Ecological Processes

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Contrasting responses of an invasive plant to herbivory of native and introduced insects

Qiu-Yue Fu[1], Guan-Wen Wei[2], Mo-Zhu Wang[3,4], Yuan Cui[5], Bi-Cheng Dong[1,6*] and Fei-Hai Yu[7]

Abstract

Background Interactions between alien plants and insect herbivores in introduced ranges may determine their invasion success. However, few studies have investigated whether alien plants respond differently to native and introduced herbivores in their introduced ranges and whether genotypes of alien plants matter. We conducted a greenhouse experiment to examine the effects of herbivory by a native insect (*Spodoptera litura*), by an introduced insect (*S. frugiperda*), and simultaneously by both insect species on growth, morphology, and biomass allocation of 17 genotypes of an invasive alien clonal plant *Hydrocotyle verticillata*, and used selection gradient analysis to test which herbivory conditions favor selection of a specific leaf or root trait value.

Results Different genotypes of *H. verticillata* showed significant variation in growth, morphology, and biomass allocation, but their responses to herbivory were relatively consistent. All three herbivory treatments significantly decreased total mass and stolon mass, but herbivory of *S. frugiperda* increased specific leaf area. Herbivory of *S. litura* and simultaneous herbivory of both insect species also decreased leaf mass, petiole mass, root mass, and ramet mass. Selection gradient analysis showed that leaf and root traits varied under different herbivory treatments. To achieve greater fitness, as measured by total mass and/or number of ramets, *H. verticillata* favored larger leaf area under herbivory by *S. frugiperda*, larger leaf area and lower specific leaf area under herbivory by *S. litura*, and larger leaf area, lower specific leaf area, and lower root-to-shoot ratio under simultaneous herbivory.

Conclusions *H. verticillata* demonstrated contrasting responses to herbivory by native and introduced insects, showing a remarkable ability to coordinate leaf trait plasticity and optimize biomass allocation. This strategy allows *H. verticillata* to achieve greater fitness under various herbivory conditions, potentially contributing to its invasion success. These findings highlight the importance of plant–herbivore interactions in shaping invasion dynamics and underscore the complex adaptive mechanism that enables invasive plants to establish and spread in introduced ranges.

Keywords *Hydrocotyle verticillata*, Invasive plant, Introduced herbivore, Native herbivore, Phenotypic plasticity, Selection gradient analysis

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Background

Interactions between alien plants and their herbivores in introduced ranges are crucial to their invasion success (Liu et al. 2022; De Oliveira et al. 2023). The Enemy Release Hypothesis (ERH) suggests that alien plants, which lack co-evolved natural enemies in their introduced ranges, often gain a competitive advantage over native species and are more likely to invade successfully (Keane 2002). Although widely acknowledged in invasion ecology (Lucero et al. 2019; Xu et al. 2021; Costan et al. 2022), the ERH remains debatable (Colautti et al. 2004; Mitchell et al. 2006; Liu and Stiling 2006; Meijer et al. 2016). Some previous studies have documented that native herbivores in introduced ranges may still regulate alien plants after establishing interactions between themselves and these novel enemies in introduced ranges (Colautti et al. 2004; Chun et al. 2010; Liu et al. 2020; Xu et al. 2022). Therefore, investigating the relationships between alien plants and various new enemies in introduced ranges is valuable for understanding invasion mechanisms.

Aboveground herbivory is the most common biotic stress experienced by plants, which can limit plant growth and development by reducing photosynthetic capacity, depleting nutrients, and altering reproductive abilities (Li et al. 2016, 2020; Heinze 2020). However, the loss from these direct or indirect damages varies widely, ranging from minimal effects to significant fitness costs, depending on the extent of damage and the ability of damaged plants to compensate through growth and repair mechanisms (Su et al. 2023). Therefore, plants may evolve various tolerance strategies to mitigate herbivory-induced damage. Tolerance allows plants to maintain fitness despite damage; this can manifest itself as rapid regrowth after herbivory (Croy et al. 2020; Allen et al. 2021), resource reallocation to replace lost tissues (Shan et al. 2023, 2024), or modification of life history traits, such as adjusting reproduction timing to offset herbivory effects (Chen et al. 2023). This tolerance strategy does not suspend herbivory, but lessens its impact on overall fitness and survival of plants (Dong et al. 2017; Kafle and Wurst 2019; Croy et al. 2020).

The tolerance strategy of alien plants can vary with the herbivores involved (Liu et al. 2020). When there are relatively long-term co-evolutionary relationships between alien plants and native herbivores, alien plants may develop specific responses tailored to the particular feeding mode or the type of damage inflicted by a herbivore (Oduor 2022). For instance, piercing and sucking insects might elicit a different plant response than chewing herbivores (Basu et al. 2023). However, when there are no co-evolutionary relationships between alien plants and native herbivores, alien plants may evolve more generalized tolerance strategies that enable them to cope with a wide range of herbivory pressure (Scherber et al. 2003). This broad spectrum tolerance and trait plasticity can be advantageous for alien plants in new environments, as it allows them to maintain their fitness and competitive ability in the face of diverse and unfamiliar herbivore communities.

