

Original Research

Leaf Morphology and Ecological Stoichiometry of C, N and P in Dioecious Invasive *Amaranthus palmeri*

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Abstract

Amaranthus palmeri is a dioecious invasive weed, which poses a great threat to agricultural production and biodiversity protection in China. Although many studies have explored the invasiveness of invasive alien plant species from the perspective of resource utilization efficiency, surprisingly few studies have investigated the sex-related traits in invasive alien plant species. In our study, four different types of *A. palmeri* were selected to investigate the leaf morphology, allometric growth patterns and ecological stoichiometry of carbon (C), nitrogen (N) and phosphorus (P) between male and female, which typical invaded regions in Jizhou District (JZ), Baodi District (BD), Xiqing District (XQ) and Jinghai District (JH) in Tianjin. Results demonstrated that the leaf width (LW), leaf length (LL), leaf area (LA) and specific leaf area (SLA) of the male plant were generally significantly higher than those of the female plants. Compared with the female plants, the traits of the male plants were closely sex-related and had an allometric growth relationship. The leaf N content (N_{mass}) and P content (P_{mass}) of *A. palmeri* were higher than the average of Chinese terrestrial plants, while the leaf carbon-nitrogen ratio (C/N) and carbon-phosphorus ratio (C/P) of *A. palmeri* were lower than the average of global terrestrial plants. It is concluded that *A. palmeri* may have different ecological response strategies, which can adapt to the habitats to achieve a successful invasion by optimizing the resource allocation and utilization efficiency between male and female plants.

Keywords: invasive alien plant species, dioecious, ecological stoichiometry, *Amaranthus palmeri*

Introduction

With the rapid development of economic globalization and modernization, the economic and

trade exchanges and economic integration continues to deepen, and invasive alien species around the world are increasing and the damage is aggravated [1]. According to IUCN (<https://www.iucn.org/theme/species/our-work/invasive-species>), the invasive alien species are defined as: “the species that are introduced, accidentally or intentionally, outside of their natural geographic range and that become problematic.” Invasive alien plant

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species (IAPS), with the human activity, cross their native habitats and invade multiple ecosystems around the world, posing a major threat to local biodiversity, social economy and human health [2]. IAPS have the potential to make a tremendous impact on global agriculture, which continues to influence food security worldwide [3-4]. Exploring the invasion mechanism of successful IAPS has become an important issue in the field of ecology and evolution, and it is also a prerequisite for effective prevention and control of invasive plants [5].

The ability of IAPS to colonize and expand in new habitats may depend on the availability of resources in the environment, the utilization rate of plants and the demand for resources [6]. The nutrient resource utilization strategies are vital to successful establishment and aggravation of IAPS [7]. Successful invaders usually have strong competitiveness, reproductive ability and adaptability in new habitats [8]. After IAPS to new habitats, they will theoretically have higher indicators of plant growth and reproductive input, such as higher specific leaf area, nutrient element content (N, P, K), resource utilization efficiency and photosynthetic rate. The C, N and P ecological stoichiometry in plants can reflect the nutrient utilization efficiency of plants [9], limited conditions [10] and growth rate [11]. Among them, N and P are the main limiting elements for the growth and distribution of terrestrial plants [11]. The leaf C/N and C/P reflect the growth rate of plants and the utilization efficiency of N and P [9]. The leaf N/P can be used to diagnose N and P nutrient limitation in plant growing environment [12]. Studies on ecological chemometrics of IAPS have found that IAPS not only have strong absorption capacity of N and enrichment capacity of P [6, 13], but also have fast growth rate and stronger ability to store assimilation products [14]. Therefore, studying the invasiveness of IAPS from the perspective of ecological stoichiometry could attribute to underlying the ecological response strategies in different environment condition [14].

