Nutrient Enrichment Enhances Growth and Competitive Ability of Invasive Giant Ragweed (Ambrosia trifida) Populations Postprint

Authors: Wei Chunqiang, Tang Saichun, Li Xiangqin, Pan Yumei

Date: 2022-02-14T21:21:03+00:00

Abstract

Understanding the effects of nutrient enrichment on the growth and competition of invasive plants, as well as the differential responses of different invasive populations to nutrient variation, is crucial for predicting invasion risk. To investigate the invasion risk of Bidens frondosa, this study employed a common garden experiment to examine the growth and competitive responses of four invasive populations from Hebei, Jiangsu, Jiangxi, and Guangxi under different nutrient levels, both in monoculture and in mixed planting with the closely related native plant Bidens biternata. The results showed that: (1) In monoculture, plant height, branch number, and total biomass of the four populations were significantly higher under high nutrient conditions than under low nutrient conditions, while reproductive ratio was significantly higher under low nutrient conditions than under high nutrient conditions (except for the Jiangsu population); in mixed planting, the competitive responses of all growth parameters for the four populations were smaller under high nutrient conditions than under low nutrient conditions. (2) Under all nutrient levels, plant height and total biomass of Guangxi and Jiangxi populations were significantly higher than those of the Hebei population, the Guangxi population exhibited the highest branch number (12\$±0.86, 16.83±0.95, *and*21.83±1.14*underlow*, *medium*, *andhighnutrientconditions*, *respectively*); *thereprod* These results demonstrate that high nutrient conditions enhance the growth and competitive ability of B. frondosa; moreover, growth and competitive abilities vary among populations. Nutrient enrichment and gene flow among invasive populations may potentially increase the invasion risk of B. frondosa.

ChinaRxiv 中X

Full Text

Increased Nutrients Enhance the Growth and Competitive Ability of Invasive Populations of *Bidens frondosa*

WEI Chunqiang, TANG Saichun*, LI Xiangqin, PAN Yumei
Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain, Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, Guilin 541006, Guangxi, China

Abstract

Understanding how nutrient enrichment affects the growth and competitive ability of invasive plants, as well as how different invasive populations respond to nutrient changes, is crucial for predicting invasion risks. To assess the invasion potential of *Bidens frondosa*, we conducted a common garden experiment examining the growth and competitive responses of four invasive populations (from Hebei, Jiangsu, Jiangxi, and Guangxi) under different nutrient levels, both when grown alone and in competition with the native congener *B. biternata*. The results showed: (1) When grown alone, all four populations exhibited significantly greater plant height, branch number, and total biomass under high nutrient conditions compared to low nutrient conditions, while reproductive ratios were significantly higher under low nutrient conditions (except for the Jiangsu population). When in competition, the competitive responses of all growth parameters were lower under high nutrient conditions than under low nutrient conditions. (2) Across all nutrient levels, the Guangxi and Jiangxi populations showed significantly greater plant height and total biomass than the Hebei population. The Guangxi population produced the most branches (12 ± 0.86, 16.83 ± 0.95, and 21.83 ± 1.14 under low, medium, and high nutrient conditions, respectively). The Hebei population exhibited the highest reproductive ratios under both low [(47.33 ± 3.29)%] and high [(25.74 ± 2.82)%] nutrient conditions, significantly exceeding those of the Guangxi population [(30.92 ± 1.78)% under low nutrient and (19.77 ± 1.22)% under high nutrient]. Under medium nutrient conditions, the Hebei population' s competitive response for total biomass (-0.51 ± 0.04) was significantly greater than that of the Guangxi population (-0.35 ± 0.06), and its competitive response for reproductive biomass (-0.46 ± 0.03) was also significantly greater than that of the Guangxi population (-0.28 ± 0.07). These findings demonstrate that high nutrient availability enhances the growth and competitive ability of *B. frondosa*, with significant variation among populations. Nutrient enrichment and inter-population gene flow may potentially increase the invasion risk of this species.

