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The invasive alien species *Bidens pilosa* (Asteraceae) has successfully invaded and acclimated to coastal areas

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The invasion of plants into specialized environments requires acclimatory changes, which can simultaneously act as barriers to further invasion in these contexts. In coastal areas, vegetation is shaped by various stresses from the marine environment; therefore, these areas are predominantly inhabited by plant species that have evolved specific acclimations to these stresses, including many endemic species. In recent years, the invasive species *Bidens pilosa* L. (Asteraceae) has been reported in the coastal areas of Japan. We conducted comparative morphological analyses of coastal and inland populations of *B. pilosa* to elucidate the background of their acclimation to coastal areas. The large leaf area of *B. pilosa* is suggested to be involved in the capture of sand blown by the wind in the unstable soil composed of sea sand in its habitat. In addition, the acclimatory changes in *B. pilosa* were achieved without considerable alterations in the resource allocation ratio between stems and leaves. The coastal population of *B. pilosa* exhibited a significantly higher ratio of resources allocated to roots, indicating that this acclimationfacilitated stable establishment in coastal soils and enhanced moisture acquisition in coastal areas subjected to severe drought stress. In contrast to the increased ratio of resource allocation to roots, the coastal population of *B. pilosa* displayed a significantly lower investment in inflorescences. The findings suggest that once a population is established, it can sustain itself with minimal investment in inflorescences. This is likely attributable to the limited number of plants in coastal areas and reduced competitive pressures in these environments. These acclimatory changes in *B. pilosa* may lead to the expansion of its habitat in various coastal areas.

KEYWORDS

resource allocation, leaf size, root, blown sand, coastal ecotype, aboveground morphology

1 Introduction

The invasion of introduced vascular plants currently poses a major threat to natural ecosystems across nearly all continents, the global economy, and human health (Theoharides and Dukes, 2007). Natural ecosystems are often plagued by the invasion of alien species, which constantly threaten native plant populations (Morgan, 1998; Wilkerson, 2013). Recent studies indicate that roads and hiking trails in high mountain regions, which host numerous endemic species, serve as corridors facilitating the introduction of alien species from lowland species pools to those of the highlands (Koyama et al., 2024). Additionally, these pathways alter the abiotic environment and establish disturbance-resistant alien species (Fuentes-Lillo et al., 2021). Invasive species can cause numerous problems in diverse environments (Marshall et al., 2003; Ellstrand et al., 2010; Jauni and Hyvönen, 2010).

The existence of locally adapted and acclimated plants indicates that disruptive selection promotes alternative trait combinations across distinct environments. This implies that trade-offs arising from phenological, physiological, morphological, and genetic constraints are critical determinants of diversification. Variations in plant populations are frequently observed when water availability changes abruptly over short spatial scales (Jackson and Jobbgy, 2005). In coastal areas, the accumulation of salts in the soil causes a decrease in its osmotic potential and results in plant dehydration; therefore, salt stress is associated with water stress (Kaspari et al., 2009). Roots, stems, and leaves can store water, and numerous studies have reported environmentally induced morphological changes in response to drought conditions within coastal areas (Tunala et al., 2012; Ohga et al., 2013; Sunami et al., 2013; Shiba et al., 2021, 2022a, b; Takizawa et al., 2022, 2023). For example, Tunala et al. (2012) demonstrated that the epidermal cells of the coastal variety of *Aster hispidus* Thunb. var. *insularis* (Makino) Okuyama (Asteraceae), a variety known to occur in coastal regions, were larger in size but fewer in number than those of *A. hispidus* Thunb. var. *hispidus*, which typically grows in inland grasslands. They also showed that these cells were involved in the ability of succulent leaves to store water. Sunami et al. (2013) found a correlation between leaf hair on the abaxial side of leaves and stomatal density in this variety. They showed that fewer leaf hairs corresponded to lower stomatal density to mitigate transpirational water loss. Ohga et al. (2013) proposed that the coastal population of *Adenophora triphylla* var. *japonica* (Regel) H. Hara (Campanulaceae) evolved relatively thick leaves via a heterochronic process for water storage. Shiba et al. (2022c) reported that the coastal population of *Eurya japonica* Thunb. (Ternstroemiaceae) exhibited smaller stomata and larger epidermal cells on both the adaxial and abaxial sides to reduce transpiration during gas exchange and retain water in leaves, respectively. Similar results regarding the differentiation between inland and coastal populations were observed in *Ligustrum japonicum* Thunb. (Oleaceae) (Takizawa et al., 2022). In addition to drought conditions, wind-induced stress also plays an important role in the speciation of plants adapted to coastal areas. Shiba et al. (2023) reported that wind speed in coastal areas contributed to reducing the lamina area and petiole length per petiole cross-sectional area in *Farfugium japonicum* (L.) Kitamura (Asteraceae) based on wind speed data from the Automated Meteorological Data Acquisition System (AMeDAS) installed at approximately 1,300 locations across Japan. Moreover, Shiba et al. (2024a) revealed that *F. japonicum* exhibited dwarfed laminae, petioles, and scaves, indicating that constant strong winds in coastal areas restricted height growth. These observations indicate that coastal areas are environments where stress-adapted and acclimated plants can invade. Because of these stresses, although only 4% of all vascular plants in Japan inhabit coastal areas, approximately 30% of all endemic species are located in these areas (Sawada et al., 2007), emphasizing their significance in terms of conservation. Oka (2010) reported an increase in invasive plants in the coastal areas of Japan, while Mabuchi et al. (2020) indicated that invasive species occupied various parts of the coastal areas affected by the tsunami resulting from the Great East Japan Earthquake in 2011. Takizawa et al. (2023) reported that *L. lucidum* Aiton, introduced to Japan as a roadside tree in the mid-1800s, invaded dry coastal areas and displayed a decrease in stomatal size. These studies indicate that invasive plants are more prevalent in coastal areas than expected; therefore, their acclimations need to be clarified.