In recent years, the trend of the spread and outbreak of alien organisms has become more and more obvious in China. In order to prevent the IAPS from further aggravating, the State Environmental Protection Administration has successively published a list of four batches of IAPS in China, among which Asteraceae (42.5%), Poaceae (15%), and Amaranthaceae (12.5%) occupy the top three of the list (http://www.mee.gov.cn/gkml/hbb/bgg/201612/t20161226_373636.htm). *Amaranthus palmeri* (*A. palmeri*), a dioecious annual weed of the family Amaranthaceae, is native to the southwestern United States to northern Mexico, and then invaded all over the world. It is now widely distributed among Europe, Oceania and Asia [15]. *A. palmeri* is one of the main agricultural weeds in America, which could lead to the letdown of crop yield by 63~91% [16]. In China, *A. palmeri* was first discovered in Fanzhuangzi Village, Fengtai District, Beijing. In recent years, it has been reported in

Beijing, Tianjin, Shandong, Jiangsu and other regions. *A. palmeri* grows rapidly, has strong adaptability and high reproduction ability, which can grow on farmlands [17], garbage dumps, roadsides [18], abandoned lands, in deserts [19] and river beds [20]. Moreover, *A. palmeri* has evolved resistance to multiple herbicidal modes of action [21], which poses a great threat to agricultural production and biodiversity protection in invaded areas.

Previous studies on ecological chemometrics of IAPS mainly focused on monoecious species, but less attention has been paid to the sex level of plants. As a dioecious IAPS, *A. palmeri* provides a good model to explore the adaptive response of plants at the sex level. In this study, male and female plants from four heavily invaded areas of *A. palmeri* were selected as the research objects. Through a combination of field investigation and laboratory analysis, the leaf morphology, allometric growth pattern, functional traits and nutrient element characteristics of male and female plants were analyzed. This study aims to explore and answer the following questions: (1) To analyze the relationship between the invasion of *A. palmeri* and leaf related traits. (2) Whether the related traits of *A. palmeri* leaves are different between sexes or not. (3) *A. palmeri*, as a dioecious invasive plant, whether there are different survival adaptation strategies between male and female during the invasion process or not.

Material and Methods

Study Sites

Four different types of *A. palmeri* typical invaded regions in Jizhou District (JZ), Baodi District (BD), Xiqing District (XQ), and Jinghai District (JH) of Tianjin were selected as sampling sites (Table 1).

Sample Design and Data Collection

From August to September 2019, heavily invaded areas with coverage more than 60% of *A. palmeri* were selected as the study sites in above mentioned regions, which covered most of the invasive habitat types of *A. palmeri*. The major accompanying species of *A. palmeri* are *Eleusine indica*, *Setaria viridis*, *Bidens maximowicziana*, *Humulus scandens*, *Chenopodium album* and *Pharbitis purpurea*, etc. Five quadrats (1 m × 1 m) were randomly selected in each site to record the number of female and male plants of *A. palmeri* and determine the plant height. 5-15 female and male plants of *A. palmeri* with relatively consistent growth were selected in each quadrat, and fully extended, disease-free and complete mature leaves were randomly selected. All samples were put into envelopes and immediately brought back to the laboratory for further analysis.

Table 1. Description of the four study sites. Notes: JZ, Jizhou District; BD, Baodi District; XQ, Xiqing District; JH, Jinghai District.

Plots	Latitude and Longitude	Habitat	Annual temperature	Annual Precipitation	Frost-free Period	Soil type
JZ	40°1'20"N, 117°23'27"E	Railroad	11.5°C	678.6 mm	195 d	Cinnamon soil
BD	39°24'52"N, 117°26'7"E	Farmland	11.6°C	612.5 mm	184 d	Fluvo-aquic soil
XQ	39°9'49"N, 116°57'12"E	Wasteland	11.6°C	586.1 mm	203 d	Fluvo-aquic soil
JH	38°54'21"N, 117°1'54"E	River bank	11.8°C	566.7 mm	193 d	Fluvo-aquic soil

Leaf area measuring instrument (YMJ-B, Zhejiang Top Instrument Co., Zhejiang, China) was used to measure leaf length (LL), leaf width (LW) and leaf area (LA) of the leaves. Then the leaves were dried at 55°C to the constant weight, and the leaf dry weight (LDW) of the leaves were determined. The dried leaves were ground using an automatic sample rapid grinding machine (JXFSTPRP-24, Jingxin, China), and then passed through a 100-mesh sieve. Leaf nitrogen (N_{mass}) and carbon (C_{mass}) contents were determined by a Vario MICRO cube elemental analyzer (Elementar, Germany). Leaf phosphorus (P_{mass}) content was determined by Mo-Sb spectrophotometers.