Key words: *Bidens frondosa*, invasive population, growth, competitive response, nutrient

Introduction

Human activities have introduced numerous alien plant species to new regions, some of which have become invasive, competing with native plants and reducing local biodiversity (Powell et al., 2011; Power & Vilas, 2020). Understanding the invasiveness of alien plants and the factors influencing it is essential for predicting invasion risks and managing invasive species. Anthropogenic activities such as fertilization and wastewater discharge increase nutrient availability in habitats, affecting the growth, reproduction, and competitive dynamics of both invasive and native plants (Zhang et al., 2017; Wan et al., 2019; Wang et al., 2021), ultimately influencing invasion success (Huang et al., 2018). For instance, increased soil nitrogen enhances the competitive ability of invasive plants such as spotted knapweed (*Centaurea stoebe*), galinsoga (*Galinsoga quadriradiata*), and Canada goldenrod (*Solidago canadensis*) relative to native species (He et al., 2012; Liu et al., 2018; Wan et al., 2019), facilitating their successful establishment. However, other studies have found that nutrient enrichment can reduce the competitiveness of certain invasive plants like marsh pennywort (*Hydrocotyle vulgaris*) and increase the invasibility resistance of native communities (Liu et al., 2017). Therefore, investigating how nutrient enrichment affects the growth and competition of different invasive plants is critical for predicting their invasion risks.

Current research on nutrient effects has primarily focused on comparisons between invasive and native plants or between invasive populations and those from the native range (He et al., 2012; Liao et al., 2013; Wan et al., 2019), with less attention paid to variation among different invasive populations. Different invasive populations may exhibit distinct plastic responses to environmental conditions, and gene flow among these populations can increase genetic diversity, enabling invasive plants to evolve greater plasticity and colonize more diverse habitats and communities (Richards et al., 2006; Lavergne & Molofsky, 2007), thereby enhancing invasion risk. Furthermore, the competitive ability of invasive plants against natives can vary among populations (He et al., 2012). Understanding whether different populations show differential responses to environmental changes can inform strategies to prevent the evolution of enhanced invasiveness (Droste et al., 2010).

Bidens frondosa L. (Asteraceae), native to North America, has expanded its range considerably in China over the past decade, now occurring in 21 provinces including Hebei, Henan, Anhui, Beijing, Guangdong, and Guangxi (Ma, 2013). This invasive species exhibits several traits associated with invasiveness, including high reproductive biomass allocation (Zhou et al., 2012), strong allelopathic potential (Yan et al., 2012), high germination rates of heteromorphic achenes under suitable temperatures (Zhou et al., 2015), strong reproductive capacity (Yan et al., 2016), high competitive ability (Pan et al., 2016), and considerable phenotypic plasticity (Wei et al., 2017). *B. biternata*, a native congener, often co-occurs with *B. frondosa* in disturbed habitats such as cultivated fields, abandoned lands, roadsides, and paddy field margins that vary in nutrient availability (Pan et al., 2016). Because closely related species have similar resource requirements, competition between them is often intense (Balestri et al., 2018). However, how nutrient enrichment affects the growth and competition of *B. frondosa* invasive populations and whether responses differ among populations remain unclear.

This study selected four typical invasive populations of *B. frondosa* from Hebei, Jiangsu, Jiangxi, and Guangxi to examine their growth and competitive responses under different nutrient levels. We compared these populations when grown alone and in competition with the native congener *B. biternata* to address two questions: (1) Does nutrient enrichment enhance the growth and competitive ability of *B. frondosa* invasive populations? (2) Do invasive populations differ in their plastic responses of growth and competitive ability to nutrient variation? The findings will provide a basis for predicting invasion risk and developing management strategies for *B. frondosa*.

Materials and Methods

1.1 Study Site and Plant Materials The experiment was conducted in 2013 at the experimental site of Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, located in Yanshan Town, Yanshan District, Guilin City (25°04 49.6 N, 110°18 01.8 E, 170 m a.s.l.). The region has a mid-subtropical monsoon climate with an average annual temperature of 17.8 °C, average January temperature of 5.8 °C, average July temperature of 28 °C, and average annual precipitation of 1,949.5 mm.

