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GROWTH STRATEGIES AND CLIMBING BEHAVIOR OF THE INVASIVE VINE WILD CUCUMBER (*ECHINOCYSTIS LOBATA*)

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Running title: *Dołkin-Lewko and Zajączkowska ……… Growth strategies and climbing behavior of wild cucumber*

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One of the significant challenges related to climate change is the migration of invasive plant species, particularly in vulnerable habitats like wetlands and river valleys. Wild cucumber (*Echinocystis lobata*), an invasive vine, has rapidly expanded across Europe, disrupting native vegetation and altering ecosystems. This study investigated the growth dynamics, climbing behavior, and plant anatomy of wild cucumber in relation to support density (5 cm, 20 cm, and 50 cm spacing). Using time-lapse imaging and biometric analysis, we observed the highest growth rates in the densest support variant (5 cm), where the mean growth rate reached 0.78 mm/min, compared to 0.57 mm/min in the 50 cm variant. Nutation movements were more intense during early growth stages and stabilized upon attachment to supports. Anatomical studies revealed a lightweight structure with a hollow pith, reinforced sclerenchyma and collenchyma, facilitating efficient climbing and mechanical stability. These findings highlight the adaptive mechanisms of wild cucumber and provide insights into its competitive advantage as an invasive species. Future research should explore its growth on natural supports to inform management strategies in ecologically vulnerable areas.

Keywords: alien species, invasive plant, growth rate, climbing mechanism, shoot anatomy

INTRODUCTION

Rapid changes in the natural environment due to climate change are reflected in the migration of organisms. Various habitat types in wetlands and river valleys are particularly vulnerable to alien species. Riparian forests, found along the banks of rivers and streams, are susceptible ecosystems, greatly impacted by invasive alien species (Richardson et al., 2007).

In these environments, invasive species significantly disrupt biodiversity and ecosystem functions by outcompeting native vegetation and altering habitat structure (Richardson et al., 2007; Kominoski et al., 2013). These species often have aggressive growth habits, leading to reduced species diversity, altered community dynamics, and degraded habitats for wildlife (Pyšek et al., 2013; Catling, 2005). Additionally, invasive plants can modify ecosystem processes, including soil properties, nutrient cycling, and hydrology, further threatening ecological integrity (Charles and Dukes, 2007; Miniat et al., 2021). This issue is particularly pronounced near urban areas, where seed availability from parks and home gardens facilitates the introduction of invasive species (Tarabon et al., 2018). Invasive vines from urban areas, such as wild cucumber further exacerbate biodiversity loss by forming dense monocultures that displace native plants (Dylewski et al., 2018; Dołkin-Lewko and Zajączkowska, 2022). Invasive species in wetlands also tend to form monotypes, which intensifies biodiversity loss (Gebauer et al., 2016).

In Europe, this problem is becoming increasingly critical, as one of the invasive species of vines, wild cucumber (*Echinocystis lobata* (Michx.) Torr. & Gray), has recently been included in the list of 100 of the most invasive alien species on the continent (Vilà et al., 2009). Wild cucumber is a North American species that became invasive in Europe at the turn of the 20th century (Bagi and Böszörményi, 2008) and is found in many Central and Southeastern European countries such as Latvia, Lithuania, Poland, Slovakia (Kostrakiewicz-Gierałt et al., 2022), Croatia (Hulina, 1998), Ukraine, Hungary (Bagi and Böszörményi, 2008), Russia (Borisova, 2011), Romania (Curtean-Bănăduc et al., 2011), and Slovenia (Zelnik, 2012). Over the last few decades, the distribution area of this species has significantly increased (Hulina, 1998).

Wild cucumber is recognized for its rapid growth and its ability to colonize new habitats by climbing onto surrounding vegetation using tendrils (Bagi and Böszörményi, 2008; Kostrakiewicz-Gierałt et al., 2022). The plant’s tendrils form spring-like structures upon contact with supports, enabling attachment to the surrounding vegetation. This mechanism allows the plant to grow rapidly, reaching lengths of 6–8 meters (Silvertown, 1985; Bagi and Böszörményi, 2008). While research has focused on its ecological impacts, such as forming dense monocultures and outcompeting native species (Kostrakiewicz-Gierałt et al., 2022), there is a notable lack of detailed anatomical and biomechanical studies on the wild cucumber growth, which are crucial for understanding of the process of colonizing new areas. The anatomical structure of wild cucumber shoots is largely unexplored, and the cross-sectional images presented in this study address this gap, contributing new knowledge to the literature on Cucurbitaceae species. While the anatomy of more well-known Cucurbitaceae species has been studied (Mohammed and Guma, 2015; Luchian and Teodosiu, 2019), wild cucumber remains under-researched in this context. Although plant growth kinetics is increasingly used to study various species (Kerckhoffs et al., 1997; Yazdanbakhsh and Fisahn, 2010; Michaletz, 2018), its application to invasive plants is still limited. Studying the growth kinetics of invasive plants, such as wild cucumber, provides valuable insights into their population dynamics, spread patterns, and ecological impacts.

In this context, it seems most effective to start research by focusing on the kinetics and biomechanics of the shoots and tendrils, whose movements determine their ability to compete with native species. Research on the kinetics of wild cucumber growth will facilitate a deeper understanding of this vine’s growth mechanisms, which can, in turn, aid development of effective control methods, especially in ecologically sensitive areas. This research is especially important given that managing the spread and abundance of this vine is a growing challenge across many European countries, a problem likely to intensify with climate change (Sundarapandian et al., 2015).

The purpose of this research is to investigate the growth dynamics, climbing behavior, and anatomical adaptations of wild cucumber (*Echinocystis lobata*) in relation to varying support densities. By analyzing the plant's growth rates, nutation movements, and shoot structure, the study aims to uncover how these factors contribute to its invasive success in riparian habitats.

Such knowledge is essential for devising effective management strategies to mitigate the negative impacts of invasive species on biodiversity and ecosystem function.

Therefore, we put forward the following hypotheses:

1. The growth rate and climbing efficiency of wild cucumber are enhanced by denser supports (5 cm), promoting faster vertical growth compared to sparser supports (50 cm).
2. The anatomical structure of the wild cucumber shoot is adapted to form a lightweight yet durable construction, supporting its rapid growth and climbing ability.

MATERIALS AND METHODS

RESEARCH MATERIAL

The seeds of plants used in the experiment were collected from a natural site near the village of Gassy, located near Warsaw, Masovian Voivodeship, Poland (52.07887291095115, 21.207374837430606). The site is located in the floodplain areas of the Vistula River and is similar to the habitat of Populetum albae Br.-Bl. 1931. The seeds were obtained at the end of the growing season (end of September and beginning of October) in 2020 and 2021.