Bidens pilosa L. (Asteraceae) is an annual herbaceous plant species that can reach a height of approximately 2 m. It features pinnate leaves and flower heads consisting of approximately four to five broad white ray florets with numerous tubular yellow disc florets (Koyama, 1995). *B. pilosa* has been utilized in traditional medicine for the treatment of various ailments (Chih et al., 1995; Ubillas et al., 2000; Chang et al., 2001; Oliveira et al., 2004; Sundararajan et al., 2006; Yuan et al., 2008; Ashafa and Afolayan, 2009; Tobinaga et al., 2009; Dagawal and Ghorpade, 2011; Adia et al., 2014). *B. pilosa* is native to the Americas, but has been introduced to various regions globally, including Eurasia, Africa, Australia, and the Pacific Islands (Koyama, 1995). In Japan, *B. pilosa* is an invasive plant that proliferates in cultivated fields, roadsides, and disturbed lands in the urban areas of Honshu, Kyushu, and Ryukyu and often becomes weedy (Koyama, 1995; Asami et al., 1999). Recently, Abe (2021) reported the invasion of *B. pilosa* in the coastal areas of Japan. Our findings corroborated this, as we identified this species in several coastal areas in Japan (Figure 1A), where it coexisted with coastal endemic species, such as *Setaria viridis* (L.) P.Beauv. var. *pachystachys* (Franch. & Sav.) Makino & Nemoto (Poaceae), *Ixeris repens* (L.) A.Gray (Asteraceae), *Canavalia lineata* (Thunb.) DC. (Fabaceae) and *Calystegia soldanella* (L.) R.Br. (Convolvulaceae). Our preliminary survey also found a population of *B. pilosa* that grew sympatrically with *Lysimachia mauritiana* Lam. (Purimulaceae), an endemic species of coastal areas, along the coast (Figure 1). *B. pilosa* has been reported to produce allelochemicals that may adversely affect the growth of native plants (Arthur et al., 2012; Balah et al., 2024). This underscores the need to clarify the acclimation patterns of this species in coastal areas to conserve coastal vegetation. Previously, comparative cultivation analyses using open-top chambers (OTC) have revealed that *B. pilosa* has acclimated to the wind by altering its leaf area and stem length (Shiba et al., 2024b). However, strong stress in coastal areas is influenced by both wind and soil moisture

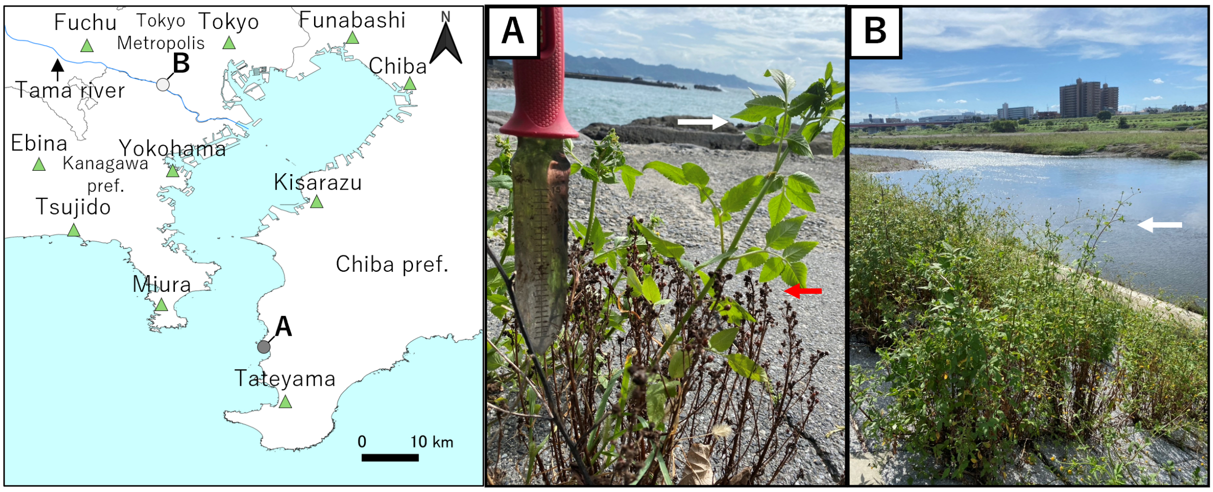

FIGURE 1
Sampling sites of *Bidens pilosa* and AMeDAS stations. AMeDAS locations are indicated by triangles. Coastal population of *Bidens pilosa*. **(A)** coastal, **(B)** inland. White arrow indicates *B. pilosa*, and red arrow indicates *Lysimachia mauritiana*.