Seeds of *B. frondosa* were collected in October 2012 from four locations along a latitudinal gradient representing the species' distribution in China: Guilin, Guangxi (25°51 34 N, 110°28 53 E, 390 m a.s.l.); Ji' an, Jiangxi (27°5 33 N, 115°1 4 E, 150 m a.s.l.); Wujiang, Jiangsu (30°56 34 N, 120°23 40 E, 2 m a.s.l.); and Baoding, Hebei (38°56 28 N, 115°57 45 E, 12 m a.s.l.). These were designated as the Guangxi, Jiangxi, Jiangsu, and Hebei populations, respectively. Seeds of the native competitor *B. biternata* were collected from Guilin, Guangxi.

1.2 Experimental Design On May 3, 2013, seeds from each *B. frondosa* population and the native *B. biternata* were sown separately in 10 plastic pots (23 cm inner diameter, 18 cm depth). After one and a half months, when seedlings reached approximately 15 cm in height, uniformly sized seedlings were selected and transplanted into plastic pots. Two planting patterns were established: monoculture (one plant per pot) and mixed culture (two plants per pot: one *B. frondosa* individual and one *B. biternata* individual). After 18 days of growth, when all plants had developed new roots, experimental treatments commenced.

The nutrient source was a compound fertilizer "Shifengyuan" (potassium sulfate type) with an N:P:K ratio of 15:15:15, purchased commercially. Three nutrient levels were established: high, medium, and low. Following Liao et al. (2013), the high nutrient treatment consisted of 4 g of compound fertilizer per pot; the medium nutrient treatment received 2 g per pot, applied in two doses with a 10-day interval; and the low nutrient treatment received no fertilizer. Throughout the experiment, plants were watered daily to ensure adequate moisture. Each treatment had six replicates, totaling 144 pots (4 populations × 2 planting patterns × 3 nutrient treatments × 6 replicates).

1.3 Measurements and Calculations On September 20, 2013, at the peak flowering stage of *B. frondosa*, plant height and branch number were measured for each individual. Plants were then harvested and separated into roots, stems, leaves, and capitula. These parts were placed in marked bags and oven-dried at 80 °C to constant weight to determine dry mass (g). Total biomass was calculated as the sum of root, stem, leaf, and capitulum dry mass. Reproductive ratio was calculated as capitulum dry mass divided by total biomass.

In mixed cultures, the competitive ability of *B. frondosa* was assessed through competitive responses of plant height, branch number, total biomass, and reproductive biomass. Competitive response indices were calculated following Armas et al. (2004). For example, competitive response of total biomass = (biomass in mixed culture - biomass in monoculture) / (biomass in mixed culture + biomass in monoculture). The index ranges from -1 to 1, where more negative values indicate stronger competitive response (greater suppression) and more positive values indicate weaker competitive response (less suppression).

1.4 Statistical Analysis All statistical analyses were performed using SPSS 18.0 software. One-way ANOVA was used to analyze differences in growth and competitive responses among nutrient levels within each population and among populations within each nutrient level. Two-way ANOVA was used to examine the effects of population, nutrient level, and their interactions on growth and competitive response parameters. The significance level for all tests was set at $P < 0.05$.

Results

2.1 Growth Responses of Different *B. frondosa* Populations to Nutrients Two-way ANOVA revealed that both population and nutrient level had significant effects on all growth parameters (plant height, branch number, total biomass, and reproductive ratio). Additionally, the population × nutrient interaction significantly affected total biomass and reproductive ratio (Table 1).

When grown alone, all populations showed significantly greater plant height, branch number, and total biomass under high nutrient conditions compared to low nutrient conditions ($P < 0.05$) (Fig. 1: a-c). Across all nutrient levels, the Guangxi and Jiangxi populations were tallest, followed by the Jiangsu population, with the Hebei population being shortest (Fig. 1: a). The Guangxi population produced the most branches (12 ± 0.86, 16.83 ± 0.95, and 21.83 ± 1.14 under low, medium, and high nutrient conditions, respectively), significantly more than the other three populations at each nutrient level (P <

0.05) (Fig. 1: b). The Guangxi and Jiangxi populations exhibited significantly greater biomass than the Hebei population, and under high nutrient conditions, also exceeded the Jiangsu population ($P < 0.05$) (Fig. 1: c).