Genotypic diversity underlies the potential of rapid evolution for the invasive populations of alien plants (Liu et al. 2010; Harms et al. 2021; Campoy et al. 2021). Different genotypes may exhibit varying tolerance-induced trait plasticity in response to herbivory pressure (Li et al. 2016; Duncan and Williams 2020). When favored by natural selection, trait plasticity may enhance plant fitness; for example, herbivory-induced damage may drive adaptive evolution by increasing plant tolerance to herbivore attacks (Tian et al. 2021; Ashra and Nair 2022). On the contrary, trait plasticity can be maladaptive if it opposes natural selection, reducing fitness (Minden et al. 2023). To date, it is unknown to what extent herbivory-induced trait plasticity is adaptive.

Through a greenhouse experiment, we tested the effect of herbivory damage caused by caterpillars of two moth species in the genus *Spodoptera*—the invasive *Spodoptera frugiperda* from the Americas and the native *S. litura* from China—on performance of 17 genotypes of invasive *Hydrocotyle verticillata*. We evaluated differences in growth (total mass, leaf mass, petiole mass, stolon mass, root mass, ramet mass, number of ramets, number of leaves, and leaf area), morphology (mean leaf area and specific leaf area), biomass allocation (root-to-shoot ratio), and plasticity in leaf morphology and biomass allocation of *H. verticillata* when subjected to separate or simultaneous herbivory by the two insects. We specifically tested the following hypotheses: (1) *H. verticillata* exhibits different responses to herbivory by invasive *S. frugiperda* and native *S. litura*, although both insect species are from the same genus. We predict that herbivory by native *S. litura* causes more adverse effects on the performance of *H. verticillata* compared to herbivory by *S. frugiperda*, due to a relatively long-term interaction between *H. verticillata* and *S. litura* in China. (2) Contrasting responses of *H. verticillata* to different herbivory types (i.e., herbivory by a single insect or by both insect species simultaneously) may depend on genotypes. We predict that some genotypes will exhibit differential responses to various herbivory types. (3) *H. verticillata* shows differential levels of trait plasticity in response to various herbivory types. We predict that plasticity in leaf and root traits varies significantly when *H. verticillata* is subjected to different herbivory types.

Materials and methods

Study species

Hydrocotyle verticillata Thunb. (previously misidentified as *Hydrocotyle vugaris* L. in China; e.g., Miao et al. 2011; Zhang et al. 2022; Begum et al. 2022, 2023), is a perennial clonal herb native to South and North America and the West Indies. However, it has now been widely distributed in tropical and subtropical regions (Umate and Deogade 2020). The species was introduced to China as an ornamental plant in the 1990s, and it is commonly planted for greening purposes in domestic and public gardens (Miao et al. 2011; Tang et al. 2020). It reproduces mainly through clonal growth through stolon fragments. The creeping solons bear peltate leaves and roots at the nodes, functioning as ramets (Dong et al. 2015; Xue et al. 2022). Due to its strong phenotypic plasticity and rapid reproductive ability, *H. verticillata* has become invasive in China. It has caused significant negative effects on native flora, particularly in wetlands, by displacing some species from their habitats and altering local biodiversity and ecosystem dynamics (Miao et al. 2011; Si et al. 2020; National Plants Specimen Resource Center 2023). So far, however, there is still no evidence that this species has resulted in the extinction of any native plants. In the field, we have observed that larvae of *S. litura* can actively feed on *H. verticillata*.

Spodoptera frugiperda Smith (Lepidoptera: Noctuidae), is a herbivorous insect whose larvae feed on over 350 plant species of 76 families (Montezano et al. 2018; Gui et al. 2022). *S. frugiperda* is native to tropical and subtropical regions of the Americas, and has spread to Asia, Africa, the Middle East, and Australia due to its strong migratory ability (Rwomushana 2019). *S. frugiperda* was first reported in Yunnan Province, China in January 2019, and has spread to southwest, central, and northern China (Xiao et al. 2020; Jing et al. 2020). The invasion of *S. frugiperda* has already caused significant losses in crop production in China. It is estimated that the maize industry alone has a potential overall economic loss of 143.2 billion RMB due to this invasion (Qin et al. 2020).

Spodoptera litura Fabricius (Lepidoptera: Noctuidae), is an omnivorous and generalist pest that feeds on crops including tobacco, cotton, soybeans, and vegetables (Yang et al. 2022; Zhang et al. 2022). *S. litura* is widely distributed in tropical and subtropical regions, including Asia, Africa, North America, and Oceania (Tang et al. 2022). The larvae of *S. litura* can cause substantial damage to crop growth by consuming their leaves (Du et al. 2022). *S. frugiperda* and *S. litura* undergo six larval instars during their holometabolic life cycles. Each instar is distinguished by specific morphological changes and a progressive increase in size (Maes 2014; Rwomushana 2019).

Although *S. frugiperda* and *S. litura* have similarities in behavior (e.g., migration, reproduction, and other habits), they differ in morphology. *S. litura* is larger than *S. frugiperda*. Compared to *S. litura*, the second-instar larvae of *S. frugiperda* can be distinguished by reddish-brown markings on the sides of the abdomen (Zhao et al. 2019).