(Nakajima and Yoshizaki, 2010; Ito and Yoshizaki, 2017, 2019). Consequently, this poses the following question: how can we analyze the acclimation patterns of *B. pilosa* to these multiple stresses in coastal areas?

Resource allocation is essential for plant development, yield formation, and tolerance to abiotic and biotic stresses. It also serves as a key indicator of plant growth and adaptation strategies and varies with environmental conditions (Kerkhoff et al., 2006; Reich et al., 2008; Sardans and Peñuelas, 2013; Shiba et al., 2024a, b; Shiba and Fukuda, 2024). Plant resource allocation reflects the trade-off in the distribution of aboveground and belowground biomass, which can be influenced by external environmental conditions (Fan et al., 2019; Poorter et al., 2012; Reich et al., 2014; Yang et al., 2010, 2018; Shiba et al., 2024b). Comparative analyses of resource allocation strategies among different environmental conditions are crucial in understanding plant adaptation or acclimation. These studies have been widely used to analyze biomass partitioning between aboveground and belowground organs (Enquist and Niklas, 2002; Cheng and Niklas, 2007; McCarthy and Enquist, 2007; Yang et al., 2010; Shiba et al., 2024b). Resource allocation patterns of five black spruce species planted along a latitudinal gradient in a boreal forest revealed that trees in the northern region budded earlier, grew less, and reached reproductive maturity earlier than those in the southern region. In addition, late frost damage affected growth capacity without seasonal adjustment in the subsequent year. This indicated that local adaptation of functional traits might lead to the inability of black spruce to adapt to future climate conditions associated with global warming or alternatively function as a powerful evolutionary force promoting rapid adaptation to changing environmental conditions (Silvestro et al., 2023). Therefore, analyzing resource allocation patterns is beneficial for research on the adaptation and acclimation of local populations to future climate changes. Consequently, plants serve as effective systems for examining environmental acclimation mechanisms. The acclimation pattern of *B. pilosa* to multiple stresses in coastal areas can clarify differences in resource allocation modes. Shiba et al. (2024b) indicated that *B. pilosa* reduced the allocation of resources to the ground under wind stress conditions. However, this study was solely conducted in a cultivated environment. Investigating how *B. pilosa* alters its resource allocation ratio in response to water stress and unstable soil due to sea sand and wind stress in outdoor coastal areas is pertinent. This study aims to clarify the changes in functional morphology and resource allocation during growth as a case study of the acclimation patterns of *Bidens pilosa* to coastal environments.

2 Materials and methods

On October 2, 2024, 58 individuals of the coastal *B. pilosa* population were collected from the coast of Kyonan Town, Awa District, Chiba Prefecture (35°06′04″ N, 139°49′31″ E). Subsequently, on October 19, 2024, 43 individuals of the inland *B. pilosa* population were collected from the Tamagawa Riverbed in Tamatsutsumi, Setagaya Ward, Tokyo (35°36′24″ N, 139°37′55″ E). During collection, slight damage was noted in individuals from the coastal population; however, both populations had developed inflorescences. The soil at the sampling sites consisted of marine sand and gravel for the coastal populations, while the inland populations were primarily found in areas with typical soil.

In addition, we presented monthly data for 2024 on temperature, precipitation, sunshine duration, wind speed, and humidity near the *B. pilosa* populations in this study using AMeDAS data from the Japan Meteorological Agency (Supplementary Materials 1; Figure 1). According to the AMeDAS Monthly Maximum Instantaneous Wind Speed data, the coastal populations (e.g., Tateyama, Miura, and Kisarazu) experienced wind speeds ranging from 19.6 to 22.7 m/s in August, while the inland populations (e.g., Fuchu, Tokyo, and Yokohama) experienced wind speeds ranging from 13.2 to 21.1 m/s, indicating that wind speeds tend to be higher in coastal areas (Supplementary Table 8).

2.1 Morphological measurements

Leaf area (cm^2) was measured by selecting up to three fully expanded leaves per individual, photographing them, and analyzing the images with ImageJ software to calculate the average value. The number of nodes was counted for each individual as an indicator of the leaf number.

Stem length (mm) was measured using ImageJ software following the capture of an image of the entire individual. Stem diameter (mm) was measured at the base using a digital caliper (CD-15APX; Mitutoyo Corporation, Kawasaki, Japan) in triplicate, and the average value was calculated.