TIME-LAPSE IMAGING

Observations were carried out at the Department of Forest Botany, Warsaw University of Life Sciences, Poland. Wild cucumber plants (*Echinocystis lobata* (Michx.) Torr. & Gray) were planted in pots with a diameter of 12 cm for the movement and growth experiments. The experiment involved three variants of support distribution: every 5 cm, every 20 cm, and every 50 cm (Fig. 3). The wooden supports were placed horizontally in relation to the plant growth direction. The lowest horizontal support was placed 30 cm above the soil surface in all experimental variants. The data was collected in the years 2020-2023. All plants were grown under controlled lighting (HPS Phytolite 600 W lamp, photon flux 1045 µmol m^{-2} s^{-1}, luminous flux 100 klm) and temperature (21 °C). The plants were watered automatically using a drip irrigation system (Gardena, Ulm, Germany). After developing their first pair of mature leaves, when they were about 20-35 cm in length, the plants were photographed with the Ricoh GR and Ricoh GX200 cameras (Ricoh, Tokyo, Japan) with a built-in intervalometer. The images were captured from one direction, with the camera lenses set perpendicular to the plant's axis. The shutter was released every 15 minutes. The resulting images were combined into a 10 fps video. The following were used for the analysis: 13 recordings of the 5 cm variant and 12 recordings of the 20 and 50 cm variants.

Next, an analysis was performed based on the resulting video using Tracker (https://www.cabrillo.edu/~dbrown/tracker/), an application based on the Open Source Physics (OSP) Java framework and designed for kinetic analysis of video objects. The recordings were used to measure the plant growth parameters. The tape measure and point mass tools were used to determine the length of the shoots and to change the position of the apex relative to the areas of the X- and Y-axis photographed over time. The center of the coordinate system is the base of the plant. The plant length after alignment refers to the length measured from the base of the plant to the apex, accounting for any distortions or deviations due to the plant's lean or position relative to the camera. To address these artifacts, a trend line was drawn (polynomial of the 2nd degree, due to the very good fit, $R^2 = 0.975–0.995$) to correct for the plant's tilt, and the corrected plant length parameters were calculated. Quantitative measurements of the increase in shoot length were complemented by observations regarding the movement of tendrils.

SHOOT GEOMETRY

To complement the research, cross-sections of the shoots of ten plants were scanned. Samples were collected at 5 cm intervals, starting from the base of the plant, in the place where the shoot emerges from the soil, which corresponds to the soil level in the pot, and finishing the last measurement directly under the top of the shoot. Using ImageJ (https://imagej.nih.gov/ij/), a program based on the OSP Java framework, the following parameters were measured: shoot cross-sectional area, tissue area (the area constituting the hollow pith was not included in the measurements), perimeter, and circularity. The circularity of the shoot cross-sections was quantified using the formula:

$$Circularity = \frac{4\pi \cdot Area}{Perimeter^2}$$

Due to variations in plant height, measurements were taken from the scanned cross-sections at five specific points along the shoot: the base, 1/4, 1/2, 3/4 shoot height, and the top.

MICROSCOPIC OBSERVATIONS

To investigate the anatomical adaptations of climbing stems, cross-sections were taken from three different stem variants during the preliminary study. However, no significant anatomical differences were observed between these variants. Based on this finding, the anatomical analysis was focused exclusively on the shoot region where tendrils attach to the support (mostly between 50–80 cm, depending on the attachment point of the tendrils). The plants were grown under controlled conditions with supports spaced every 5 cm to ensure tendril attachment. For anatomical studies, fresh fragments of shoots were sampled from the places where the tendrils were attached to the support and cut immediately after collection. Shoot fragments were attached to the microtome holder with commercial glue and serial-sectioned at 60µm using a VT1000 S vibratome (Leica). Unstained sections were examined under a light microscope in a bright field (BF). The sections were then immersed in a drop of aniline blue and incubated for 5 min. They were then viewed using UV-excited autofluorescence (NU). Another section of the same sample was treated with commercial Herzberg reagent to distinguish the lignified cell walls from non-modified ones, and with Mayer's Mucicarmine stain solution with Lugol solution (Łotocka, 2023) to confirm general anatomical conclusions and detect starch grains. Observations were carried out using a Provis AX70 light microscope (Olympus Corporation) equipped with a UC90 digital camera (Olympus Corporation). Images were saved at 3384 × 2708 pixel resolution as tiff files using the OLYMPUS cellSens Standard 1.18 software (Olympus Corporation). For publication purposes, selected representative images were adjusted using nondestructive tools of Photoshop CS6 Extended (Adobe Systems Inc.). Images of uneven sections were prepared using focus-stitching of several optical “sections”; (Auto-Blend Layers tool), and images of large areas were obtained by combining several images using the Automate-Photomerge tool.

GROWTH QUANTIFICATION AND STATISTICAL ANALYSIS

The analysis adopted a significance level (α) of 0.05 for all statistical tests. A linear mixed model (LMM) was used for all analyses of plant growth, estimated using Restricted Maximum Likelihood (REML) with the nloptwrap optimizer. Multicollinearity among predictors was assessed using the Variance Inflation Factor (VIF), with a VIF below 3.0 indicating a low correlation (Zuur et al., 2010). The Shapiro-Wilk test was used to assess the normality of the variable distributions. Plant growth data were analyzed using the R Statistical language (version 4.1.1; R Core Team, 2021). The plant growth rate was quantified as the aggregate of differences in plant length after alignment between two successive measurements (at times t+1 and t), separated by 15-minute intervals. This was calculated using the formula:

$$\textit{plant growth rate}_{t+1} = \textit{length after alignment}_{t+1} - \textit{length after alignment}_{t}$$

The term "length after alignment" refers to the adjusted length of the plant, accounting for any deviations from the camera's perspective. This adjustment is necessary to correct for any artifacts or distortions caused by the plant’s lean or tilt relative to the camera during image capture.