From July to August 2016, 128 individual plants of *H. verticillata* were collected from ten field populations in different cities of China [refer to Table S1 and Wang et al. (2020) for more details]. In summary, 20 genotypes were identified using AFLP (Amplified Fragment Length Polymorphism), based on the original protocol of Vos et al. (1995) with several modifications. These genotypes were isolated and vegetatively propagated using stolon fragments in a common garden at Taizhou University, ensuring recovery and consistency for future research. In July 2021, we selected 17 genotypes of *H. verticillata* that had sufficient material for the experiment. The larvae of *S. frugiperda* and *S. litura* were obtained from Henan Jiyuan Baiyun Industry Co., Ltd. (http://www.keyunnpv.cn/).

Experimental design

The experiment employed a two-factorial design comprising 17 genotypes and four levels of herbivory treatments: control (no herbivory), herbivory by *S. frugiperda*, herbivory by *S. litura*, and simultaneous herbivory by *S. frugiperda* and *S. litura*. Each combination of genotype and herbivory treatment had six replicates.

On 12 July 2021, 1224 stolon fragments from the 17 genotypes of *H. verticillata* with similar sizes were selected for pre-cultivation. Each fragment comprised one stolon node bearing a peltate leaf attached to a long petiole and two adjacent 1-cm-long internodes. To facilitate rooting, these fragments were initially cultivated for four weeks in aquatic containers (52.5 cm long × 34.5 cm wide × 6.5 cm high). The containers were filled with a mixture of tap water and commercial nutrient solutions (Miracle-Gro All Purpose; Scotts Miracle-Gro Company, Wuhan, China) at a volume ratio of 1:400, following the manufacturer's instructions. The solutions were refreshed once every two weeks. On 10 August 2021, three plants of each genotype with adventitious roots were transplanted into individual plastic pots (18 cm in diameter × 16 cm high) and then thinned into one plant per pot. The pots were filled with a 3-L mixture of loess and sandy soil at a 1:1 volume ratio. Water was added every two days. There were 408 pots in total.

On 19 September 2021, 17 separate pots containing the 17 different genotypes of *H. verticillata* were randomly placed inside a net cage (180 cm long × 60 cm wide × 60 cm high) made of 0.5 mm nylon mesh. There were a total of 24 net cages, with four different herbivory treatments and six replicates per treatment. This nested

design ensured consistent environmental conditions for all genotypes within each replicate, facilitating systematic evaluation of treatment effects while controlling for between- and within-cage variability (Schielzeth and Nakagawa 2013). In the control treatment, the 17 genotypes of *H. verticillata* were grown without herbivores. In treatments involving separate herbivory by *S. frugiperda* or *S. litura*, the 17 genotypes of *H. verticillata* were subjected to herbivory conditions at a density of four second-instar larvae of one species per pot, each having 3–6 cm in body length, released at the start of the experiment. In the treatment of simultaneous herbivory by *S. frugiperda* and *S. litura*, the 17 genotypes of *H. verticillata* were subjected to two second-instar larvae of each species per pot, also released at the start of the experiment. The herbivory treatments were repeated twice during the experiment: first from 19 September to 5 October 2021, and again from 13 to 26 October 2021. The timing of each treatment allowed the larvae of both insect species to complete development through the 2nd to the 6th instars, simulating the damage commonly caused during these stages. The mean temperature and relative humidity during the experiment were 29.80 ± 0.12 °C and 78.95 ± 0.35%, respectively.

Due to the large spacing between plots within each cage, the larval movement of *S. frugiperda* and *S. litura* between plants was effectively controlled. Furthermore, we conducted daily visual inspections of each pot to ensure that the number of larvae remained consistent with the intended treatment densities. These measures were crucial to maintaining experimental accuracy and ensuring well-controlled herbivore conditions.

The experiment lasted for 15 weeks and ended on 26 October 2021. At harvest, the number of ramets and leaves was counted for each plant of *H. verticillata*. Leaf area was measured using WinFOLIA software (Regent Instruments Inc., Quebec City, QC, Canada). The leaves, petioles, stolons, and roots were separated, dried at 70 °C for 48 h, and weighed.

Data analysis

Before analysis, mean leaf area was calculated by dividing total leaf area by number of leaves. Specific leaf area (SLA) was calculated by dividing total leaf area by leaf mass (Wang et al. 2018). Root-to-shoot ratio was calculated by dividing root mass by shoot mass (i.e., leaf mass + stolon mass + petiole mass) (Wang et al. 2022). Ramet mass was calculated by dividing total mass by number of ramets (Chen et al. 2019). To better meet the assumptions of normality and homogeneity of variance, total mass, leaf mass, root mass, ramet mass, number of leaves, number of ramets, leaf area, mean leaf area, and SLA were natural-log(x) transformed; stolon mass and petiole mass were natural-log($x+1$) transformed; root-to-shoot ratio was square-root transformed.

Effects of genotype and herbivory

We employed linear mixed models to examine the effects of genotype and herbivory on growth (total mass, leaf mass, stolon mass, petiole mass, root mass, ramet mass, number of ramets, number of leaves, and total leaf area), morphology (mean leaf area and SLA), and biomass allocation (root-to-shoot ratio) of *H. verticillata*. In the models, we specified three custom contrasts of the herbivory treatments (control *vs*. herbivory by *S. frugiperda*, control *vs*. herbivory by *S. litura*, and control *vs*. simultaneous herbivory by both insect species) and their interactions with genotypes. This allowed us to compare the performance differences between plants grown without herbivory and those subjected to herbivory by different species of *Spodoptera*. For all dependent variables except number of ramets, a random effect was included to account for variability between cages within each replicate level. For number of ramets, the random effect was limited to replicate levels only, because of the singularity problem. Mixed linear models were fitted using the "lmer" function from the "lme4" package (Bates et al. 2015). The significance of these contrasts and their interactions was assessed using the "anova" function.