2.2 Biomass of roots, stems, leaves, and inflorescences

Following morphological measurements, the samples were divided into roots, stems, leaves, and inflorescences and subsequently dried in a drying oven (FS-405, Advantec Toyo Co., Ltd., Tokyo, Japan) at 75°C for at least 72 h. After drying, the samples were immediately removed from the oven, and the dry mass (g) of each organ was measured using an electronic balance (ATX224R, Shimadzu Corporation, Kyoto, Japan).

Additionally, the above/belowground ratio was calculated for each population by defining the dry mass of stems, leaves, and inflorescences as the aboveground biomass and the dry mass of roots as the belowground biomass.

2.3 Statistical analysis

Statistical analyses were conducted using R software (R Core Team, 2024). After confirming the normality of the data using the Shapiro–Wilk test, Levene's test was used to assess the homogeneity of variances for the normally distributed data. A Student's t-test was conducted under the assumption of equal variances. The Mann–Whitney U test was performed for data that did not conform to a normal distribution.

Scatter plots were generated for each environment to examine the relationship between the two variables. After performing a statistical test for correlation and the Shapiro–Wilk test, if normality was confirmed for one or both variables and a statistically significant correlation was found between the two environments, an analysis of covariance (ANCOVA) was performed. The relationship between the two variables was analyzed for stem basal diameter versus stem length and root versus inflorescence dry mass.

3 Results

In this study, the comparison data between the two groups included the node number, leaf area, and dry weight of various organs (roots, stems, leaves, and inflorescences), as well as the above/belowground ratio. Only the node number was compared using Student's t-test. Other variables did not follow a normal distribution and were consequently compared using the Mann–Whitney U test. For stem basal diameter versus stem length, both environments showed a normal distribution and statistically significant correlation; therefore, an ANCOVA was performed. However, for root versus inflorescence dry mass, neither variable followed a normal distribution and no statistical correlation was found in the coastal population; therefore, an ANCOVA was not conducted.

3.1 Leaf and stem morphological measurements

A statistically significant difference was observed in the number of nodes between the coastal and inland populations ($p < 0.001$). The number of nodes in the coastal population was 17.34 ± 0.48 (mean ± SE), whereas those in the inland population were significantly higher at 20.05 ± 0.53 (Figure 2A). A statistically significant difference was also observed in the leaf area between the coastal and inland populations ($p < 0.01$). The leaf area in the coastal population was 2,141.12 ± 158.62 mm^2, while that of the inland population was significantly smaller at 1,500.00 ± 109.66 mm^2 (Figure 2B). These results suggest that the leaf morphology of the coastal population may represent an acclimation pattern characterized by larger but fewer leaves (Figure 2).

The relationship between basal stem diameter and stem length in *B. pilosa* demonstrated a statistically significant positive correlation in both populations (coastal: $p < 0.001$, inland: $p < 0.001$). In addition, the ANCOVA results revealed no interaction effect ($p = 0.11$). This suggests that the stem development of *B. pilosa* is not influenced by the environment, with a consistent addition of stem length corresponding to increases in stem diameter, irrespective of whether the plant is situated in a coastal or inland environment (Figure 3).

3.2 Resource allocation to each organ

The dry mass of each organ is shown in Figure 4. No significant difference was observed between the two groups regarding the dry mass of stems and leaves (stems: $p = 0.44$, leaves: $p = 0.85$; Figures 4B, C). However, significant differences were observed between roots and inflorescences (roots: $p < 0.01$, inflorescences: $p < 0.001$; Figures 4A, D). The dry mass of roots in the coastal population was 1.06 ± 0.15 g, whereas that in the inland population was significantly lower at 0.58 ± 0.01 g (Figure 4A). Additionally, the dry mass of inflorescences in the coastal population was 0.11 ± 0.01 g, whereas that in the inland population was significantly higher at 0.44 ± 0.08 g (Figure 4D). Furthermore, the above/belowground ratio was significantly different between the coastal and inland populations ($p < 0.001$). The ratio in the coastal population was 7.23 ± 0.41, whereas that in the inland population was significantly higher at 12.41 ± 0.65 (Figure 4E). These results suggest that *B. pilosa* in coastal environments allocates more resources to roots while