Reporting of the regression coefficients for interaction effects was based on evaluation of estimated marginal means (EMMs) and contrast analyses to decipher the relationship between plant growth rate and different levels of support, while maintaining the normalized plant length after alignment constant at 0 mm (corresponding to a non-normalized value of 508 mm). The deviation of a plant's apex from the X- and Y-axes was quantified as the aggregate of absolute differences in position deviations between two successive measurements (at times t+1 and t), separated by 15-minute intervals. This was calculated using the formula:

$$\Delta x_{t+1} + \Delta y_{t+1} = |x_{t+1} - x_t| + |y_{t+1} - y_t|$$

The frequency of the nutation movement was estimated for each plant based on full-day observations. Due to the varying number of measurement points for individual plants, this approach was adopted to maintain consistency. Nutation movement was characterized as the range between the two minimum deviation values along the x-axis, as defined by the following equation:

$$Nutation\ movement = min\Delta x_{i+1} - min\Delta x_i,\ where\ i = 1, ..., k$$

Here, Δx_i represents the difference between two successive measurements, defined as $\Delta xi = x_{t+1} - x_t$, where $t = 1, ..., T$. In these equations, k represents the daily frequency of nutation movements for the plant under observation and T denotes the number of measurement points per day, which is a fixed value specific to each plant. Analyses of shoot cross-section data were conducted using the PAST (https://past.en.lo4d.com/), a program based on the OSP Java framework. Due to the different lengths of plant shoots, and thus the variable number of cross-sections, fragments from shoots of different heights were selected for the statistical analysis. The data were subjected to statistical analysis to determine the differences between particular cross-sections. One-way ANOVA tests were performed, and Tukey's post-hoc test was used to determine the differences between the groups.

RESULTS

TIME-LAPSE IMAGING

Each measurement provided a detailed account of the plant's length and the deviation values of the shoot tips along both the X- and Y-axes, categorized by support conditions (Supp. table 1).

The study of plant movements showed significant differences in growth rates depending on the density of supports. Plants with 5 cm supports exhibited the highest mean growth rate (0.78 mm/15 min), followed by those with 20 cm supports (0.75 mm/15 min), and lastly, those with 50 cm supports (0.57 mm/15 min) (Fig. 1a). The variability in growth rates was the highest for the 20 cm support (0.30 mm/15 min), followed by the 5 cm support (0.25 mm/15 min), and the 50 cm support (0.16 mm/15 min). Over time, the changes in growth rates of individual shoots were slightly skewed in the 20 cm support group, as suggested by the median (0.77 mm/15 min) being higher than the mean. Shapiro-Wilk tests confirmed normality for most distributions, except for slight skewness in the 20 cm support group. Plants with unlimited access to supports (5 cm) grew faster than those that could not attach themselves to a support and had to explore the space horizontally (50 cm) (Fig. 1a). The EMMs confirmed these growth trends (Fig. 1b). For 5 cm supports, the estimated growth rate was 0.78 mm/15 min (95% CI: [0.664, 0.891]). Increasing support spacing to 20 cm resulted in a slight and statistically insignificant increase to 0.80 mm/15 min (95% CI: [0.685, 0.921]), due to overlapping confidence intervals. For 50 cm supports, the growth rate significantly decreased to 0.55 mm/15 min (95% CI: [0.432, 0.668]), confirmed by non-overlapping confidence intervals. A significant decrease in the growth rate was observed as the support height increased from 5 cm to 50 cm ($p = 0.019$). These results indicate a non-linear relationship between the plant growth rate and the support height. Similarly, in the case of supports with a 20 cm step size, the growth rate was significantly higher than that of plants grown on supports with a 50 cm step size.

The analyses also showed that support density significantly influenced the deviation of the plant's apex from the X- and Y-axes (Fig. 2a). The 5 cm support variant exhibited the highest variability in nutation movements, which is reflected in the larger difference between the mean and median of X-axis deviations. This suggests that shoots in this variant changed their growth direction more frequently while searching for a stable support. For plants grown with 5 cm supports, the mean deviation was 24.93 mm (SD = 33.73 mm), with a median of 20.07 mm. The range (0–1,775.06 mm) and skewness (24.27) indicated frequent extreme values. For 20 cm supports, the mean deviation was 28.78 mm (SD = 32.87 mm), with a range of 0–1,116.36 mm. The distribution was more uniform, with skewness (15.29) and kurtosis (410.69) lower than in the 5 cm group. For 50 cm supports, the mean deviation was 25.77 mm (SD = 27.29 mm), with the narrowest range (0–677.66 mm) and the lowest skewness (7.96) and kurtosis (127.47), indicating the least variability. The time covariate had a significant positive effect on apex deviation ($B1 = 0.16$, 95% CI: 0.15 to 0.17, $p < 0.001$), suggesting that the plant apex deviation from the X- and Y-axes tended to increase with time (Fig. 2b).

Nutation frequency per day tended to increase with support density, peaking in the 50 cm support group (Fig. 2c). The mean nutation frequencies were 24.25 (SD = 4.32) for the 5 cm support, 24.72 (SD = 3.58) for the 20 cm support, and 26.01 (SD = 4.49) for the 50 cm support (Suppl. Table 2). Despite this trend, statistical tests revealed no significant differences in nutation frequency across the different support densities ($p > 0.05$). The EMMs for the nutation movement frequency per day on day 5.44 were 23.1, 24.2, and 22.9 for the 5 cm, 20 cm, and 50 cm support groups, respectively, with small standard errors (SE = 0.78, 0.81, and 0.88). This suggests no significant variability in nutation frequency across the support heights. Figure 2c illustrates the predicted nutation frequency as a function of observation day and support variant, emphasizing that while support density influenced the trend, it did not have a statistically significant impact on nutation frequency per day.

As shown in the photos of individual plants (Fig. 3), supports placed at high (5 cm) and medium (20 cm) densities promoted vertical growth of the plant. Tendrils can attach to a support, fix, and stabilize plants. First, the plant is attached to the support and then can continue to grow and search for the next support. As the plant grew, the nutation movements became more intense and they stopped after attaching another tendril or in the presence of a support. While searching for a place to get attached to, the plant increases its range of nutation movements. Plants growing with limited access to supports (50 cm) at the beginning also grow in a vertical plane but when they have no chance to attach themselves to another support, they begin to explore the space horizontally. This is usually accompanied by a rapid displacement of the apex, caused by the plant tipping over, due to excessive weight. Under these conditions, the plants continue to grow by catching hold of the current support.