$$\text{Specific leaf area (SLA, cm}^2\cdot\text{mg}^{-1}) = \text{LA/LDW}$$

Data Analysis

The data were preliminarily processed by Excel 2016, and the analysis of variance and correlation test were performed by SPSS 22.0, and the figures were created in SigmaPlot 14, and the statistical data were expressed as mean and standard error. The difference between male and female plant traits were tested by independent-samples t test, and the Pearson correlation analysis was analyzed on leaf traits. The significance test level was $P < 0.05$.

The growth relationships between LL, LW, LA, and SLA were described by the classic allometric equation $Y = \beta X^\alpha$. After logarithmic transformation, each variable was expressed as a linear regression equation: $\log Y = \log \beta + \alpha \log X$, where X and Y represented different leaf traits, $\log \beta$ was the intercept of the equation, and α was the slope of the equation, that was, allometric growth index. If $\alpha = 1$ (approximately equal), indicates that the traits grow at the same rate, and if $\alpha \neq 1$ (significant deviation), it means that there is allometric growth among the traits. The data mainly used the standardized major axis (SMA) regressions analysis to calculate the slope α of the allometric growth equation, and compare the slopes of each group and the difference between each slope and 1. If regression slopes were found to be homogenous then a common slope was fitted, and the WALD statistic was used to test for

the significance of the differences in trait values along the common regression slope and shifts in intercepts of SMA regression slopes. All data were performed using the software (S) MATR Version 2.0.

Results and Discussion

The Leaf Morphological Characteristics of Male and Female Plants of *A. palmeri*

There were significant gender differences in the leaf morphology of male and female plants of the four regions (Fig. 1). The LW, LA and SLA of male plants were significantly higher than those of female plants ($P < 0.05$, Fig. 1a, b, d). The LL of male plants of JZ and JH were significantly higher than female plants ($P < 0.05$, Fig. 1b), and there was no significant difference in LL between male and female plants of BD and XQ ($P > 0.05$, Fig. 1b). Among them, the LW, LA and the SLA of the male plants of the four sampling sites were all higher than that of female plants. The results indicated a certain difference in leaf morphology between male and female plants.

The Allometric Relationships of Leaf Traits between the Male and Female Plants of *A. palmeri*

All leaf traits were positively correlated: except the correlation between SLA and LW, LL and LA of female plants were not significant ($P > 0.05$, Table 2), most paired trait combinations had significant allometric relationship with R^2 values ranging from 0.500 to 0.884 ($P < 0.05$). Among them, the SMA slopes of LW and LL, SLA and LA were 1.157 to 1.271, significantly greater than 1, and the SMA slopes of other pairwise traits were 0.500 to 0.739, which were all less than 1, and reached a very significant level ($P < 0.01$). SMA slopes between male and female leaf pairwise traits of *A. palmeri* were found to be homogeneous ($P > 0.05$, Fig. 2 a, b, c). Common regression slopes were then fitted and tested whether there was a shift in elevation of the slope for each pairwise trait relationship. There