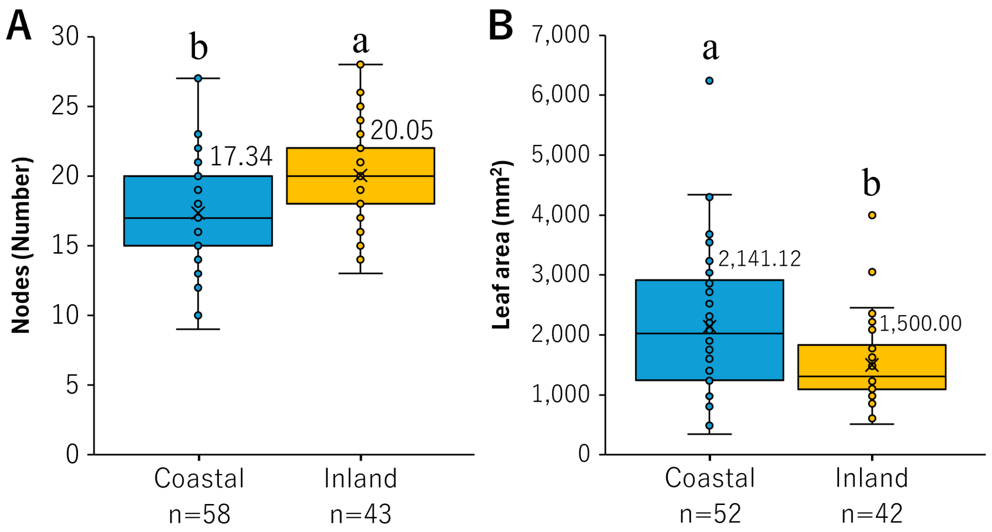

FIGURE 2
Comparison of **(A)** nodes and **(B)** leaf area. The values denoted by different letters in the box plot exhibit significant differences for nodes, as determined by the Student's t-test, and for leaf area, as determined by the Mann–Whitney U test ($p < 0.05$). The means are plotted at cross marks, with the figures located in the top right corner of the diagram.

maintaining similar allocations to stems and leaves, despite a decrease in resource allocation to inflorescences (Figure 4).

Because the dry mass of roots and inflorescences varied between environments, an analysis of their relationship revealed a statistically significant positive correlation in *B. pilosa* from the inland population (coastal: $p = 0.27$, inland: $p < 0.001$; Figure 5). This suggests that *B. pilosa* from inland environments increases resource allocation to roots and inflorescences, whereas *B. pilosa* from coastal environments continues to invest resources in roots, with minimal investment in inflorescences (Figure 5).

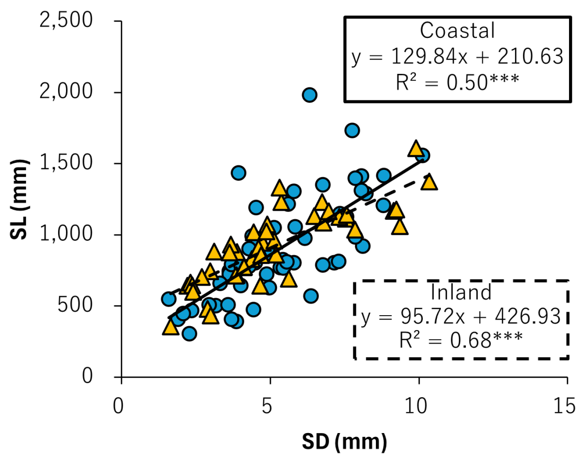

FIGURE 3
Stem diameter (SD) versus stem length (SL) for coastal (blue circle and solid line) and inland (orange triangle and dashed line) plant samples. The linear regression equation, coefficient of determination, and statistical evaluation of the correlation are presented. The significance of the correlation coefficient is indicated as follows: ***$p < 0.001$.

4 Discussion

Coastal ecosystems play many important roles in coastal defense, such as attenuating high wind stress (Hesp, 1989, 1991; Carter, 1991; Morris et al., 2018; Hanley et al., 2020). However, introduciung alien plant species severely threatens local biodiversity, ecosystem services, and environmental quality (Pejchar and Mooney, 2009; Pyšek and Richardson, 2010; Jones and McDermott, 2018). Therefore, it is imperative to elucidate the mechanisms by which invasive plants acclimate to coastal areas. Our analysis revealed that the number of leaves of *B. pilosa* in the coastal area was lower than that in the inland areas (Figure 2A). Shiba et al. (2024b) demonstrated that wind stress reduced the number of leaves in *B. pilosa*. This suggests that high wind speeds in coastal areas reduce the number of leaves of this species to avoid breakage by alleviating the load on the leaves and supporting stems. Interestingly, the leaf area of *B. pilosa* was significantly greater in coastal areas (Figure 2B), while no significant differences were observed in the relationship between stem basal diameter and height across environments (Figure 3). Therefore, allocation of resources to stems and leaves in the coastal population of *B. pilosa* did not significantly differ from that in the inland population (Figures 4B, C). Shiba et al. (2024b) showed that *B. pilosa* exhibited a reduced number of leaves, leaf area, and stem height in windy areas. In contrast, our results contradict the findings of Shiba et al. (2024b), suggesting that stress other than wind may contribute to the observed increase in leaf area in coastal areas. Why is there a contradiction, and what stresses other than wind affect coastal populations? For example, Ohga et al. (2013) showed that coastal of *Adenophora triphylla* var. *japonica* had increased leaf area by enlarging leaf cells, allowing them to retain water, and similar results have been shown for *Aster hispidus* var. *insularis* (Tunala et al., 2012). Nonetheless, since our study did not