Plasticity of leaf and root traits under herbivory treatments

The relative fitness of each genotype was calculated as the mean fitness (i.e., mean total mass or number of ramets) of one genotype averaged over replicates relative to the mean fitness of all genotypes in the corresponding herbivory treatment encountered by that genotype (Lande and Arnold 1983). Total mass was chosen as a fitness proxy, as it reflects overall plant growth, resource accumulation, and competitive ability. Ramet number was selected because *H. verticillata* mainly reproduces through clonal growth, making it a key indicator of reproductive success and potential for population expansion. The trait values were the mean values of leaf morphology (mean leaf area and SLA) and biomass allocation (root-to-shoot ratio) for each genotype in a specific herbivory treatment. Before analysis, trait values were standardized using Z-score transformation.

To test the cross-environment genotypic selection (control *vs.* herbivory by *S. frugiperda*, control *vs.* herbivory by *S. litura*, and control *vs.* simultaneous herbivory by both insect species), we performed ANCOVAs using relative fitness as dependent variable, herbivory as fixed factor, and trait values as covariates. The treatment effect was estimated using the likelihood ratio test. A significant trait-by-herbivory interaction indicates that the selection pattern differs between environments

(Bell and Galloway 2008). To test selection differential in each specific environment, a within-environment phenotypic selection analysis was used to calculate selection differentials by regressing each plant's relativized fitness on its standardized traits in each environment (Caruso et al. 2006; Liu et al. 2010). The sign and magnitude of a regression coefficient (for cross-environment genotypic selection analysis) or selection differential (for within-environment phenotypic selection analysis) describe the direction and strength of linear selection. All analyses were performed using R version 4.0.5 (R Core Team 2021).

Results

Effects of genotype and herbivory

Different genotypes of *H. verticillata* exhibited significant differences in growth (total mass, leaf mass, stolon mass, petiole mass, root mass, ramet mass, number of ramets, number of leaves, and total leaf area), morphology (mean leaf area and SLA) and biomass allocation (root-to-shoot ratio; Table 1).

Compared to the control (no herbivory), total mass and stolon mass of *H. verticillata* were significantly lower under all herbivory treatments, but SLA was higher under herbivory of *S. frugiperda* (Table 1, Figs. 1A and 2F). Compared to the control, total mass, leaf mass, petiole mass, root mass, and ramet mass were significantly reduced by herbivory of *S. litura*, and also by simultaneous herbivory by both insect species (Table 1, Figs. 1B–E and 2A). There was a significant interaction effect between genotype and simultaneous herbivory on root mass (Table 1).

Plasticity of leaf and root traits under herbivory conditions

Cross-environment analyses indicated significant covariate effects of mean leaf area and root-to-shoot ratio when total mass was used as a fitness proxy. This suggests environment-independent selection for larger leaf area and lower root-to-shoot ratio (Tables 2 and 3).

When comparing the control with herbivory by *S. frugiperda*, significant trait-by-herbivory interactions were observed in mean leaf area and SLA when total mass was used as a fitness proxy, and in mean leaf area when number of ramets was used [significant effects of Cov:(CK vs. Sf) in Table 2]. Within-environment analyses further showed that selection favored larger leaf area, although this selection was weaker under herbivory by *S. frugiperda* compared to the control (Table 3). In addition, selection of lower SLA became neutral under herbivory of *S. frugiperda* (Table 3).

When comparing the control with herbivory of *S. litura*, significant trait-by-herbivory interactions were observed in SLA when total mass and number of ramets were used as a fitness proxy [significant effects of Cov:(CK vs. Sl) in Table 2]. Within-environmental analyses showed that selection favored lower SLA to increase

Table 1 Results of ANOVAs testing effects of different genotypes [Gen], herbivory (control [CK], herbivory by *S. frugiperda* [Sf], herbivory by *S. litura* [Sl], and simultaneous herbivory by *S. frugiperda and S. litura* [Sf + Sl]), and their interactions on growth, morphology, and biomass allocation of *H. verticillata*.

Variables	Gen	CK *vs.* Sf	CK *vs.* Sl	CK *vs.* Sl + Sf	Gen: (CK *vs.* Sf)	Gen: (CK *vs.* Sl)	Gen: (CK *vs.* Sl + Sf)
Growth							
Total mass[a]	**30.2*** **	**5.1***	**22.0*** **	**18.4*** **	0.9	0.6	1.4
Leaf mass[a]	**17.0*** **	4.2	**15.4****	**9.3****	0.9	0.4	1.0
Petiole mass[b]	**15.7*** **	0.8	**12.6*** **	**6.9****	1.5	0.4	0.3
Stolon mass[b]	**30.9*** **	**4.9***	**13.0****	**12.0****	1.0	1.0	1.3
Root mass[a]	**18.3*** **	1.2	**5.4***	**7.6***	1.1	1.3	**1.8***
Ramet mass[a]	**32.1*** **	1.5	**10.6****	**8.2***	0.8	0.3	1.3
No. ramets[a]	**11.8*** **	1.2	1.2	1.0	1.1	0.6	1.2
No. leaves[a]	**63.7*** **	0.1	2.6	0.2	0.5	1.2	0.7
Leaf area[a]	**10.3*** **	1.4	1.4	< 0.1	0.7	0.8	0.7
Morphology							
Mean leaf area[a]	**44.1*** **	1.9	1.6	< 0.1	0.7	1.3	1.2
SLA[a]	**11.2*** **	**4.9***	2.0	3.7	1.2	0.9	0.8
Allocation							
Root-to-shoot ratio[c]	**4.4*** **	0.1	0.2	0.2	1.1	1.5	0.9