All four populations maintained high reproductive ratios across nutrient levels (ranging from 19.77% to 47.33%). Except for the Jiangsu population, the Guangxi, Jiangxi, and Hebei populations showed significantly higher reproductive ratios under low nutrient conditions compared to medium and high nutrient conditions ($P < 0.05$) (Fig. 1: d). Under low nutrient conditions, the Hebei population had the highest reproductive ratio [(47.33 ± 3.29)%], significantly greater than the other three populations ($P < 0.05$). Under medium nutrient conditions, no significant differences in reproductive ratio were observed among populations ($P > 0.05$). Under high nutrient conditions, the Hebei population again showed the highest reproductive ratio [(25.74 ± 2.82)%], significantly exceeding that of the Guangxi population [(19.77 ± 1.22)%] ($P < 0.05$) (Fig. 1: d).

Table 1 Effects of population, nutrient, and their interaction on the growth and competitive response of *Bidens frondosa* (F-value)

Variable	Population (P)	Nutrient (N)	Population × Nutrient (P×N)
Plant height	66.46***	214.85***	2.32*
Branch number	33.25***	42.93***	2.89*
Total biomass	15.88***	234.69***	5.78**
Reproductive ratio	27.30***	24.66***	12.97***
Competitive response of plant height	34.55***	5.78**	2.81*
Competitive response of branch number	2.96*	2.96*	2.96*
Competitive response of total biomass	2.96*	2.96*	2.96*

Variable	Population (P)	Nutrient (N)	Population × Nutrient (P×N)
Competitive response of reproductive biomass	2.96*	2.96*	2.96*

Note: * indicates significant differences (*0.01 < P < 0.05,* ***0.001 < P < 0.01,*** P < 0.001)

Figure 1 Effects of nutrient on the growth of invasive populations of *Bidens frondosa*. Data are means ± SE. Different capital letters indicate significant differences among nutrient levels for the same population, and different lowercase letters indicate significant differences among populations at the same nutrient level, P < 0.05. The same below.

2.2 Competitive Responses of Different *B. frondosa* Populations to Nutrients When grown in competition with the native congener, two-way ANOVA indicated that population had no significant effect on competitive responses of plant height and branch number, but significantly affected competitive responses of total biomass and reproductive biomass. Nutrient level significantly affected competitive responses of all parameters (Table 1).

No significant differences were observed among populations in competitive responses of plant height or branch number (P > 0.05) (Fig. 2: a-b). However, under medium nutrient conditions, the Hebei population showed significantly greater competitive responses for total biomass (-0.51 ± 0.04) and reproductive biomass (-0.46 ± 0.03) compared to the Guangxi population (-0.35 ± 0.06 and -0.28 ± 0.07, respectively) (P < 0.05). No other significant differences among populations were detected for these parameters at other nutrient levels (P > 0.05) (Fig. 2: c-d).

The competitive response of plant height for the Guangxi and Jiangsu populations was significantly lower under high nutrient conditions than under low nutrient conditions (P < 0.05), while the Jiangxi and Hebei populations showed no significant differences across nutrient levels (P > 0.05) (Fig. 2: a). The Guangxi population exhibited no significant differences in branch number competitive response across nutrient levels (P > 0.05), whereas the other three populations showed significantly lower competitive responses under high nutrient conditions compared to low nutrient conditions (P < 0.05) (Fig. 2: b). All four populations demonstrated significantly lower competitive responses for total biomass and reproductive biomass under high nutrient conditions compared to low nutrient conditions (P < 0.05) (Fig. 2: c-d), indicating reduced competitive suppression and enhanced competitive ability under high nutrient availability.

Figure 2 Effects of nutrient on the competitive response of invasive populations of *Bidens frondosa*

Discussion

3.1 Growth and Competitive Responses of *B. frondosa* Populations to Nutrients Nutrient enrichment generally facilitates plant invasion (Huang et al., 2016; Nackley et al., 2017). Our study found that increased nutrient availability enhanced plant height, branch number, and total biomass across all four invasive populations of *B. frondosa*. This response likely reflects the species' high phenotypic plasticity (Wei et al., 2017), enabling it to maximize fitness in resource-rich environments (Dawson et al., 2012). Additionally, *B. frondosa* possesses traits associated with high resource capture and utilization efficiency, including high specific leaf area, high net photosynthetic rate, and high relative growth rate (Pan et al., 2017), allowing rapid growth and biomass accumulation under favorable conditions and thereby enhancing competitive ability. These results align with findings for congeneric invasive species *B. pilosa* and *B. alba* (Liu et al., 2012).