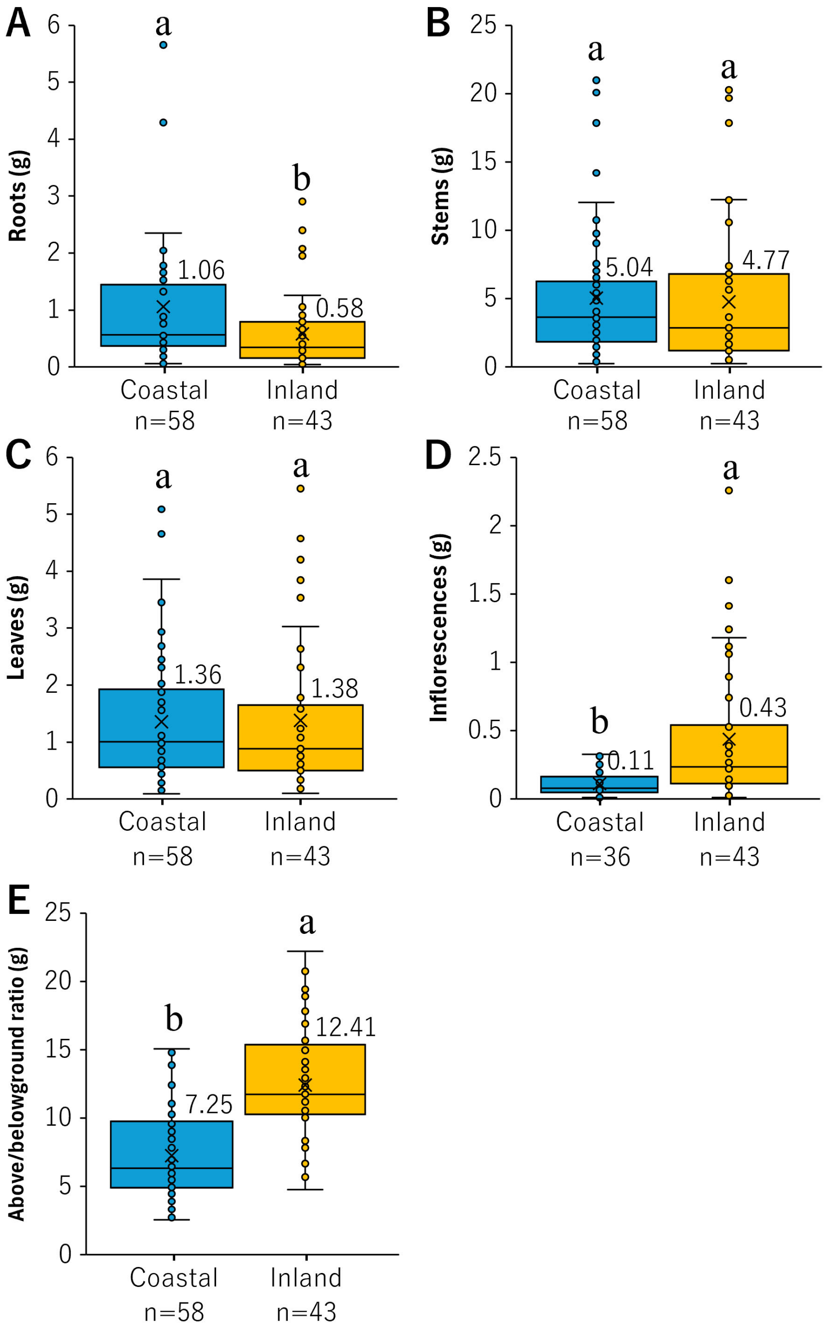

FIGURE 4
Comparison of **(A)** roots, **(B)** stems, **(C)** leaves, **(D)** inflorescences, **(E)** above/belowground biomass ratio. The values denoted by different letters in the box plot exhibit significant differences, as determined by the Mann–Whitney U test ($p < 0.05$). The means are plotted at cross marks, with the figures located in the top right corner of the diagram.

directly measure environmental factors such as drought or salinity, causal relationships between these factors and leaf morphology could not be determined. Meanwhile, it is known that sand carried by the wind accumulates around plants in coastal regions (Hesp, 2002; Zarnetske et al., 2015; Hesp et al., 2019), and plant height and leaf size are thought to influence their sand-trapping capacity (Hesp, 2002; Feagin et al., 2015; Zarnetske et al., 2015). As the frequency and intensity of strong winds increase due to climate change, the enlargement of leaf area in *B. pilosa* in such environments may play a role in trapping sand for moisture retention and plant anchorage. These findings suggest that coastal populations of *B. pilosa* reduce the number of leaves in response to strong winds, while elongating stems to maximize leaf production and stabilize growth by increasing leaf area. Such acclimation likely