Values for which $P < 0.05$ are in bold

[a] These variables were natural-log(x) transformed; [b]These variables were natural-log($x + 1$) transformed; [c]This variable was square-root transformed. F-values are given. The significance levels are: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, and no symbol $p \geq 0.05$. Significant values ($p < 0.05$) are formatted in bold

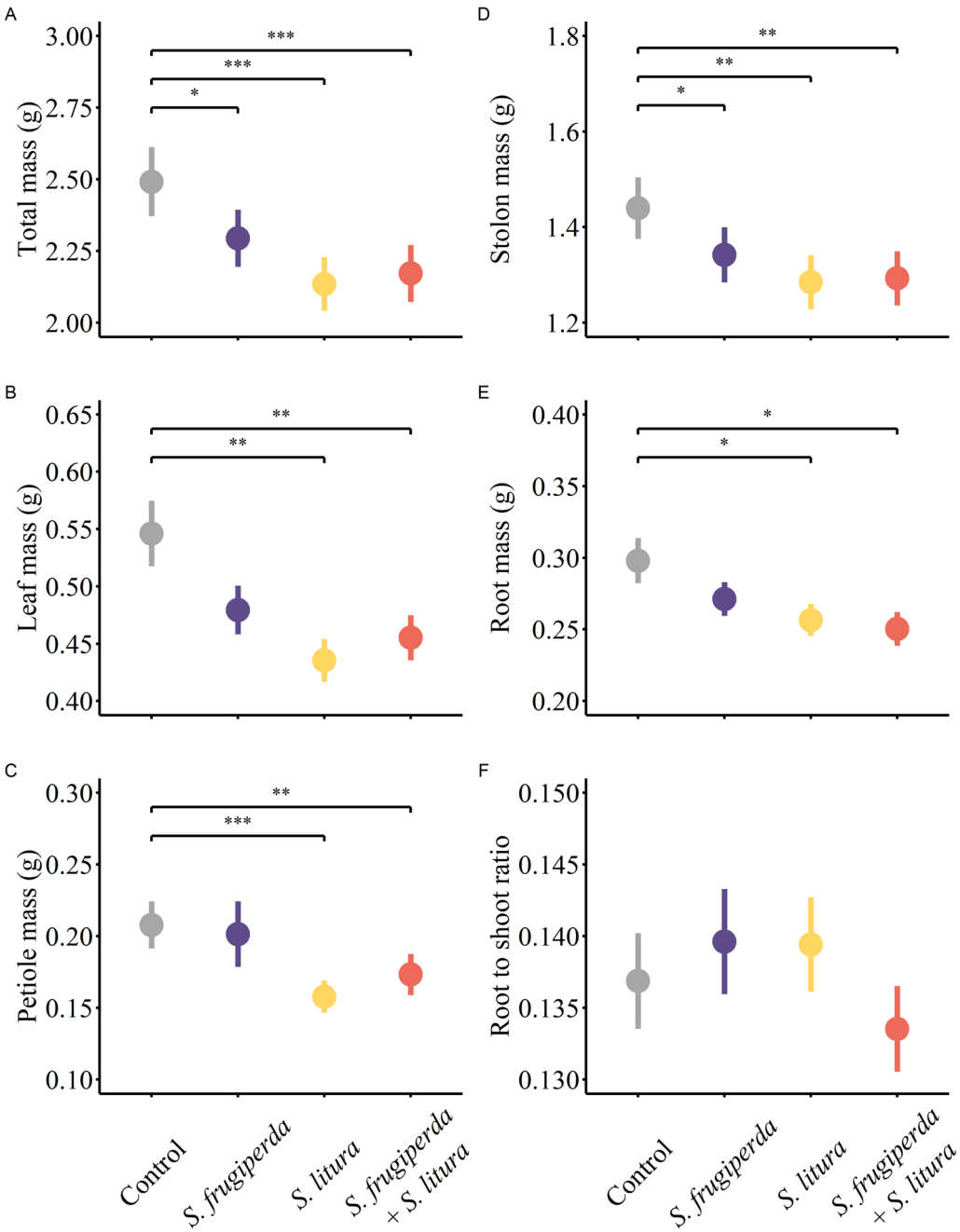


Fig. 1 Scatter plots with error bars for effects of herbivory (control, herbivory by *S. litura*, herbivory by *S. frugiperda*, and herbivory by *S. frugiperda* and *S. litura*) on (**A**) total mass, (**B**) leaf mass, (**C**) petiole mass, (**D**) stolon mass, (**E**) root mass, (**F**) root-to-shoot ratio of *H. verticillata*. The significant levels of pairwise comparisons (control *vs.* herbivory by *S. litura*, control *vs.* herbivory by *S. frugiperda*, and control *vs.* herbivory by *S. frugiperda* + *S. litura*) are shown: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, and no symbol $p \geq 0.05$. Mean ± SE are given

total mass, but favored higher SLA to promote ramet production (Table 3).