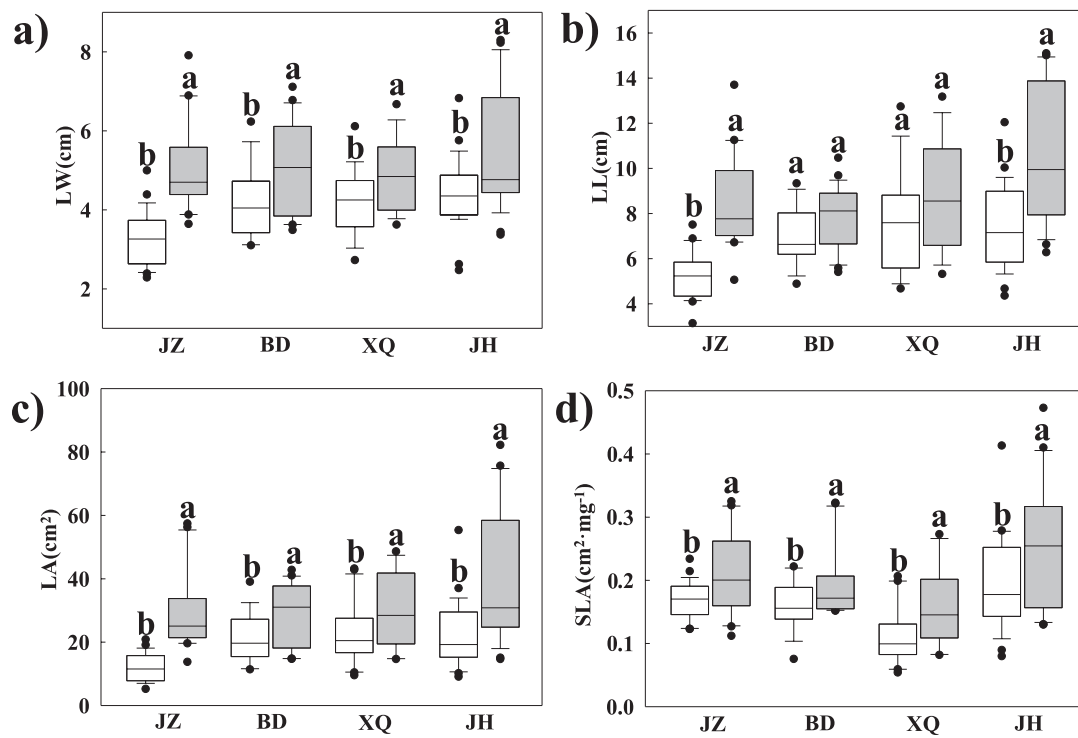


Fig. 1. The leaf morphology characteristics between male (grey boxes) and female (white boxes) of *A. palmeri* in different regions. Notes: different letters indicate significant difference between male and female plants (independent-sample t test), the same below. LW, leaf width; LL, leaf length; LW, leaf width; SLA, specific leaf area.

was no significant difference in elevation of the common slope between male and female leaf pairwise traits ($P > 0.05$), but there were significant shifts along the common fitted slope ($P < 0.01$).

The Resource Utilization Efficiency of Male and Female Plants of *A. palmeri*

The leaf N_{mass} and P_{mass} of the male plants of JZ and XQ were significantly higher than that of the female

Table 2. Standardized major axis regression analyses for leaf traits of male and female *A. palmeri*.

Trait (y-x)	Sex	R ²	Slope	Intercept	Slope Homogeneity (P)	Shift in Elevation (P)	Shift along slope (P)	Test of isometry	
								F	P
lgLL-lgLW	Female	0.620**	1.162	0.126	0.913	0.933	<0.001**	5.319	0.023*
	Male	0.546**	1.175	0.117				4.930	0.029*
lgLW-lgLA	Female	0.884**	0.500	-0.029	0.444	0.241	<0.001**	431.188	0.000**
	Male	0.876**	0.522	-0.066				333.513	0.000**
lgLL-lgLA	Female	0.860**	0.581	0.093	0.355	0.256	<0.001**	205.409	0.000**
	Male	0.827**	0.614	0.040				126.884	0.000**
lgLW-lgSLA	Female	0.016 ^{ns}	NA	NA	NA	NA	NA	NA	NA
	Male	0.500**	0.604	1.130				46.987	0.000**
lgLL-lgSLA	Female	0.028 ^{ns}	NA	NA	NA	NA	NA	NA	NA
	Male	0.573**	0.710	1.445				24.306	0.000**
lgLA-lgSLA	Female	0.018 ^{ns}	NA	NA	NA	NA	NA	NA	NA
	Male	0.614**	1.157	2.291				4.723	0.033**

Notes: NA indicates that there were insufficient significant correlations between the traits among male and female to justify analysis. ns indicates $P > 0.05$, * indicates $P < 0.05$, ** indicates $P < 0.01$, the same below.

