Module Biomass and Allocation Patterns of the Invasive Plant Tagetes minuta Across Different Habitats (Postprint)

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Abstract

Tagetes minuta is a recently introduced invasive species in Tibet, with its detrimental impacts becoming increasingly apparent; however, research on its invasion mechanisms remains scarce in China. To investigate the biomass and allocation patterns of population modules of *Tagetes minuta* in heterogeneous environments, and to further elucidate its survival strategies and invasion-prone habitats, this study measured and analyzed the biomass of population modules during the flowering and fruiting period in five typical invaded habitats, including vegetable gardens, orchards, roadsides, wastelands, and riverbanks, and calculated phenotypic plasticity index values. The results indicated: (1) The general pattern of biomass allocation among modules of *Tagetes minuta* populations followed the order stem > flower/fruit > leaf > root, with maximum values observed in roadside habitats and minimum values in vegetable gardens, and all parameters showed significant differences between these two habitats ($P < 0.05$). (2) The mean values of the total coefficient of variation (CV) and plasticity index (PI) for biomass of all modules of *Tagetes minuta* were 46.93% and 61.44%, respectively. (3) The ratio of reproductive to vegetative module biomass of *Tagetes minuta* followed the pattern wasteland > roadside > orchard > riverbank > vegetable garden; the root-to-shoot ratio exhibited the pattern vegetable garden > wasteland > riverbank > roadside > orchard. (4) Significant positive correlations existed among all modules and between each module and total biomass in *Tagetes minuta*, reflecting an integrated and coordinated survival strategy. These results demonstrate that *Tagetes minuta* can adapt to heterogeneous habitats through adjustments in biomass allocation among modules, exhibiting high phenotypic plasticity. High reproductive output and adaptability to heterogeneous environments may be key factors underlying its successful invasion.

Module Biomass and Its Allocation of Invasive Plant *Tagetes minuta* Populations in Different Habitats

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Abstract: *Tagetes minuta* is a newly invasive species in Tibet whose damaging impacts are beginning to emerge, yet few studies have examined its invasion mechanisms in China. To investigate the biomass and allocation characteristics of population modules of *T. minuta* in heterogeneous environments and further understand its survival strategies and vulnerable habitats, this study measured and analyzed the biomass of population modules during the flowering and fruiting stages across five typical invasion habitats: vegetable gardens, orchards, roadsides, wastelands, and river beaches. Phenotypic plasticity indices were also calculated. The results showed: (1) The general pattern of module biomass in *T. minuta* populations was stem > flower and fruit > leaf > root, with the highest values observed along roadsides and the lowest in vegetable gardens, showing significant differences between these two habitats ($P < 0.05$). (2) The mean total coefficient of variation (CV) and phenotypic plasticity index (PI) across all modules were 46.93% and 61.44%, respectively. (3) The biomass ratio of reproductive to vegetative modules ranked as wasteland > roadside > orchard > river beach > vegetable garden, while the root-shoot ratio showed the opposite trend: vegetable garden > wasteland > river beach > roadside > orchard. (4) Significant positive correlations existed between all modules and between each module and total biomass, reflecting an integrated and coordinated survival strategy. These results indicate that *T. minuta* can adapt to heterogeneous habitats through biomass adjustment of its modules, demonstrating high phenotypic plasticity. High reproductive output and adaptability to heterogeneous environments may be important factors contributing to its successful invasion.

Keywords: invasive plant, *Tagetes minuta*, different habitats, population module, biomass allocation, Tibet

Introduction

Biological invasion represents a major cause of species endangerment and extinction worldwide (Tan et al., 2014), with plant invasion ranking among the three most challenging environmental problems globally (Zheng and Xue, 2018). Phenotypic plasticity is a crucial factor enabling plants to maintain broad ecological amplitudes and higher tolerance, playing a significant role in species distribution (Dostál et al., 2016; Lu et al., 2007). Compared with native plants, invasive species often exhibit greater phenotypic plasticity (Godoy et al., 2011; Thompson, 1991), with approximately 50% of invasive plants' success linked to this trait (Zheng et al., 2018). Furthermore, phenotypic plasticity can vary among different populations of the same species (Vilela et al., 2008). As one manifestation of phenotypic plasticity, biomass directly affects plant growth and reproduction (Weiner, 2004) and reflects both environmental impacts on plants and their adaptive responses (Zhou et al., 2015). Shifts in biomass allocation patterns can drive the expansion of invasive plants (Qi et al., 2006). In recent years, numerous scholars have investigated phenotypic plasticity in invasive plants through quantitative analysis of population module biomass and allocation characteristics (Zhou et al., 2015; Tan et al., 2014; Zhu and Ma, 2010), which is crucial for revealing invasion mechanisms.