When comparing the control with simultaneous herbivory, significant trait-by-herbivory interactions were observed in all leaf and root traits when total mass was used as a fitness proxy [significant effects of Cov:(CK vs. Sf + Sl) in Table 2]. Within-environmental analyses showed that selection favored larger leaf area, lower SLA, and lower root-to-shoot ratio, and such selection became stronger under simultaneous herbivory compared to the control (Table 3).

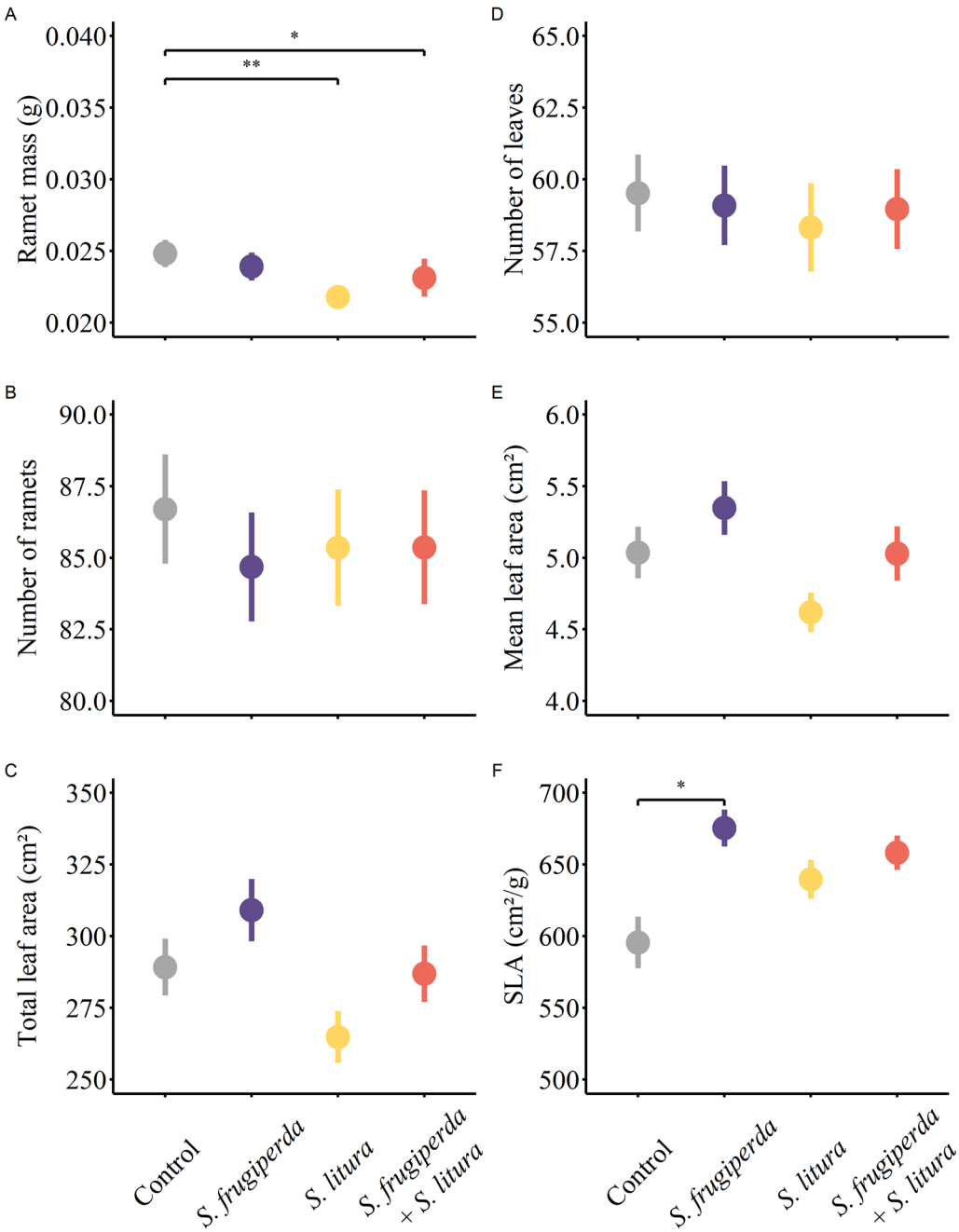


Fig. 2 Scatter plots with error bars for effects of herbivory (control, herbivory by *S. litura*, herbivory by *S. frugiperda*, and herbivory by *S. frugiperda* and *S. litura*) on (**A**) ramet mass, (**B**) number of ramets, (**C**) total leaf area, (**D**) number of leaves, (**E**) mean leaf area, (F) SLA of *H. verticillata*. The significant levels of pairwise comparisons (control *vs.* herbivory by *S. litura*, control *vs.* herbivory by *S. frugiperda*, and control *vs.* herbivory by *S. frugiperda* + *S. litura*) area shown: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, and no symbol $p \geq 0.05$. Mean ± SE are given

Discussion

Our study sheds light on the life history strategies of *H. verticillata* in its introduced ranges, particularly focusing on its responses to various herbivory pressure. We found substantial genotypic variation in growth, morphology, and biomass allocation, as well as relatively consistent plastic responses to herbivory in different genotypes. These findings highlight the adaptability and tolerance of *H. verticillata*, which are likely to contribute to its invasive success.