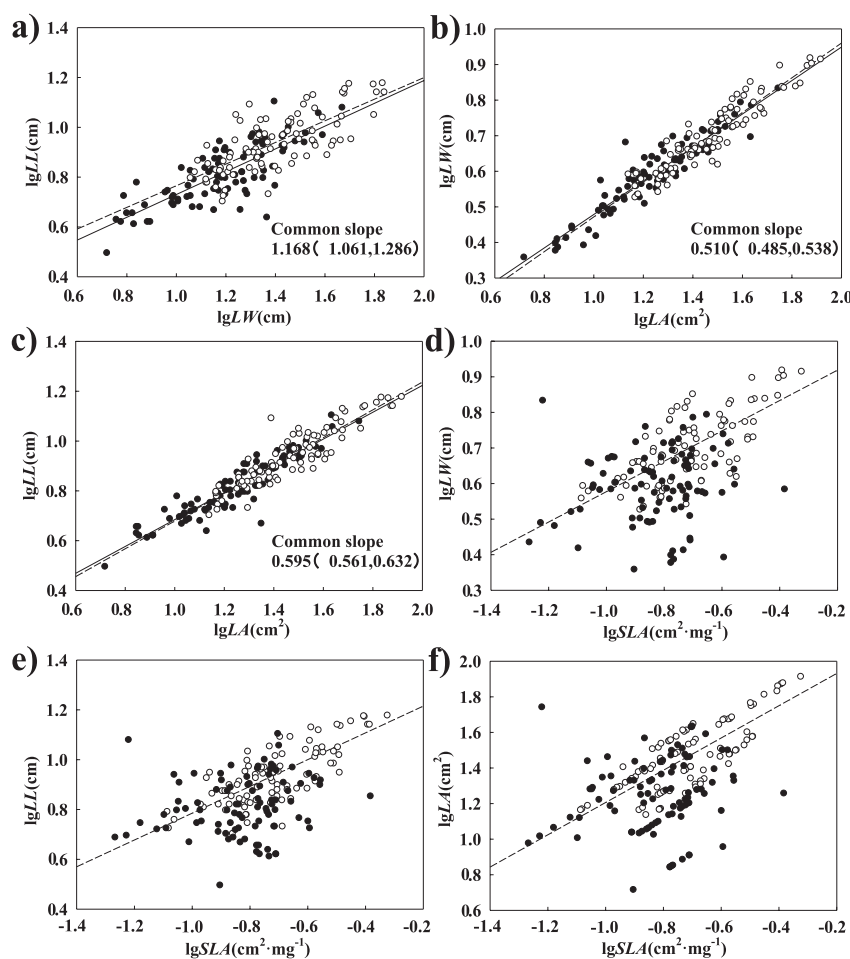


Fig. 2. Standardized major axis regression relationships for leaf traits of male (open circle, dashed line) and female (closed circle, solid line) *A. palmeri*. Notes: LW, leaf width; LL, leaf length; LW, leaf width; SLA, specific leaf area.

plants ($P < 0.05$), while the leaf N_{mass} and P_{mass} of the female plants of BD and JH were significantly higher than that of the male plants ($P < 0.05$, Fig. 3 a, c). The leaf C_{mass} of the male plants of JZ was significantly higher than that of the female plants ($P < 0.05$), while the leaf C_{mass} of XQ was just the opposite, and there was no significant difference in the leaf C_{mass} of male and female plants in other regions (Fig. 3b). The leaf C/N and C/P of the female plants of JZ and XQ were significantly higher than that of the male plants ($P < 0.05$), while the leaf C/N and C/P of the male plants of BD and JH were significantly higher than that of the female plants ($P < 0.05$, Fig. 3 d, e). The leaf N/P of the male plants of XQ and JH was significantly higher than that of the female plants ($P < 0.05$, Fig. 3 f), while there was no significant difference in the leaf N/P of male and female plants in other regions.

