranged from 140 to 190 stomata per mm² and did not show significant differences among leaves from the three zones; however, the mean value recorded for the lower zone was lower than those of the middle and upper zones (*Figure 16*).

The average number of epidermal cells in the lower, middle, and upper leaf zones was 363, 414, and 441, respectively (*Figure 16*). A significant difference ($p < 0.05$) was observed between the abaxial

epidermal cell numbers of leaves from the lower and upper zones (Figure 16). No significant differences were detected in stomatal index values among the zones (Figure 17).

Light microscopic analysis revealed that the plant is delimited by epidermal cells with undulating anticlinal walls, arranged in a linear pattern with stomata (Figure 18a). The epidermal architecture indicates a mesophytic water-regulation strategy, accompanied by dense coverage of non-glandular trichomes. These trichomes are predominantly located along the leaf veins. Two types of covering hairs contribute to the effective reduction of cuticular transpiration. The leaf surface is characterized by unicellular, bicellular, and tricellular trichomes, with no essential oil-containing structures detected (Figure 18b, c).



Figure 19. Light micrographs of *Fallopia x bohemica* pollen following fuchsin staining at 400× magnification. Photos: Krisztina Csákné Nemoda.

Pollen morphological analysis was performed using a light microscope at 400× magnification following fuchsin staining. The results indicated that the plant produces small pollen grains (15–20 µm) with a granulate surface, belonging to the tricolporate type, characterized by three pores and three colpi (Figure 19).

CONCLUSIONS

Fallopia x bohemica owes much of its invasive potential to its relatively large total leaf area with strong shading capacity, zone-specific variation in petiole length that optimizes light interception, rapid biomass production, and the consequent efficient displacement of surrounding vegetation. Within a single phenophase, biomass among individuals belonging to the same population is highly variable, largely due to spatial position and the continuous formation of new shoots. Precise delimitation of individual plants is difficult, as rhizome connections are not visible

without excavation. The hybrid is capable of developing a dense, highly branched shoot architecture within a very short period.

Although seed reproduction is limited, *Fallopia × bohemica* spreads efficiently through vegetative means, primarily via rhizomes. Rhizomes have a substantial spatial requirement, and their role as nutrient and carbohydrate storage organs has been less well documented in the literature; targeted investigation of this aspect is planned for future studies.

The hybrid exhibits a mesophytic water balance, and detached shoots lose water relatively quickly. However, its dense trichome cover reduces cuticular transpiration. No natural herbivores or pests have been identified so far. Despite its invasiveness, *Fallopia × bohemica* is insect-pollinated, and its numerous flowers provide an important nectar source for bees.

Management of the species poses a serious challenge. Mechanical control by mowing is ineffective, as plants rapidly regenerate their branching structure, and mowing can result in rhizome fragments that may be transported by streams and establish new populations downstream. Chemical control is also not recommended due to the proximity of streams and aquatic habitats.

Fallopia × bohemica owes its invasiveness to hybrid vigor, broad stress tolerance, and allelopathic interference with native plants. Research gaps include the precise identification of allelochemicals, long-term soil ecosystem recovery post-eradication, and climate-based modelling of future distribution. Integrative management approaches combining ecological restoration with community awareness programs are crucial for sustainable control.

Our findings highlight that the invasive success of *Fallopia × bohemica* is strongly rooted in its structural and biomass-related traits rather than in reproductive output alone.

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