Table 2 Results of ANCOVA testing for overall selection (Cov) and differences in selection of *H. verticillata* between the control and one of three herbivory treatments

Fitness proxy	Variables	Cov	Cov: (CK *vs.* Sf)	Cov: (CK *vs.* Sl)	Cov: (CK *vs.* Sl + Sf)
Total mass	Mean leaf area	**29.8*** **	**9.8** **	0.3	**11.4** **
	SLA	2.6	**7.6** **	**4.8***	**18.6*** **
	root-to-shoot ratio	**8.3** **	0.3	3.3	**7.5** **
No. ramets	Mean leaf area	0.6	**4.6***	1.6	2.5
	SLA	1.4	2.5	**4.2***	2.4
	root-to-shoot ratio	2.1	3.3	0.2	0.6

The abbreviations used to represent the different treatments were as follows: CK for the control; Sf for herbivory of *S. frugiperda*; Sl for herbivory of *S. litura*, and finally, Sf + Sl to represent the simultaneous herbivory of both *S. frugiperda* and *S. litura*

χ^2 values are given. The significance levels are: ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, and no symbol $p \geq 0.05$. Significant values ($p < 0.05$) are formatted in bold

Table 3 Selection gradients for leaf and root traits of *H. verticillata* under each specific herbivory environment

Fitness proxy	Variables	CK	Sf	Sl	Sf + Sl
Total mass	Mean leaf area	**0.156*** **	**0.142*** **	**0.216*** **	**0.230*** **
	SLA	− **0.165*** **	− 0.104	− **0.110***	− **0.239*** **
	root-to-shoot ratio	− 0.083	− 0.066	− 0.028	− **0.157***
No. ramets	Mean leaf area	**− 0.052***	− 0.061	− 0.068	− 0.014
	SLA	0.034	0.071	**0.070***	0.020
	root-to-shoot ratio	0.036	0.064	0.008	0.025

The abbreviations used to represent the different treatments were as follows: CK for the control; Sf for herbivory of *S. frugiperda*; Sl for herbivory of *S. litura*, and finally, Sf + Sl to represent the simultaneous herbivory of *S. frugiperda and S. litura*

Selection gradients are expressed as standardized regression coefficients of relative fitness (relative total mass and relative number of ramets) on leaf (mean leaf area and SLA) or root (root-to-shoot ratio) traits under the control or one of three herbivory treatments. Regression coefficients are given. The significance levels are: ***$p < 0.001$, *$p < 0.05$, and no symbol $p \geq 0.05$. Significant values ($p < 0.05$) are formatted in bold

Genotypic variation in growth, morphology, and biomass allocation

Our study revealed significant variations in growth, morphology, and biomass allocation among different genotypes of *H. verticillata*, suggesting high levels of trait plasticity in the invasive populations. Specifically, ramets of the genotypes from Taizhou and Ningbo were relatively large, while those of the genotypes from Lishui, Wenzhou, and Chongqing were relatively small. Moreover, ramets of the genotypes from Taizhou with faster growth rates and greater biomass allocation to leaves (e.g., TZ-8 and TZ-1) may be better suited to resource-rich or low-stress environments. In contrast, ramets of the genotypes from Lishui and Wuhan with slower growth and greater allocation to roots (e.g., LS-3 and WH-1) may be better adapted to resource-poor or high-stress environments. This is possible because *H. verticillata* has already been widely distributed throughout southern China, so different invasive populations may have evolved to optimize their growth and resource allocation strategies in response to local environments. Indeed, a recent study showed that spatial environmental heterogeneity can drive the variation of the functional traits of *H. verticillata* (Wan et al. 2019). The differential responses of genotypes may further enhance the potential of *H. verticillata* in introduced ranges, for natural selection and adaptation in response to environmental changes.

Effects of herbivory on growth, morphology, and biomass allocation

Herbivory by *S. frugiperda* and *S. litura* both reduced the overall fitness (total mass) and stolon development of *H. verticillata*. This aligns with the field observation that, even in the introduced ranges, invasive *H. verticillata* was still subjected to some regulation by native herbivores that it encountered (Liu et al. 2017; Xu et al. 2024). This is also common in other aquatic invasive plants such as *Alternanthera philoxeroides* and *Eichhornia crassipes* in the introduced ranges (May et al. 2022; Fu et al. 2023). For example, the larvae of *S. litura* could directly postpone and retard the development of the leaf organ, resulting in a significant reduction in the aboveground growth and overall fitness of damaged plants (Fu et al. 2023).