Tagetes minuta (Asteraceae) is an annual herb native to South America that has now spread across more than 20 countries and regions in North America, Europe, Asia, Africa, and Oceania (Zhang et al., 2019). In China, it has successfully established populations in Taiwan, Beijing, Hebei, Shandong, and Jiangsu (Zhang et al., 2019) and represents one of the most damaging and aggressively invasive alien species in Tibet (Yang et al., 2018). This species exhibits strong allelopathic inhibition (Arora et al., 2016), high stress resistance (Zhang et al., 2019), a broad ecological amplitude (Zhang et al., 2014), and rapid reproduction and dispersal (Zhang et al., 2019), enabling it to quickly occupy ecological niches and form monospecific dominant communities. Since its first detection in Tibet in 2009 (Xu and Taslii, 2015), both its population size and distribution area have shown explosive growth (Tu et al., 2018), making research on its invasion biology particularly urgent.

Current domestic research on *T. minuta* has primarily focused on naturalized distribution (Xu and Taslii, 2015; Zhang et al., 2014; Dong et al., 2013), competitive ability (Tu et al., 2018), pollination networks (Tu et al., 2019), and risk assessment (Zhang et al., 2019). This study aims to quantitatively analyze the biomass characteristics of *T. minuta* modules across different habitats to understand its phenotypic plasticity, explore its invasion mechanisms and ecological adaptability, predict its most vulnerable habitats, and provide a basis for prevention and control strategies.

1.1 Study Area

The study area is located in southeastern Tibet, spanning from Milin County to Lang County in Nyingchi City (92°28 -95°12 E, 28°39 -29°50 N, elevation 3,200–3,700 m), where *T. minuta* invasion is particularly severe. The region features a plateau temperate semi-humid monsoon climate with annual precipitation of 350–641 mm, mean annual temperature of 8.2–11.0°C, annual sunshine duration of 2,000–2,500 hours, and a frost-free period of 130–170 days.

1.2.2 Data Processing

Data processing and regression analysis were performed using Excel software. Pearson correlation analysis and one-way ANOVA were conducted in SPSS 19.0 to analyze correlations and significant differences ($P < 0.05$) between plant height and module biomass, with LSD tests for multiple comparisons. Figures were generated using Origin 2018. After weighing all modules of *T. minuta*, mean biomass values were used to calculate phenotypic plasticity expressions: the total coefficient of variation (CV) and plasticity index (PI) based on maximum and minimum means (Wang and Zhou, 2017; Valladares et al., 2006). In this study, mean CV and PI values were used to represent the phenotypic plasticity of *T. minuta*.

The formulas are:

$$PI = \frac{\text{maximum mean} - \text{minimum mean}}{\text{maximum mean}} \times 100\%$$

Where maximum and minimum means refer to the average biomass values across replicate quadrats in different habitats, with the larger value being the maximum mean and the smaller being the minimum mean.

Results

2.1 Module Biomass and Allocation Characteristics of *T. minuta* Populations in Different Habitats

As shown in Table 2 , stem biomass distribution across habitats ranked as roadside > orchard > wasteland > river beach > vegetable garden, while other modules followed the pattern roadside > wasteland > orchard > river beach > vegetable garden. Total plant biomass and individual module biomass were highest along roadsides and lowest in vegetable gardens, with root, stem, leaf, flower-fruit, and total biomass in vegetable gardens accounting for only 2.71%, 1.68%, 4.14%, 1.36%, and 2.14% of roadside values, respectively. Roadside habitats showed significant differences from all other habitats, while vegetable gardens showed no significant differences from river beaches but differed significantly from other habitats. Orchards and wastelands also showed no significant differences between them but differed from other habitats ($P < 0.05$).

Table 3 reveals similar patterns of biomass allocation across habitats, with stems showing the highest allocation and roots the lowest. In orchards, roadsides, and wastelands, allocation ranked as stem > flower-fruit > leaf > root; in vegetable gardens as leaf > stem > flower-fruit > root; and in river beaches as stem > leaf > flower-fruit > root. Roots showed no significant differences across habitats. Stems showed no significant differences between roadsides and river beaches but differed significantly among other habitats. Leaves differed significantly between vegetable gardens/river beaches and other habitats. Flower-fruit biomass showed significant differences among all habitats except between roadsides and wastelands ($P < 0.05$).