SHOOT GEOMETRY

Significant differences between individual plant parts were found in the shoot geometry of wild cucumber (Fig. 4). In the case of shoot cross-sectional area, tissue area, and circularity, two homogeneous groups were distinguished (Fig. 4 a, b, d). The first included the base of the shoot and the second included values from the other heights. The shoot base had a higher cross-sectional area value, on average 12.72 mm^2. As for the other values, they decreased with height and ranged from 3.29 mm^2 to 1.28 mm^2 on average. The tissue area at the shoot base averaged 9.07 mm^2 and differed significantly from the values for the other heights, which on average ranged from 2.16 mm^2 to 1.11 mm^2. In terms of circularity, the shoot base had the highest value (0.94), so it was largely similar in shape to a circle and significantly different from the other cross-sections from other heights. As the height increased, this shape changed, and the circularity values decreased. They ranged from 0.81 to 0.74. The most significant differences were observed in the perimeter, where three homogeneous groups were identified (Fig. 4c). The base, 1/4, and 1/2 of the shoot formed one group, 1/4, 1/2, and 3/4 formed another, while the top section had the smallest perimeter (average 4.48 mm), compared to the base (12.96 mm). All results are available in Table 3 in Supplementary Material.

MICROSCOPIC OBSERVATIONS

Wild cucumber is an annual species and has the typical structure of a dicotyledonous plant and, as a member of Cucurbitaceae, exhibits a stem structure with bicollateral vascular bundles, a common trait in this family. While dicots typically undergo secondary growth, wild cucumber exhibits only limited secondary thickening, due to its annual life cycle (Fig. 5). The stem was five-ridged and characterized by distinct ridges and furrows with vascular bundles at two locations. Five or six smaller vascular bundles were located at the ridges, and three or four larger bundles were located at the furrows (Fig. 5a). The usually uniseriate and cutinized epidermis contained occasional stomata. The cortex consisted of two or three layers and was widened at the ridges and narrowed at the furrows (Fig. 5 b-e). The outermost hypodermis varied in thickness, consisting of a few layers of collenchyma at the stem ridges that tapered into photosynthetic chlorenchyma at the furrows (Fig. 5d-e). The middle cortical layer consisted of several layers of loosely arranged parenchyma cells. Numerous starch grains were present in the parenchyma cells (Fig. 5f-g). A ring of sclerenchyma overlayed parenchyma that followed the outer contour of the vascular bundles (Fig. 5a). The vascular bundles were bi-collateral (Fig. 5d-f). The central xylem is bound by an inner and outer cambium and topped by a larger outer and smaller inner phloem. Sieve tubes, companion cells, and phloem parenchyma were evident in the phloem. The xylem was well-developed, with numerous protoxylem visible toward the inside and a very large metaxylem to the outside of the bundles. The xylem consisted primarily of large vessels and xylem parenchyma. The vascular bundles were separated by zones of internal parenchyma. Probably, the variability in the vascular bundle structure reflects the plant’s rapid growth (Fig. 5d,e). The central pith-disintegrated early, forming a pith cavity (Fig. 5a).

DISCUSSION

In this study, the growth of wild cucumbers was strongly influenced by the density of support spacing. Initially, the plant grew vertically, but in the absence of support, it bent under its weight and explored the space horizontally (Fig. 3). The unlimited availability of supports stimulated faster plant growth than in their absence. Den Dubbelden and Oosterbeek (1995) found that herbaceous vines held by supports grew better than those unsupported. However, these studies lacked specific growth speed data for comparison, unlike our study, where the growth rate ranged around 0.21 mm/15 min between extreme variants of the support step size. Our research results indicate that wild cucumber exhibits a very fast growth rate not only when supports are available (0.78 mm/15 min), but also when growing horizontally (0.57 mm/15 min), especially in conditions where there is a lack of support for vertical growth. This ability to grow in any plane favors the spread of this species. Similar growth behaviors were observed in other vines (Paul and Yavitt, 2011). Typically, vines use external structures as support for vertical growth. Since such plants are unable to maintain an upright position, their functioning in natural vegetation is limited by the availability of appropriate support structures and the climbing efficiency of the plants (den Dubbelden and Oosterbeek, 1995; Paul and Yavitt, 2011).

Rapid growth and appropriate climbing mechanisms allow vines to compete for resources and cause mechanical damage to plants (Schnitzer and Bongers, 2002). Lambers and Poorter (1992) reported that plant species from fertile and productive habitats tend to have higher relative growth rates and nutrient uptake than species from less favorable environments. This is of particular importance in the context of the spread of wild cucumber, which has a rapid growth rate and prefers nutrient-rich habitats (Kostrakiewicz-Gierałt et al., 2022). Harris et al. (2007) also indicate that invasive vine species can become a threat to native species, disturbing the balance of ecosystems, including forests. Wild cucumber’s growth allows it to dominate natural plant communities, particularly in riparian zones, where it has been observed to displace native vine species such as *Humulus lupulus* and *Calystegia sepium* (Celka et al., 2022; Stanković et al., 2022). Its ability to colonize habitats rapidly and outcompete local flora may contribute to long-term shifts in plant community composition, particularly in areas where support structures are abundant (Celka et al., 2022). The presence of wild cucumber in riparian zones, alongside other invasive species such as *Amorpha fruticosa* and *Bidens frondosa* (Stanković et al., 2022), suggests that its spread could contribute to habitat degradation. This invasion may lead to reduced structural diversity in vegetation, affecting native species and altering ecosystem services, particularly in protected habitats such as alluvial forests and oxbow lakes (Celka et al., 2022).

Many vines are often observed to have delayed leaf development (French, 1977). French's (1977) research on 37 species of vines showed that the lateness of leaf development allows shoots to seek support to remain light, and nutation movements can be more intense and deviate over longer distances than in the case of shoots that additionally have to bear the weight of developed leaves and all plant structures. Similar behaviors were observed in wild cucumber, which first developed a searching shoot, and only during elongation did it develop leaves, which is characteristic of the Cucurbitaceae family (Liu et al. 2021). Additionally, it exhibits circular movements during shoot elongation, a phenomenon previously observed in other plants (Kiss, 2009). Nutation movements did not significantly differ between the variants with 5, 20, and 50 cm step supports. However, the deviation of the apex of the plant from the axis increased significantly over the observation period. The key to plant stabilization and continued growth was the attachment of tendrils to the supports, aiding the plants in maintaining an upright position. This was evident in the 5 and 20 cm variants. In the 50 cm variant, the plant could grow vertically only up to a certain point; when it was unable to hook onto anything, it fell and utilized the current support for further climbing. Adaptation to climbing was also evident in the shoot structure of wild cucumbers. The base is significantly larger and rounder than the climbing stem part. This makes the plant stable and allows it to grow vertically so it can attach itself to a potential support. The upper parts of the stem were much smaller and less able to withstand loads during climbing.