Consistent with the first hypothesis, our findings from the control conditions provided clear evidence that both insect species reduced total biomass and stolon

development of *H. verticillata*, but their impacts on plant performance varied. Compared to *S. frugiperda*, herbivory of *S. litura* caused more severe damage to the aboveground organs and resulted in a greater reduction in ramet production and development of belowground organs, suggesting greater herbivory pressure caused by *S. litura* on *H. verticillata*. This difference may be attributed to several reasons. First, *S. litura* typically exhibited a larger body size than *S. frugiperda* at comparable developmental stages, which required increased food consumption from host plants (personal observation). Second, feeding preferences may influence the damage intensity of the two *Spodoptera* species to host plants (Stewart et al. 2021; Zhou et al. 2023). For instance, *S. frugiperda* prefers gramineous plants, particularly *Zea mays* L. (Zhang et al. 2021; Wei et al. 2024), while *S. litura* feeds on a broader range of species, including dicotyledons such as *H. verticillata* (Zhao et al. 2019; Tang et al. 2022; Wang et al. 2023). Third, *S. litura* larvae may induce changes in the release of volatile compounds (e.g., geranylacetone and prohydrojasmon) in host plants (e.g., *Capsicum annuum* L.), inducing feeding preferences of subsequent larvae and causing lasting damage (Ming et al. 2023). This is possible because these herbivory-induced plant volatiles likely serve as chemical cues, signaling the presence of pre-existing damage or altered plant chemistry. These cues may guide larvae to host plants with higher nutrients, fewer defensive compounds, or favorable structures, thereby enhancing feeding efficiency and larval development (Ming et al. 2023). It is important to note that herbivory-induced changes in plant volatiles are commonly found in many plant–insect interactions, but the exact compounds involved and their effects on subsequent herbivory may vary between species. For *S. frugiperda*, a similar mechanism has not yet been reported in previous studies. Thus, further studies are needed to explore this potential mechanism.

Contrary to our second hypothesis, the responses of *H. verticillata* to different herbivory types were largely consistent across genotypes, implying that *H. verticillata* may have evolved a generalized tolerance strategy against herbivores that is relatively uniform across its genotypes. The exception in root mass response to simultaneous herbivory indicates that some genotype-specific responses may occur under more intense herbivory pressure, possibly reflecting differences in resource allocation strategies of plants when facing multiple herbivores. This mechanism allows *H. verticillata* to maintain potential adaptability to diverse environmental changes while also exhibiting consistent responses to specific herbivores. Therefore, such a strategy may finally contribute to its successful invasion in various ecological niches.

Plasticity of leaf and root traits under herbivory conditions

Despite lack of genotype-by-herbivory interactions, we observed significant plasticity in leaf and root traits in response to different herbivory types, which significantly affected plant fitness (measured by total mass and ramet production). This is possible because different genotypes started with different baseline trait values. Consequently, the absolute fitness outcomes after herbivory may still differ among genotypes, even though the pattern of response is similar.

Our cross- and within-environment analyses revealed intriguing patterns in the adaptive responses of *H. verticillata* to different herbivory types. When facing herbivory from *S. frugiperda*, damaged plants that developed larger leaves exhibited greater fitness, as evidenced by increased biomass production. Similarly, when facing herbivory by *S. litura*, damaged plants that developed larger and thicker leaves also exhibited greater fitness. This strategy may potentially compensate for the loss of biomass and nutrients caused by herbivory. In other words, by increasing leaf area and leaf thickness, *H. verticillata* can enhance its photosynthetic capacity and light capture efficiency, allowing it to produce more photosynthates to support growth and recovery from damage (Si et al. 2020; Di Iorio et al. 2024).

Additionally, when facing simultaneous herbivory by both insect species, damaged plants that used a combined strategy of increasing leaf area and thickness and lowering belowground investment appeared to have an advantage. This approach may allow them to further balance their resource allocation between the aboveground and belowground organs, subsequently facilitating the capture of sufficient light resources to sustain aboveground growth and stolon expansion. The contrasting selection of leaf and/or root traits under different herbivory pressure is consistent with the third hypothesis, reflecting the complex interactions between various signaling pathways and defensive mechanisms in *H. verticillata*. This highlights the remarkable adaptability and tolerance of *H. verticillata* in diverse environments (Croy et al. 2020; Wise 2024).

Conclusions

The populations of *H. verticillata* demonstrated differential tolerance strategies in response to native and introduced herbivores. Plasticity of leaf and root traits in *H. verticillata* under herbivory pressure allowed damaged plants to compensate for the loss of biomass and resources caused by herbivory. By increasing leaf area and leaf thickness, *H. verticillata* may enhance its photosynthetic capacity and light capture efficiency to support growth and recovery from damage. Simultaneously, biomass allocation tradeoff between aboveground and

belowground organs may also help damaged plants ensure sufficient resources to sustain growth and reproduction. These coordinated responses in trait plasticity and biomass allocation potentially allowed *H. verticillata* to achieve higher fitness under herbivory pressure, facilitating its invasion in China. It is worth pointing out that while our greenhouse study provided valuable information on the invasion mechanism of *H. verticillata*, it could not fully replicate field conditions and natural herbivore pressure. We acknowledge that field experiments can be conducted to validate our findings under natural herbivory conditions, which is a challenge but helps improve our confidence in understanding of plant invasion dynamics in China.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-024-00560-2.

Additional file 1.

Acknowledgements
This work is supported by the National Natural Science Foundation of China (Grant Nos. 31500331, 32071527).

Author contributions
Conceptualization: BCD and FHY; methodology: BCD, FHY, and QYF; experiments conducted & data collection: BCD, QYF, and YC; data analysis: BCD, QYF, GWW and MZW; writing-original draft preparation: QYF; writing-review & editing: BCD, FHY, QYF, GWW, MZW, YC; supervision: BCD.

Funding
This work is supported by the National Natural Science Foundation of China (Grant Nos. 31500331, 32071527).

Availability of data and materials
The datasets used and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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Received: 9 July 2024 Accepted: 11 October 2024
Published online: 23 October 2024

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