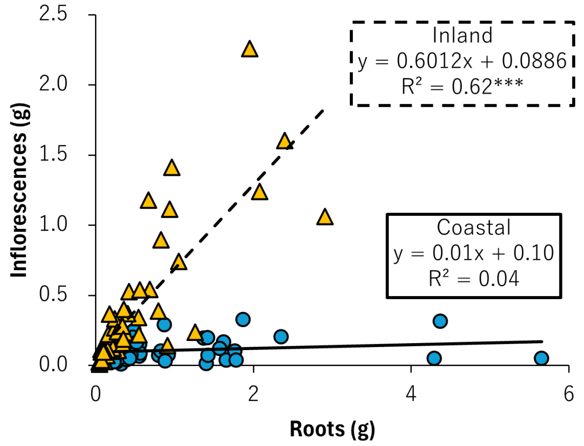

FIGURE 5
Root biomass versus inflorescence biomass for coastal (blue circle and solid line) and inland (orange triangle and dashed line) plant samples. The linear regression equation, coefficient of determination, and statistical evaluation of the correlation are presented. The significance of the correlation coefficient is indicated as follows: ***p < 0.001.

reflects a structural strategy that differs significantly from that of inland populations in terms of resource allocation to stems and leaves. Yoshizaki et al. (2023) showed that the leaves of coastal plants became increasingly susceptible to desiccation and salt intrusion after the leaf surface was damaged by blown sand. This implies that the coastal population of *B. pilosa* faces challenges related to establishment and damage caused by blowing sand. Mechanical stress on plants in coastal areas is considerably influenced by wind pressure, which is the primary environmental factor responsible for stem lodging. This phenomenon occurs when the forces exerted on plants exceed the maximum force their stems can withstand before breaking. Cooper and Mendiola (2004) noted that dwarfing could enhance plant species resistance to strong winds and lodging resistance. This suggests that this response can be adaptive because these plants are less susceptible to wind damage. Shiba et al. (2024b) demonstrated that an increase in wind speed correlated with a decrease in the rate of resource investment in stems and leaves. Consequently, based on the acclimation patterns revealed in our study, *B. pilosa* is unlikely to invade coastal areas characterized by elevated wind speeds, as wind pressure can likely cause lodging, given the resource investment rate in stems and leaves revealed in our study. In addition to wind stress, salt stress is also a major abiotic factor in coastal environments. Salt spray can damage leaf surfaces, reduce leaf area, increase water stress, and impair photosynthetic performance, thereby compounding the challenges faced by plants in these environments (Du and Hesp, 2020). Although coastal habitats may share general features such as soil type, local variations in wind conditions and salinity levels could lead to distinct acclimation patterns in other coastal populations of *B. pilosa*. Therefore, future studies should compare *B. pilosa* populations across coastal sites with differing wind regimes and salinity gradients to better understand the diversity of acclimation patterns.

The importance of the aboveground structures of plants in coastal areas is well established; however, considerable uncertainty remains regarding their belowground structures. Research has examined the differences in above- and belowground resource allocation patterns in response to nutrients and sand burial in coastal areas (Day, 1996; Brown and Zinnert, 2018; Dech and Maun, 2021). Belowground resource in coastal areas are critical for sediment stabilization and erosion mitigation (Charbonneau et al., 2017; Bryant et al., 2019; Feagin et al., 2019; De Battisti and Griffin, 2020). Our study revealed that the coastal population of *B. pilosa* exhibited significantly higher root weights and resource investment rates than those of the inland population (Figures 4A, E). Strong winds enhance plant anchorage by promoting root development (Danjon et al., 2005; Tamasi et al., 2005; Štofko and Kodrık, 2008). Several studies have shown that wind affects root growth and biomass allocation to roots (Cleugh et al., 1998; Poorter et al., 2012; Gardiner et al., 2016; Feng et al., 2019). Shiba et al. (2024b) reported that there was no significant difference in root biomass between wind-exposed and control populations of *B. pilosa*. This result suggests that the significant increase in resource investment in roots observed in the coastal population (Figure 4A) cannot be explained by strong winds and that other environmental factors in coastal areas may be involved. Other environmental factors in coastal soils—such as burial, nutrient limitation, and salt stress—should also be considered. Roots play an important role in sediment dynamics (Gyssels et al., 2005; Reubens et al., 2007; Comino et al., 2010). Several studies have reported that roots provide physical reinforcement through sediment entanglement, sediment particle incorporation into their tissue, and sediment transport resistance (Gregory, 2006; Reubens et al., 2007; Feagin et al., 2015). Additionally, root structures can provide anchoring forces for plants and biomechanical reinforcement in coastal areas (Gregory, 2006; Reubens et al., 2007; Klimešová et al., 2018). Coastal soil erosion, driven by strong winds, consistently undermines plant growth and establishment. However, Davidson et al. (2020) found that increased investment in deepening root systems enhanced plant stability under unstable conditions. The increased investment in roots observed in this study may also be attributed to such functional roles. However, these factors were not directly examined in this study, and further experimental investigation is required to identify the causes of the increased root biomass.