As observed in the anatomical structure, the stem is mostly filled with parenchyma, making it more flexible. In the study of Hebeler et al. (2000) on the species *Acanthosicyos horridus* (Cucurbitaceae), the parenchyma also constituted most of the interior of the stem. Fisher and Ewers (1995) highlighted the potential role of the parenchyma in dicotyledonous vines in initiating regeneration after injury. Starch grains were visible near the vascular bundles in the parenchymal cells of wild cucumbers. The presence of starch in the parenchyma can be an energy source for plants with fast growth dynamics. Carlquist (1985) drew attention to the presence of starch grains in the parenchyma adhering to vessels in many dicotyledonous plants. Wild cucumber exhibits a typical Cucurbitaceae family vascular bundle arrangement, characterized by well-developed metaxylem cells supporting rapid water transport, which is also typical of other species of climbers (Putz and Mooney, 1991; Carlquist, 1996; Tamaio et al., 2010). The lack of a pith contributes to a lightweight structure that allows the plant to climb up the surrounding supports and makes it extremely competitive. The lack of a pith has also been observed in other species of the *Cucurbitaceae* family (Corredor et al., 2009; Aguoru and Okoli, 2012; Mohammed and Guma, 2015). Shtein et al. (2018) indicate modifications of shoots, e.g., in buttercup (*Ranunculus repens*), where the mechanical stability of this plant requires only a reinforced stem circumference, while the empty pith allows to save matter and does not cause mechanical destabilization, and in *Galium aparine*, a climbing herbaceous plant characterized by a rectangular stem structure with collenchyma at the corners and an empty pith. In anatomical studies on the structure of wild cucumbers, both sclerenchyma and collenchyma, have been observed to strengthen the stem, which is of great importance in the case of invasive vines, characterized by rapid growth (Crang et al., 2018). Hebeler et al. (2000) also identified the presence of sclerenchyma cells that formed a continuous ring along the entire diameter of the stem. In adult plants, the band of sclerenchyma consisted of up to 10 cells. In the vines of the *Lardizabalaceae* family, a ring of sclerenchyma lies between the phloem and periderm (Putz and Mooney, 1991).

Wild cucumber is very invasive, and keeping it under control poses a problem. Understanding of the climbing and growth mechanisms of this plant may contribute to finding ways to limit its expansion. Mechanical removal is the primary control strategy for wild cucumber, with early uprooting being most effective (Kołaczkowska, 2016). However, its rapid growth necessitates repeated efforts. Chemical control is rarely used due to environmental risks (Starfinger et al., 2003), and no effective biological regulators have been identified in Europe. While some animals consume its seeds, they may also contribute to its spread (Dylewski et al., 2019). It is therefore advisable to deepen our understanding of the climbing mechanisms of this plant and extend the research to include studies that would assume the growth of this plant on natural supports, such as herbaceous plants and trees, which may help develop strategies to limit this species.

CONCLUSIONS

The results of our research have shown that wild cucumbers have a very fast growth rate, not only when support is available, but also when growing horizontally, especially in conditions where there is no support for vertical growth. This suggests that its growth strategy is highly adaptable, allowing it to persist in various conditions. During the initial growth phase of wild cucumbers, both the intensity of nutation movements and elongation were lower than those of mature plants. We also observed that nutation movements and elongation were less intense during the initial growth phase but increased as the plant matured and engaged with support structures. These findings highlight the importance of tendril attachment in maintaining vertical growth and enhancing climbing efficiency. A better understanding of the climbing and growth mechanisms of this plant may contribute to identifying ways to limit its expansion. Continued research should be conducted to better understand the climbing mechanism of this plant and to expand the research to include studies that would assume the growth of this plant on natural supports such as herbaceous plants and trees.

AUTHORS' CONTRIBUTIONS

ADL: a collection of plant material, conducting plant movement experiments, data analyses, microscopic work and observation, preparation of graphics, literature review, writing the article draft, UZ: research conception, supervising the research, manuscript comments and editing.

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Figures:

Fig. 1. (**a**) Temporal heterogeneity of the growth rate parameter for individual plants, categorized by support group (5 cm, 20 cm, and 50 cm), over 0–10,000 min. Each plant is represented by a distinct gray line, that illustrates a unique growth trajectory. The blue lines depict the linear fit for each support group, providing a generalized representation of the growth trends in each group. (**b**) Predicted growth rate as a function of plant length after alignment and support variant, based on the fitted regression model (the opaque line indicates the midpoint of the interval, providing a central estimate of the growth rate. The 95% CI offered a range of plausible values for the growth rate, indicating the uncertainty associated with the estimate).