Plant height, branch number, and total biomass represent key indicators of growth status and competitive ability. Greater height and more branches enable invasive plants to avoid shading, capture more light, and shade neighboring plants, suppressing their growth (Wang & Feng, 2005; Gupta & Narayan, 2012). Taller plants also enjoy reproductive advantages, typically producing more seeds (Annapurna & Singh, 2003).

Biomass is a critical parameter characterizing plant invasiveness (Hwang & Lauenroth, 2008), as plants with higher biomass generally exhibit stronger reproductive capacity and greater fitness (Droste et al., 2010). If an alien plant can produce high biomass in a particular habitat, it indicates high invasiveness in that environment (Wang et al., 2010). In our study, total biomass of all four *B. frondosa* populations was significantly higher under high nutrient conditions than under low nutrient conditions, consistent with the performance of *B. pilosa* and *B. alba* (Liu et al., 2012). This suggests that high nutrient availability strongly favors biomass accumulation in invasive *Bidens* species.

The reproductive ratios of *B. frondosa* populations were consistently high across nutrient levels (19.77%–47.33%), similar to field observations by Zhou et al. (2012) and exceeding those reported for the invasive aster *Parthenium hysterophorus* (10.6%–21.6%) (Tang et al., 2012). Moreover, reproductive ratios were significantly higher under low nutrient conditions than under high nutrient conditions, indicating that *B. frondosa* not only invests heavily in reproductive structures but can also increase reproductive allocation in unfavorable environments to ensure adequate seed production. Zhou et al. (2015) reported that *B. frondosa* achenes have high germination rates exceeding 90%, leading to high seedling densities. High plant density enhances the probability of establishment, spread, and invasion in new areas (Gupta & Narayan, 2012).

In competition with the native congener *B. biternata*, competitive responses of plant height, branch number, total biomass, and reproductive biomass were all lower under high nutrient conditions than under low nutrient conditions. This reduced competitive suppression under high nutrient availability demonstrates that nutrient enrichment favors *B. frondosa* in competitive interactions. This advantage likely stems from the species' high resource capture and utilization efficiency, combined with significant improvements in height, branching, and biomass under high nutrient conditions, which collectively enhance competitive ability. Wei et al. (2016) similarly found that nutrient addition increased the competitive ability of *B. frondosa* against the native congener *B. tripartita*, possibly due to its high phenotypic plasticity enabling enhanced growth and competition in nutrient-rich habitats. Elevated nutrients have also been shown to increase competitive ability in other invasive plants such as spotted knapweed, galinsoga, and Canada goldenrod (He et al., 2012; Liu et al., 2018; Wan et al., 2019).

3.2 Variation in Growth and Competition Among *B. frondosa* Populations Our results revealed significant variation among populations: the Guangxi and Jiangxi populations showed the greatest height and biomass across all nutrient levels, while the Hebei population had the lowest; the Guangxi population produced significantly more branches than the other three populations; the Hebei population exhibited the highest reproductive ratio under low nutrient conditions and significantly higher ratios than the Guangxi population under high nutrient conditions; and under medium nutrient conditions, the Hebei population showed significantly greater competitive responses for total and reproductive biomass than the Guangxi population. These findings indicate that plastic responses of growth and competition to nutrient variation differ among the four invasive populations. Such variation may reflect different rapid adaptive responses to local invasion environments or genetic differentiation among populations. Differential plastic responses among invasive populations can enable the evolution of greater plasticity, allowing invasion of more diverse habitats and communities (Richards et al., 2006; Lavergne & Molofsky, 2007). For example, invasive populations of Japanese stiltgrass (*Microstegium vimineum*) in southern Indiana showed variation in plastic responses to light and moisture, suggesting potential for evolving greater invasiveness (Droste et al., 2010). Similarly, Luo et al. (2019) found that different invasive populations of *Plantago virginica* exhibited varying plastic responses to nitrogen. The observed variation in plastic responses to nutrients among *B. frondosa* populations suggests that gene flow among populations could increase genetic diversity and evolutionary potential, potentially leading to enhanced invasiveness.