Plants can adjust their resource allocation to prioritize growth or reproduction in different environments, thereby optimizing their fitness (Mironchenko and Kozlowski, 2014). Moreover, reproductive allocation varies considerably among populations of a species growing under different environmental conditions. Semelparous annual species allocate a greater proportion of their resources to reproduction than that of iteroparous perennials (Weiner, 2004). It is questionable whether coastal populations of *B. pilosa* can invest resources in their reproductive organs due to ongoing investment in their roots. A previous study showed that *B. pilosa* maintained consistent resource allocation to inflorescences despite exposure to strong wind conditions (Shiba et al., 2024b). Our results suggest that the coastal population of *B. pilosa* invests significantly fewer resources in inflorescences (Figure 4D). The inland population of *B. pilosa* exhibited a larger increase in inflorescences corresponding to an increase in root mass, whereas the coastal population allocated more resources to root development at the expense of inflorescences (Figure 5). Reduced height growth is the most common response to wind stress because diminished stature enhances the ability of plants to resist forces and experience reduced drag (Jaffe et al., 1984; Liu et al., 2007). Studies have indicated that plants exposed to wind are shorter than those grown under wind-still conditions (Russell and Grace, 1978; Telewski and Jaffe, 1986). This suggests that this response may be adaptive, as shorter plants are less susceptible to wind damage. However, as mentioned above, coastal populations of *B. pilosa* maintain a stem height comparable to inland populations but reduce leaf number while increasing leaf area, which may enhance sand capture, stabilize the plant base, and slightly reduce wind impact. Nevertheless, it remains unclear whether sand capture is effective in mitigating broader environmental stresses, and further investigation is needed. This shift in resource allocation is expected to reduce seed production in the coastal population and may substantially affect their fitness. Coastal vegetation is a unique ecosystem, characterized by high morphological, ecological, and dynamic diversity. In such environments, plants may acclimate more readily due to reduced competition. Consequently, *B. pilosa* is one of the plant species that has acclimated to coastal areas and may thrive in this environment despite a limited number of seeds. In addition to these ecological traits, the thorny awns of the fruit of this species get caught on people's clothing and are artificially dispersed (anthropochory), expanding the distribution range of this plant throughout urban areas in Japan (Shiba et al., 2024b). The coastal areas we surveyed is shallow and safe for small children to play in, so it is a popular spot with many people coming and going, attracting many swimmers and anglers from nearby prefectures and areas (Chiba Prefectural Government, 2025; Chiba Prefecture Tourism Information, n.d). Therefore, the high level of human traffic in this coastal area may have contributed to the invasion of this species. This study provides the first report demonstrating that, in addition to its known remarkable reproductive capacity and epizoochorous dispersal strategy, *B. pilosa* has also invaded coastal environments—typically resistant to inland species—by altering its resource allocation and functional morphology through phenotypic plasticity.

The Mediterranean region, as a single region, is the world's largest tourist destination, attracting about one-third of the world's international tourists and generating more than one-quarter of international tourism revenues, and international tourist arrivals in the Mediterranean region are expected to reach 500 million by 2030 (UNWTO, 2012). Several reports have stated that *Bidens pilosa* species complex has already invaded countries surrounding the Mediterranean (Rojas-Sandoval, 2018; El Mokni et al., 2022; Plants of the World Online, 2025; Portal to the flora of Italy, 2025). In particular, the characteristic of *B. pilosa* fruits is that they can spread by adhering to people's clothes, etc (Shiba et al., 2024b), so it is expected that the distribution of *B. pilosa* will continue to expand in the Mediterranean region in the future. Furthermore, our study showed that *B. pilosa* have the characteristics to acclimate to special environments such as coastal areas, so there is a concern that *B. pilosa* will spread regardless of the environment in the Mediterranean region. *B. pilosa* also have the troublesome property of increasing the number of seeds in places where wind speed is reduced due to urban buildings, structures, and buildings (Shiba et al., 2024b). In addition, Fan et al. (2025) showed based on future climate scenarios that although populations of *B. pilosa* will decrease in tropical regions, the higher the latitude, the more adaptive the environment for this species will be, suggesting that the Mediterranean region is changing into an environment suitable for *B. pilosa* in the future. Unless proactive measures are taken to cull *B. pilosa*, which grows by acclimating its morphology to a variety of locations, from mountains to the sea, and from cities to the countryside, it is feared that an irreparable tragedy may befall the Mediterranean region, the world's largest tourist destination.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

UE: Investigation, Methodology, Project administration, Software, Validation, Writing – original draft. MS: Conceptualization, Funding acquisition, Methodology, Software, Supervision, Validation, Writing – original draft, Writing – review & editing. TF: Funding acquisition, Investigation, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that this study was conducted in the absence of any commercial or financial relationships that could be construed as potential conflicts of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2025.1604666/full#supplementary-material

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