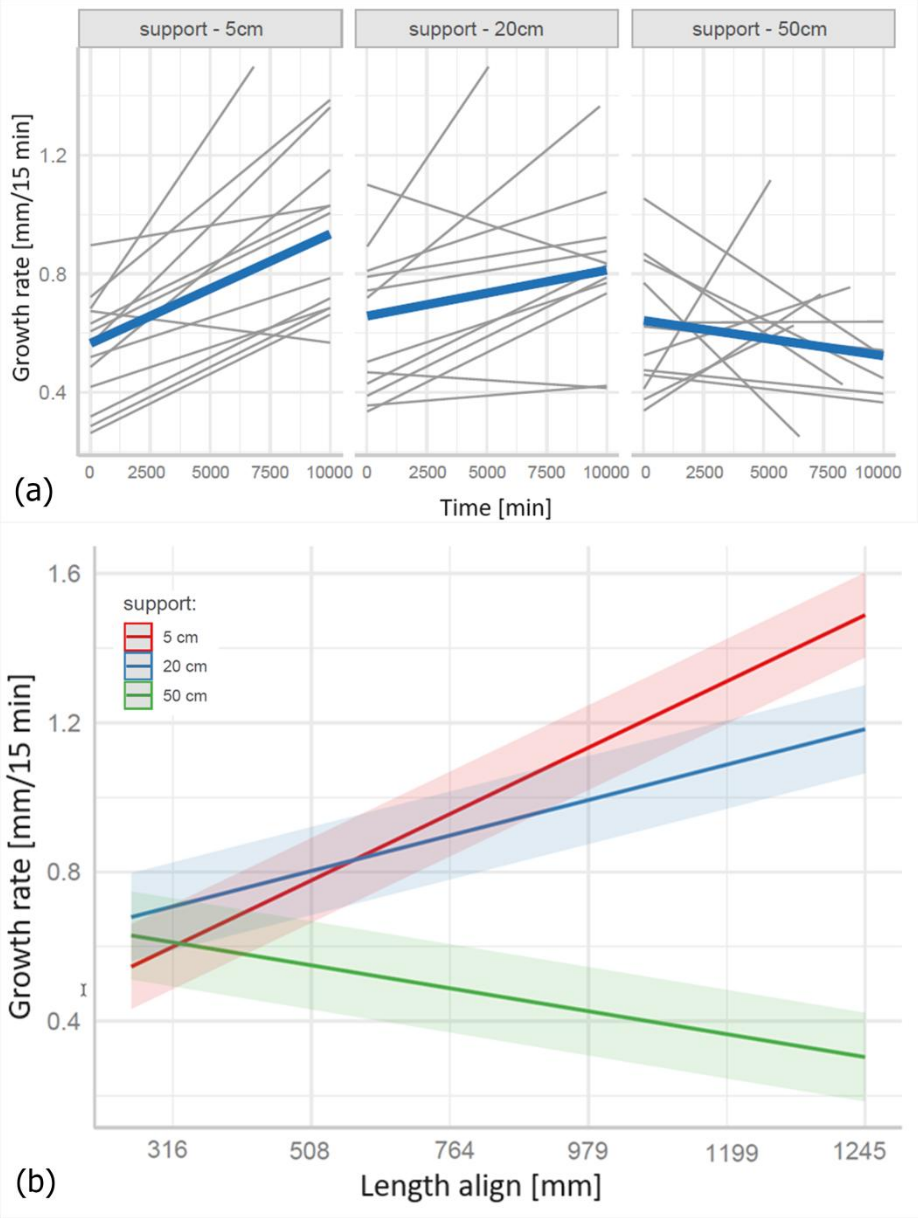
Fig. 2. (**a**) Illustration of temporal heterogeneity in plant apex deviation from the X- and Yaxes, by support group (5 cm, 20 cm, 50 cm) over a 0-10,000-minute time interval. The plant deviation trajectories are shown with the grey lines, emphasizing their unique growth patterns. The overarching deviation trends in each support group are captured by the blue lines, which represent the linear fit for each group, offering a simplified yet comprehensive view of the overall deviation tendencies. (**b**) Predicted plant apex deviation from the x and y axes as a function of time and supports variant, based on the fitted regression model (c) Predicted frequency of nutation movements as a function of the day of observation and support variants, based on the fitted regression model. (b) and (c) the opaque line indicates the midpoint of the interval, providing a central estimate of the growth rate. The 95% CI offered a range of plausible values for the frequency of nutation movements, indicating the uncertainty associated with the estimate.

Fig. 3. Photos of the growth of wild cucumber in three observation time points: initial, middle, and final, in three variants of supports: 5 cm, 20 cm, 50 cm. The red arrowhead shows the horizontal growth of the plant. Photos taken in 2023.

Fig. 4. Changes in biometric features of wild cucumber shoot cross-sections at different heights: (**a**) cross-sectional area, (**b**) tissue area, (**c**) perimeter, and (**d**) circularity. The uppercase letters A and B in charts (a), (b), and (d) represent two homogeneous groups, while A, B, and C in chart (c) represent three homogeneous groups.

Fig. 5. Cross-sections of wild cucumber shoots. Anatomical structures are labeled as follows: ep – epidermis, pc – pith cavity, vb – vascular bundle, pa – parenchyma, xy – xylem, ph – phloem, sc – sclerenchyma, co – collenchyma, sg – starch grains, chl – chlorophyll. (**a**) Unstained, BF; (**b**) Herzberg reagent, BF; (**c**, **f**, **g**) Mayer's mucicarmine stain solution with Lugol solution, BF; (**d**, **e**) Aniline blue, NU.

Figure1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support - 20cm
support - 50cm
Growth rate [mm/15 min]
1.2
0.8
0.4
0
2500
5000
7500
10000
Time [min]
(a)
1.6
1.2
0.8
0.4
support:
5 cm
20 cm
50 cm
Growth rate [mm/15 min]
316
508
764
979
1199
1245
Length align [mm]
(b)