In conclusion, nutrient enrichment enhances the growth and competitive ability of invasive *B. frondosa* populations, with high nutrient conditions particularly favoring invasion. *B. frondosa* exhibits ruderal characteristics: it thrives in disturbed, nutrient-rich habitats, possesses high reproductive capacity and growth rates, and can increase reproductive allocation under low nutrient conditions to ensure seed production (Grime, 1979). Moreover, variation in growth and competitive responses to nutrients among populations suggests that hybridization could potentially lead to the evolution of greater invasiveness. Management of *B. frondosa* should focus not only on monitoring highly disturbed, nutrient-rich habitats but also on preventing inter-regional population dispersal to avoid gene flow that could enhance evolutionary potential and invasiveness. These findings provide important insights for predicting invasion risk and developing management strategies for this species.

References

ANNAPURNA C, SINGH JS, 2003. Variation of *Parthenium hysterophorus* in response to soil quality: implications for invasiveness [J]. Weed Res, 43(3): 190-198.

ARMAS C, ORDIALES R, PUGNAIRE FI, 2004. Measuring plant interactions: a new comparative index [J]. Ecology, 85(10): 2682-2686.

BALESTRI E, VALLERINI F, MENICAGLI V, et al., 2018. Biotic resistance and vegetative propagule pressure co-regulate the invasion success of a marine clonal macrophyte [J]. Sci Rep, 8(1): 16621.

DAWSON W, ROHR RP, VAN KLEUNEN M, et al., 2012. Alien plant species with a wider global distribution are better able to capitalize on increased resource availability [J]. New Phytol, 194(3): 859-867.

DROSTE T, FLORY SL, CLAY K, 2010. Variation for phenotypic plasticity among populations of an invasive exotic grass [J]. Plant Ecol, 207(2): 297-306.

GRIME JP, 1979. Plant strategies and vegetation processes [M]. New York: John Wiley & Sons.

GUPTA S, NARAYAN R, 2012. Phenotypic plasticity of *Chenopodium murale* across contrasting habitat conditions in peri-urban areas in Indian dry tropics: Is it indicative of its invasiveness [J]? Plant Ecol, 213(3): 493-503.

HE WM, MONTESINOS D, THELEN G, et al., 2012. Growth and competitive effects of *Centaurea stoebe* populations in response to simulated nitrogen deposition [J]. PLoS ONE, 7(4): e36257.

HUANG QQ, FAN ZW, LI XX, et al., 2018. Effects of nutrient addition and clipping on biomass production of invasive and native annual Asteraceae plants [J]. Weed Res, 58(4): 318-326.

HUANG QQ, SHEN YD, LI XX, et al., 2016. Invasive *Eupatorium catarium* and *Ageratum conyzoides* benefit more than does a common native plant from nutrient addition in both competitive and non-competitive environments [J]. Ecol Res, 31(1): 145-152.

HWANG BC, LAUENROTH WK, 2008. Effect of nitrogen, water and neighbor density on the growth of *Hesperis matronalis* and two native perennials [J]. Biol

Invasions, 10(5): 771-779.

LAVERGNE S, MOLOFSKY J, 2007. Increased genetic variation and evolutionary potential drive the success of an invasive grass [J]. PNAS, 104(10): 3883-3888.

LIAO ZY, ZHANG R, BARCLAY GF, et al., 2013. Difference in competitive ability between plants from nonnative and native populations of a tropical invader relates to adaptive responses in abiotic and biotic environments [J]. PLoS ONE, 8(8): e71767.

LIU G, YANG YB, ZHU ZH, 2018. Elevated nitrogen allows the weak invasive plant *Galinsoga quadriradiata* to become more vigorous with respect to inter-specific competition [J]. Sci Rep, 8: 3136.

LIU L, QUAN H, DONG BC, et al., 2017. Nutrient enrichment alters impacts of *Hydrocotyle vulgaris* invasion on native plant communities [J]. Sci Rep, 6(1): 39468.

LIU MC, WEI CQ, TANG SC, et al., 2012. Bionomics of two invasive weeds, *Bidens alba* and *B. pilosa*, and their native congeners grown at different nutrient levels [J]. J Biosafety, 21(1): 32-40.

LUO X, XU XY, ZHENG Y, et al., 2019. The role of phenotypic plasticity and rapid adaptation in determining invasion success of *Plantago virginica* [J]. Biol Invasions, 21(8): 2679-2692.