Correlation Analysis of Leaf Traits

It is of great significance to understand the gender differences of dioecious plants by comparing the correlation between female and male leaf characters. The Pearson correlation analysis of leaf traits between

male and female plants of *A. palmeri* showed that there was a significant negative correlation between leaf C/N and N_{mass} , and also significant negative correlation between leaf C/P and P_{mass} in male and female plants ($P < 0.05$, Table 3). The leaf C_{mass} of female plants was significantly positively correlated with leaf C/N and C/P, but significantly negatively correlated with leaf N_{mass} and P_{mass} . The leaf N_{mass} of female plants was significantly positively correlated with leaf P_{mass} , but significantly negatively correlated with leaf C/P. And the leaf C/N of female plants was significantly positively correlated with leaf C/P, but significantly negatively correlated with leaf P_{mass} . The leaf N/P of male plants was significantly positively correlated with leaf C/N, but significantly negatively correlated with leaf N_{mass} ($P < 0.05$).

Discussions

There are differences in physiological and morphological adaptability among individuals of different sexes of dioecious plants, leaves are important organs, which are extremely sensitive to

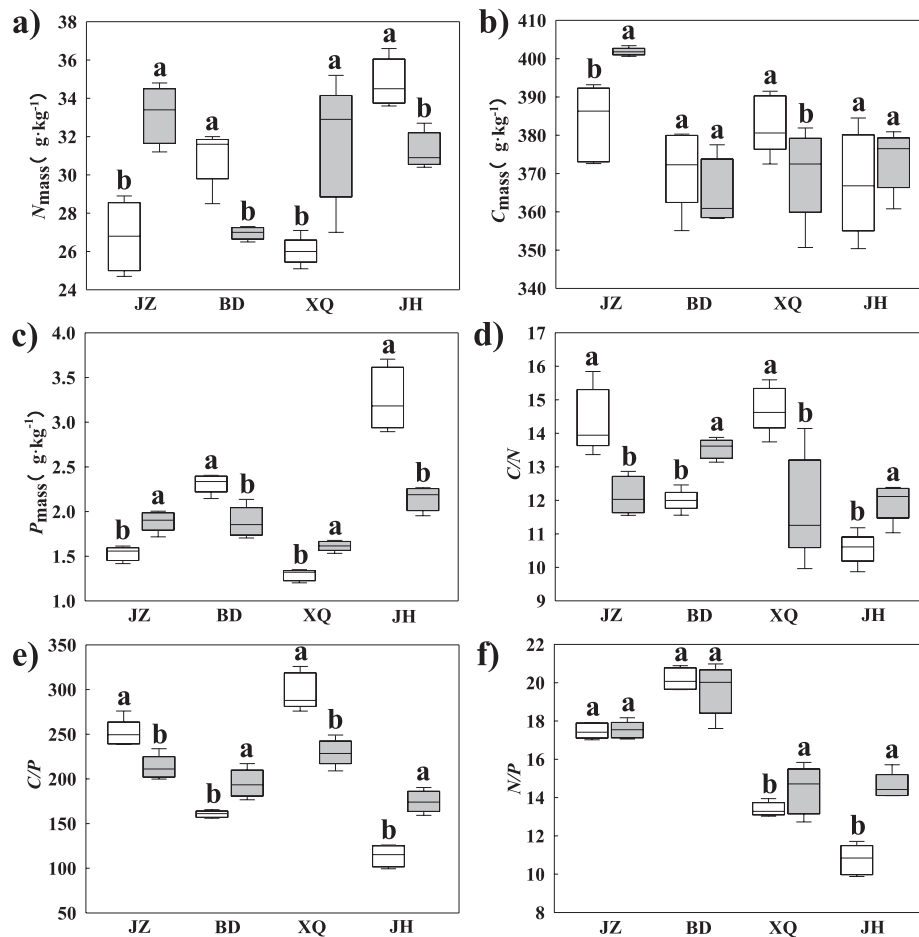


Fig. 3. The resource use efficiency between male (grey boxes) and female (white boxes) *A. palmeri* in different regions. Notes: N_{mass} , leaf nitrogen content; C_{mass} , leaf carbon content; P_{mass} , leaf phosphorus content; C/N, leaf carbon-nitrogen ratio; C/P: leaf carbon-phosphorus ratio; N/P: leaf nitrogen-phosphorus ratio.

environmental changes and have great plasticity [22]. The morphological and physiological characteristics of plant leaves can show different changes to adapt to the external living environment. In this study, the LW, LL and LA of the male plants of *A. palmeri* were significantly higher than those of the female plants

($P < 0.05$), indicating that there were differences in leaf morphology between the male and female plants of *A. palmeri*, which was consistent with the results on the leaf morphology of dioecious plants of *Cercidiphyllum japonicum* [23]. SLA is the leaf area per unit dry mass, which to a certain extent, it reflects

Table 3. The correlation analysis of leaf traits of male and female *A. palmeri*.