Figure 2

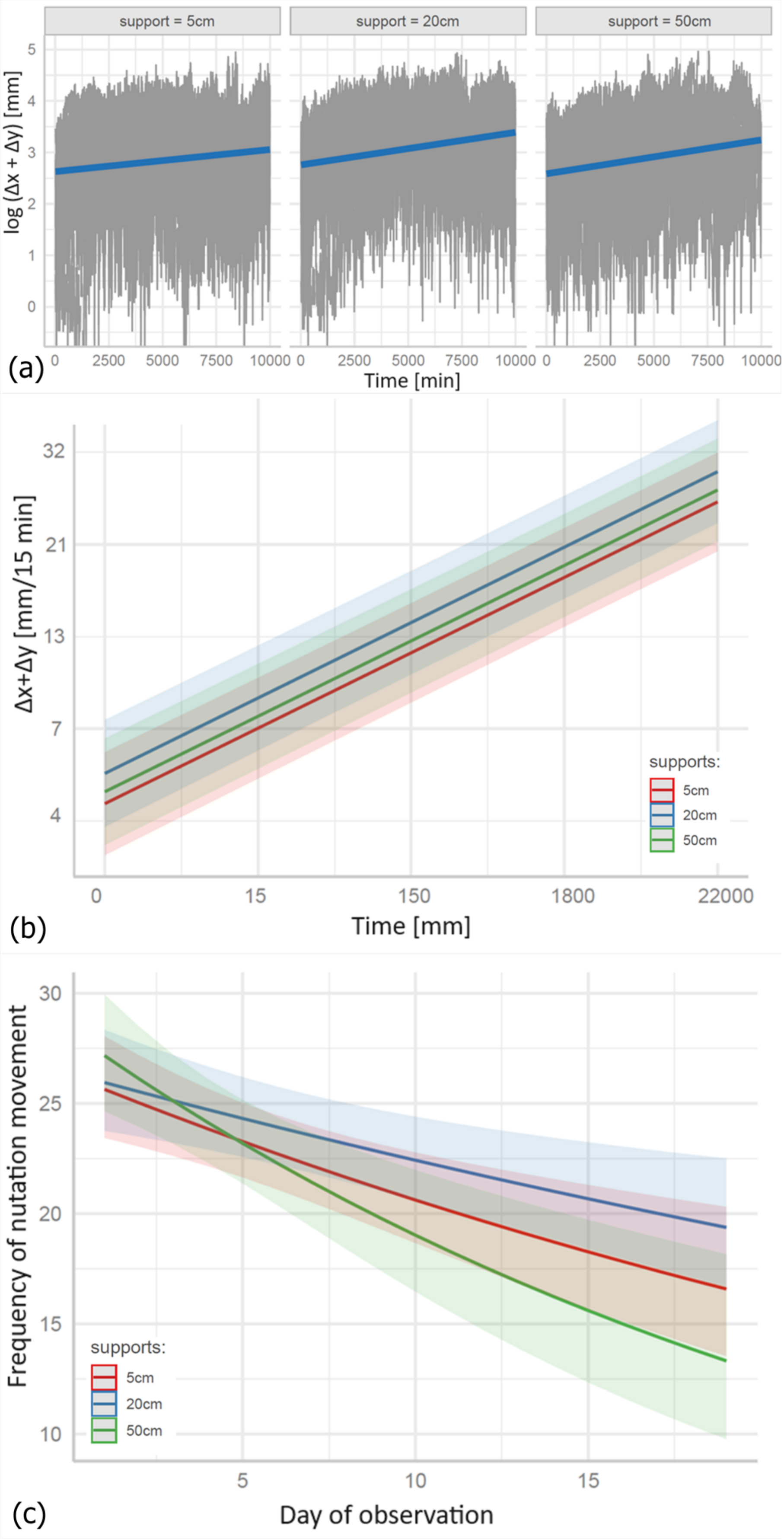

support = 5cm
support = 20cm
support = 50cm
log (Δx + Δy) [mm]
5
4
3
2
1
0
0
2500
5000
7500
10000
Time [min]
(a)
Δx+Δy [mm/15 min]
32
21
13
7
4
0
15
150
1800
22000
Time [mm]
supports:
5cm
20cm
50cm
(b)
Frequency of nutation movement
30
25
20
15
10
5
10
15
Day of observation
supports:
5cm
20cm
50cm
(c)