MA JS, 2013. The checklist of the Chinese invasive plants [M]. Beijing: Higher Education Press.

NACKLEY L, HOUGH SN, KIM SH, 2017. Competitive traits of the invasive grass *Arundo donax* are enhanced by carbon dioxide and nitrogen enrichment [J]. Weed Res, 57(2): 67-71.

PAN YM, TANG SC, WEI CQ, et al., 2016. Effects of global risks-nitrogen additions on growth and competitive relations among invasive and native congeneric species—*Bidens frondosa* [J]. Pol J Ecol, 64(4): 443-52.

PAN YM, TANG SC, WEI CQ, et al., 2017. Growth and photosynthetic responses of invasive *Bidens frondosa* to light and water availability: A comparison with invasive and native congeners [J]. Weed Biol Manag, 17(1): 36-44.

POWELL KI, CHASE JM, KNIGHT TM, 2011. A synthesis of plant invasion effects on biodiversity across spatial scales [J]. Am J Bot, 98(3): 539-548.

POWER G, VILAS JS, 2020. Competition between the invasive *Impatiens glandulifer* and UK native species: the role of soil conditioning and pre-existing resident communities [J]. Biol Invasions, 22(4): 1527-1537.

RICHARDS CL, BOSSDORF O, MUTH NZ, et al., 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions [J]. Ecol Lett, 9(8): 981-993.

TANG SC, WEI CQ, PAN YM, et al., 2010. Reproductive adaptability of the invasive weed *Parthenium hysterophorus* L. under different nitrogen and phosphorus levels [J]. J Wuhan Bot Res, 28(2): 213-217.

WAN LY, QI SS, XOU CB, et al., 2019. Elevated nitrogen deposition may advance invasive weed, *Solidago canadensis*, in calcareous soils [J]. J Plant Ecol, 12(5): 846-856.

WANG K, YANG J, CHEN JK, 2010. Comparison of morphological traits between alligator weed and two congeners under different water and nutrient conditions [J]. Biodivers Sci, 18(6): 615-621.

WANG ML, FENG YL, 2005. Effects of soil nitrogen levels on morphological, biomass allocation and photosynthesis in *Ageratina adenophora* and *Chromoleana odorata* [J]. Acta Phytoecol Sin, 29(5): 697-705.

WANG Y, WANG WQ, WANG QK, et al., 2021. Effects of soil nutrients on reproductive traits of invasive and native annual Asteraceae plants [J]. Biodivers Sci, 29(1): 1-9.

WEI CQ, TANG SC, PAN YM, et al., 2016. Effects of nutrient on competition between invasive species *Bidens frondosa* and native congener *B. tripartita* [J]. J Trop Subtrop Bot, 24(6): 609-616.

WEI CQ, TANG SC, PAN YM, et al., 2017. Plastic responses of invasive *Bidens frondosa* to water and nitrogen addition [J]. Nordic J Bot, 35(2): 232-239.

YAN XH, ZENG JJ, ZHOU B, et al, 2012. Allelopathic potential of the extracts from alien invasive plant *Bidens frondosa* [J]. J Yangzhou Univ (Agric Life Sci Ed), 33(2): 88-94.

YAN XH, ZHOU B, YIN ZF, et al. 2016. Reproductive biological characteristics potentially contributed to invasiveness in an alien invasive plant *Bidens frondosa* [J]. Plant Spec Biol, 31(2): 107-116.

ZHANG HJ, CHANG RY, Guo X, et al., 2017. Shifts in growth and competitive dominance of the invasive plant *Alternanthera philoxeroides* under different nitrogen and phosphorus supply [J]. Envir Exper Bot, 135: 118-125.

ZHOU B, YAN XH, XIAO YA, et al., 2012. Module biomass structure traits of the alien invasive *Bidens frondosa* population [J]. Guihaia, 32(5): 650-655.

ZHOU CQ, TANG SC, PAN YM, et al., 2015. Effects of light and temperature on germination of heteromorphic achenes of *Bidens frondosa* L. [J]. J Trop Subtrop Bot, 23(6): 662-668.

Note: Figure translations are in progress. See original paper for figures.