Index	SLA	N_{mass}	C_{mass}	P_{mass}	C/N	C/P	N/P
SLA	—	-0.121 ^{ns}	0.066 ^{ns}	0.250 ^{ns}	0.150 ^{ns}	-0.210 ^{ns}	0.054 ^{ns}
N_{mass}	0.043 ^{ns}	—	0.366 ^{ns}	0.091 ^{ns}	-0.904 ^{**}	0.033 ^{ns}	-0.475 [*]
C_{mass}	0.072 ^{ns}	-0.480 [*]	—	0.081 ^{ns}	0.060 ^{ns}	0.262 ^{ns}	0.027 ^{ns}
P_{mass}	0.023 ^{ns}	0.971 ^{**}	-0.531 [*]	—	-0.084 ^{ns}	-0.934 ^{**}	-0.019 ^{ns}
C/N	-0.034 ^{ns}	-0.975 ^{**}	0.644 ^{**}	-0.946 ^{**}	—	0.105 ^{ns}	0.545 [*]
C/P	-0.055 ^{ns}	-0.946 ^{**}	0.622 ^{**}	-0.957 ^{**}	0.967 ^{**}	—	-0.041 ^{ns}
N/P	-0.017 ^{ns}	-0.304 ^{ns}	0.117 ^{ns}	-0.357 ^{ns}	0.225 ^{ns}	0.121 ^{ns}	—

Notes: The female plant is below the diagonal, and the male plant is above the diagonal. SLA, specific leaf area; N_{mass} , leaf nitrogen content; C_{mass} , leaf carbon content; P_{mass} , leaf phosphorus content; C/N, leaf carbon-nitrogen ratio; C/P: leaf carbon-phosphorus ratio; N/P: leaf nitrogen-phosphorus ratio.

the expected return on previously captured resources [24-25]. Besides, it also reflects the adaptability characteristics of plants to the habitat [26], and the plants with a higher specific leaf area are less capable of preserving the acquired resources, but have a stronger ability to return. Therefore, species with higher SLA have a higher growth rate [27]. In this study, the SLA of male plants of *A. palmeri* were significantly higher than that of female plants ($P < 0.05$), which may be a functional adaptation pattern of leaf growth of male plants in order to rapidly accumulate higher biomass and more nutrients.

At present, most ecologists believe that among many plant traits, the leaf traits can reflect the survival strategies formed by plants adapting to the environment and the ability to utilize resources [28]. The allometric growth of plants is closely related to the allocation of biomass, the utilization of resources and the morphological adaptation to heterogeneous environment. Plants have evolved to respond to many selection pressures and constraints with allometric growth, and these methods can explain many behaviors of plant individuals and populations. In this study, the growth rate of the leaf traits of the male and female plants of *A. palmeri* was as follows: $LA > LL > LW$, which was consistent with the results of the study on leaf traits of *Distylium chinense* [29]. The SLA of male plants were more closely related to LW, LL and LA, while the SLA of female plants were not closely related to these traits. When the SLA is constant, the male plants of *A. palmeri* tended to have smaller LW, LL and higher LA, which reflected the flexible resource allocation strategy of dioecious invasive plants, that was, in order to successfully establish in the new habitat, the allometric growth characteristics of *A. palmeri* within its population were as follows: the male populations may use most of the sources in the process of photosynthesis, such as increasing the light capture area, while the female populations may invest more in reproductive organs under the pressure of reproduction.

As the organ with the largest contact area between plants and the external environment, the traits of leaf directly affect the basic behavior and function of the plants. The differences of leaf functional traits reflect the adaptability of plants to the environment and the characteristics of resource utilization [30]. The leaf C_{mass} , N_{mass} and P_{mass} are closely related to plant growth, species adaptation and distribution [31], and the leaf C/N, C/P and N/P and other indicators reflect the plant's resource utilization efficiency to a certain extent. The leaf N_{mass} is the main limiting factor for plant growth, which can affect the photosynthesis of plants by changing chlorophyll content, photosynthesis-related enzyme content, and enzyme activity [32-33].