Figure 3

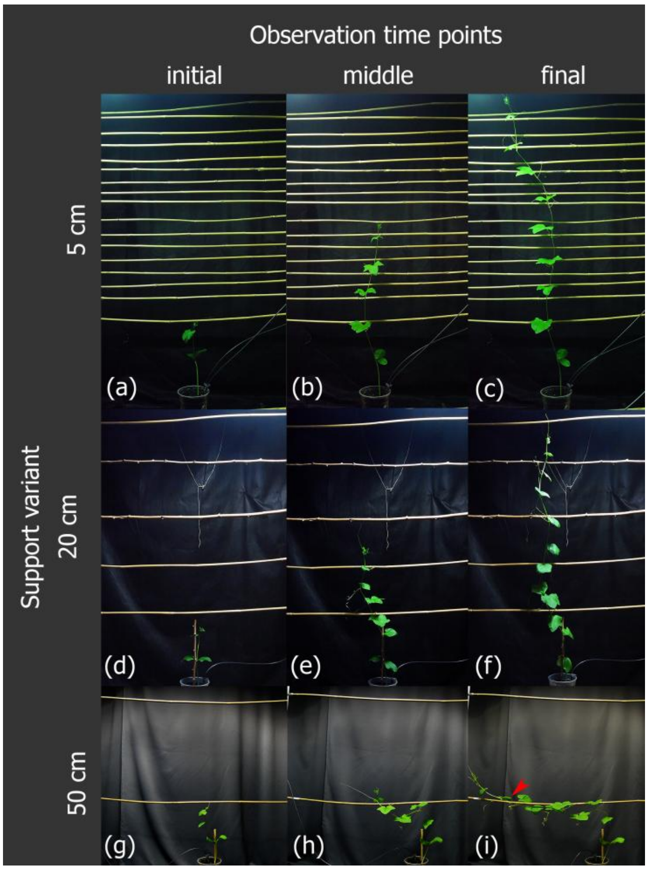


Figure 4

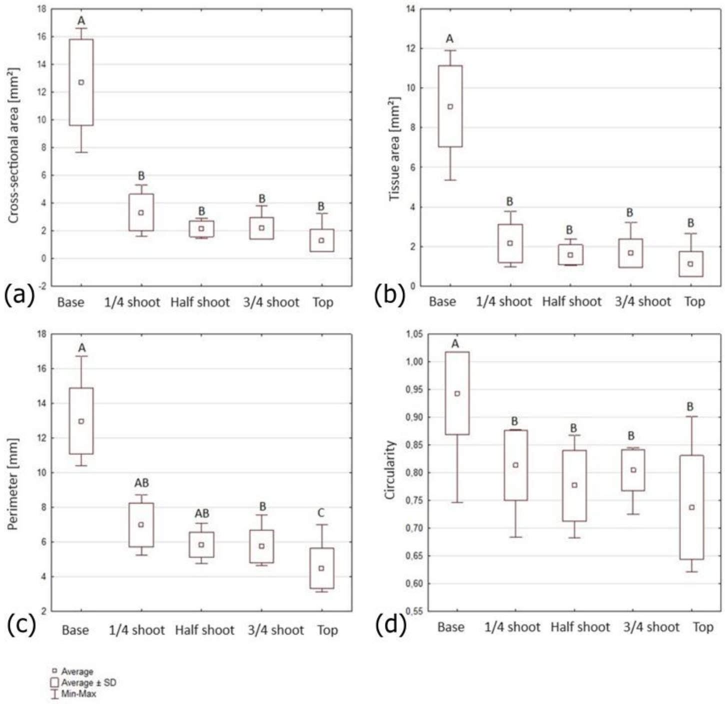
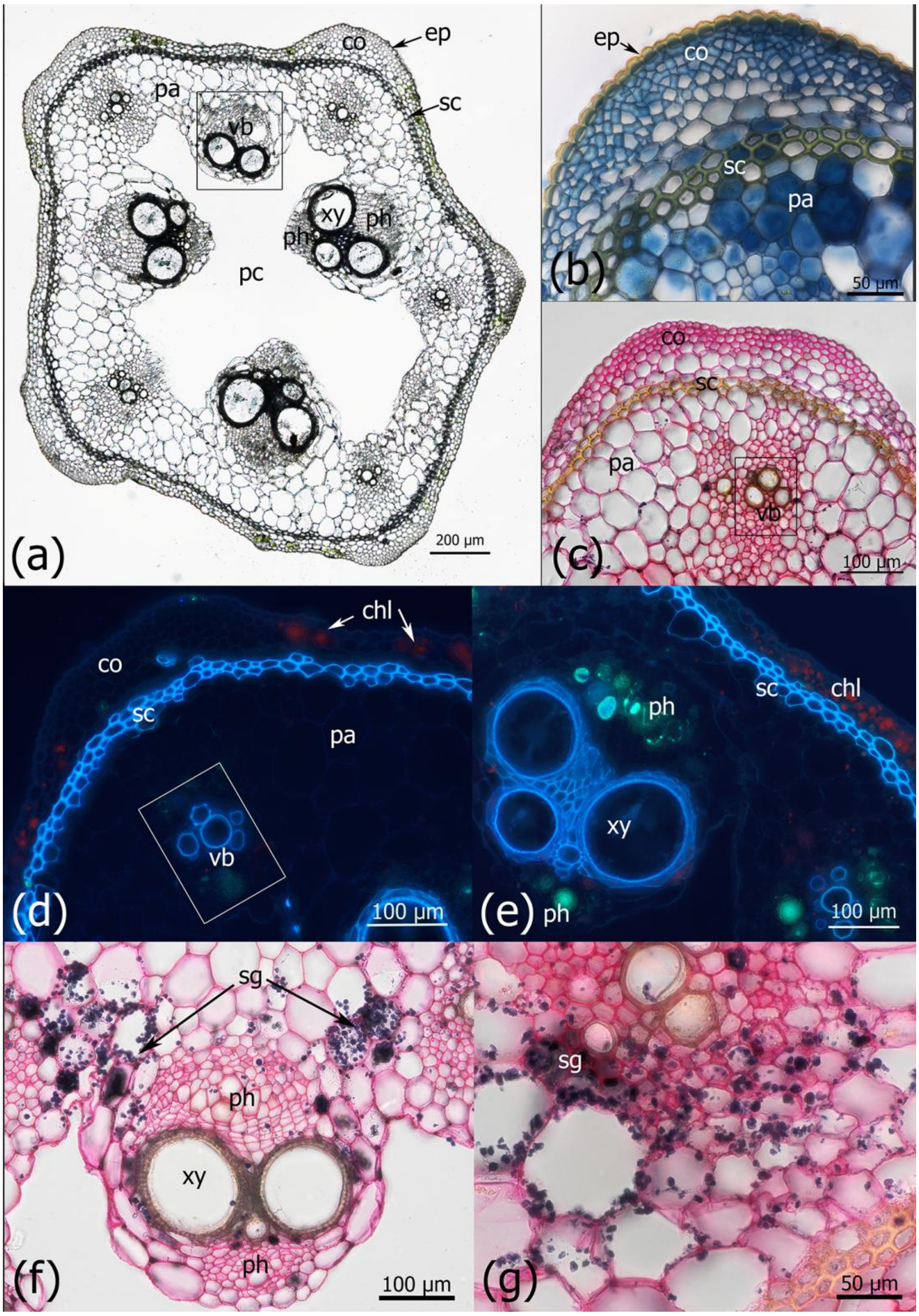


Figure 5


co
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(g)
50 µm

Supplementary Material

The supplementary material provides detailed descriptive statistics that support the investigation of wild cucumber (*Echinocystis lobata*) growth dynamics in relation to different support densities, and biometric features from different parts of the plant shoot. Table 1 summarizes the sample variables across three support densities (5 cm, 20 cm, and 50 cm), offering insights into how these densities influence growth rates and other plant characteristics. Table 2 presents data on the observation duration and frequency of nutation movements, highlighting how the proximity of supports affects the intensity and timing of these movements. Table 3 includes the mean biometric measurements of wild cucumber shoot cross-sections at different heights (base, 1/4 shoot, half shoot, 3/4 shoot, and top). It provides valuable information about the plant's structure and how it adapts to varying environmental conditions. The data presented in these tables contribute to understanding of the plant's adaptive mechanisms, particularly its ability to climb efficiently and establish itself in different habitats, which is critical in assessing its competitive advantage as an invasive species in vulnerable ecosystems like wetlands and river valleys.

Symbols

N – sample size;

M – mean;

SD – standard deviation;

Mdn– median;

Min – minimum value;

Max – maximum value;

Skew. – skewness;

Kurt. – kurtosis;

Table 1 Descriptive statistics of sample variables for support groups.

Variable	Support	N	M	SD	Mdn	Min	Max	Skew.	Kurt.
Length after alignment, mm	5 cm	10931	565.28	199.50	550.63	162.16	1045.83	0.17	-0.97
	20 cm	12021	565.40	235.84	543.68	114.52	1245.02	0.38	-0.66
	50 cm	7592	445.46	141.94	443.56	120.68	767.73	0.08	-0.66
Deviation of shoot tips from x axis, mm	5 cm	10931	-5.88	175.22	-40.86	-240.76	981.54	3.23	11.76
	20 cm	12021	74.90	121.78	51.28	-273.66	417.37	0.36	0.19
	50 cm	7592	5.31	156.88	5.71	-445.65	415.37	0.17	-0.03
Deviation of shoot tips from y axis, mm	5 cm	10931	538.35	190.09	521.72	160.30	998.07	0.21	-0.90
	20 cm	12021	488.21	198.43	459.58	153.20	1090.63	0.63	-0.24
	50 cm	7592	340.78	113.39	350.61	-66.52	572.30	-0.75	0.82

Table 2 Descriptive statistics for the duration of observation (in full days) along with the frequency of nutation movements in relation to support density.

Variable	Support	N	M	SD	Mdn	Min	Max	Skew.	Kurt.
Rate of nutation movement per day	5 cm	106	24.25	4.32	24.00	14.00	33.00	-0.58	0.42
	20 cm	119	24.72	3.58	24.00	17.00	31.00	-0.10	-1.04
	50 cm	73	26.01	4.49	27.00	14.00	35.00	-0.38	-0.86
Duration of observation, days	5 cm	13	9.15	1.77	9.00	6.00	13.00	0.37	-0.35
	20 cm	12	10.92	3.34	10.00	7.00	19.00	1.02	0.30
	50 cm	12	7.00	1.71	7.00	4.00	9.00	-0.20	-1.50

Table 3 Mean values of biometric features of wild cucumber shoot cross-sections at different heights.

Height localization	Cross-sectional area [mm^2]	Tissue area [mm^2]	Perimeter [mm]	Circularity
Base	12.72	9.07	12.96	0.94
1/4 shoot	3.29	2.16	6.97	0.81
half shoot	2.14	1.66	5.83	0.80
3/4 shoot	2.18	1.58	5.75	0.78
Top	1.28	1.11	4.48	0.74