In this study, the average N_{mass} (30.22 g/kg) and P_{mass} (1.99 g/kg) in leaf of *A. palmeri* were higher than the average of Chinese terrestrial plants [34]. However, the leaf C/N (average value of 12.63) and C/P (average value

of 204.36) of *A. palmeri* were lower than the average of global terrestrial plants [34]. Generally, higher leaf N_{mass} and P_{mass} or lower C/N and C/P represent better resource acquisition strategies and growth rates of plants [35-36]. Therefore, the results showed that *A. palmeri* exists fast growth rate and high photosynthetic efficiency. Particularly, the leaf N_{mass} and P_{mass} of male plants were significantly higher than those of female plants in JZ and XQ areas, while the results in BD and JH areas were opposite. Besides, the leaf C/N and C/P in of female were significantly higher than those of males in JZ and XQ areas, while the results in BD and JH areas were opposite. Previous studies have also shown that the leaf N/P can be widely used to indicate relative nutrient limitation to plants. The leaf $N/P < 14$ is indicative of N limitation, while the leaf $N/P > 16$ indicates P limitation. At the leaf N/P between 14 and 16, either N or P can be limiting or plant growth is limited by N and P together [20]. More recently, the researchers found that the leaf $N/P < 10$ and > 20 often correspond to N and P limitation [37]. But the new research showed that compared to the thresholds of 14 and 16, the N/P thresholds of 10 and 20 had lower error risks [38]. At the same time, a growing number of researches are questioning the universality of N/P thresholds in determining nutrient limits [39]. In this study, the leaf N/P of *A. palmeri* (average value of 16.00) was higher than the average of global terrestrial plants [35]. It is worth mentioning that the leaf N/P of male plants was significantly higher than that of female plants in XQ and JH areas. According to the results of previous researches, *A. palmeri* may be limited by either N or P or N and P together. However, the average of leaf N_{mass} and P_{mass} in *A. palmeri* were both above the adequate threshold, so the conclusion could not be completely confirmed, and more research needs to be confirmed.

Besides, the correlation between leaf N_{mass} and P_{mass} of female plants and most indexes was stronger than that of male plants. Successful invasive species in nutrient-rich environments usually have low leaf C/N nutrient [17] and high leaf N/P [40] in their tissues, but the effect of leaf N/P on the success of invasive plants is still unclear. We speculated that the resource allocation and utilization efficiency of the male and female plants of *A. palmeri* may be greatly affected by the site environment, and in different invasion environments, *A. palmeri* may have different ecological response strategies, which can adapt to the habitats to achieve a successful invasion.

Conclusions

In conclusion, our results showed that the traits of the male plants were closely related and had an allometric growth relationship compared with the female plants, which reflected the faster growth of the male plants of *A. palmeri* and stronger photosynthetic capacity. The higher leaf N_{mass} and P_{mass} and the lower

leaf C/N and C/P than the average of global terrestrial plants represented high resource acquisition strategies and growth rates of *A. palmeri*. In different invasion environments, *A. palmeri* may have different ecological response strategies, which can adapt to the habitats to achieve a successful invasion by optimizing the resource allocation and utilization efficiency between male and female plants. Further research needs to integrate various environmental factors, and explore the correlation between nutrient utilization and resource allocation of male and female plants of *A. palmeri* in heterogeneous habitats.

Abbreviations

C: Carbon; C/N: Carbon-nitrogen ratio; C/P: Carbon-phosphorus ratio; C_{mass} : Carbon content; IAPS: Invasive alien plant species; LA: Leaf area; LDW: Leaf dry weight; LL: Leaf length; LW: Leaf width; N: Nitrogen; N/P: Nitrogen-phosphorus ratio; N_{mass} : Nitrogen content; P: Phosphorus; P_{mass} : Phosphorus content; SLA: Specific leaf area; SMA: Standardized major axis

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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