2.2 Phenotypic Plasticity Characteristics of *T. minuta* Population Modules

As shown in Table 4 , phenotypic plasticity values for *T. minuta* modules and whole plants varied considerably among habitats, being highest in river beach habitats and lowest along roadsides. Among modules, flower-fruit showed the highest plasticity value (59.66%). The mean CV across habitats was 46.93%, with values of 41.69%, 45.25%, 48.71%, 52.09%, and 46.43% for root, stem, leaf, flower-fruit, and whole plant biomass, respectively. The mean PI was 61.44%, with values of 55.93%, 60.51%, 61.60%, 67.22%, and 62.28% for the respective modules.

2.3 Biomass Ratio of Reproductive to Vegetative Modules of *T. minuta* Populations

Figure 1 [Figure 1: see original paper] shows that the ratio of reproductive (flower-fruit) to vegetative (root-stem-leaf) module biomass across habitats ranked as wasteland > roadside > orchard > river beach > vegetable garden, with values of 42.28%, 39.80%, 33.75%, 27.91%, and 22.12%, respectively. No significant differences were found among orchards, roadsides, and wastelands, nor among vegetable gardens, orchards, and river beaches. However, roadsides and wastelands both differed significantly from vegetable gardens and river beaches, with the maximum value being 1.91 times the minimum ($P < 0.05$).

2.4 Root-Shoot Ratio of *T. minuta* Populations in Different Habitats

As shown in Figure 2 [Figure 2: see original paper], the root-shoot ratio across the five habitats ranked as vegetable garden > wasteland > river beach > roadside > orchard, with values of 15.49%, 13.60%, 11.88%, 11.85%, and 11.01%, respectively. Vegetable gardens showed significant differences from all other habitats except wastelands ($P < 0.05$), while no significant differences were detected among orchards, roadsides, wastelands, and river beaches.

2.5 Effects of Soil Physicochemical Properties on Biomass Allocation of *T. minuta*

Pearson correlation analysis between module biomass and soil moisture content, carbon, nitrogen, phosphorus, and pH revealed that *T. minuta* biomass was significantly negatively correlated only with moisture content and pH (Table 5), indicating weak correlations between biomass and soil nutrients. Moisture content and pH may be the primary factors constraining biomass allocation in *T. minuta*.

Significant positive correlations ($P < 0.01$) existed among root, stem, leaf, flower-fruit biomass and total biomass across all five habitats. When data from all habitats were pooled, these relationships remained significantly positive ($P < 0.01$) (Table 6). Each module showed the strongest correlation with total biomass ($R = 0.977$-0.995), with stem biomass showing the highest correlation (0.995) and root-flower-fruit biomass showing the lowest (0.951), though still exceeding 0.950.

Discussion

3.1 Module Biomass and Allocation Characteristics of *T. minuta* Populations

The variation in module biomass of *T. minuta* populations across different habitats demonstrates that integrated habitat conditions influence this species and that its biomass accumulation exhibits considerable adjustability and phenotypic plasticity. The highest biomass occurred along roadsides and the lowest in vegetable gardens, likely related to soil fertility, light availability, and human disturbance. Roadsides lack tall tree shading, providing good light conditions, air circulation, and relatively high soil nutrients, resulting in maximum biomass. Vegetable gardens, being semi-natural with long-term vegetable cultivation but minimal fertilization, had organic carbon content of only $8.35\ \mathrm{g \cdot kg}^{1}$, with nutrient deficiency limiting biomass accumulation. Additionally, cultivation practices involving frequent physical and chemical weed removal likely eliminated taller *T. minuta* individuals.

The similarities and differences in biomass allocation patterns across habitats reflect important allocation strategies and relatively stable patterns. In vegetable gardens, human removal suppressed height advantages, prompting greater energy investment in photosynthetic leaf construction to ensure adequate productivity. In other habitats, priority was given to stem growth, with larger stem biomass facilitating acquisition of space and light resources and enhancing competitiveness and invasiveness. Invasive plants often show stronger reproductive capacity in invaded regions (Marcia et al., 2017), a key factor for rapid colonization and spread (Yan et al., 2017). The flower-fruit biomass allocation ratio of *T. minuta* (18.12%-29.72%) was significantly higher than that of the strongly invasive congener *Ageratum conyzoides* (3.19%-6.20%) (Zhou et al., 2015), favoring stable population development. Similar allocation patterns have been observed in *Bidens frondosa* (Zhou et al., 2012), *Mikania micrantha* (Xu et al., 2014), and three Amaranthaceae species (Xiang et al., 2017). The adaptive mechanism of differential allocation responses to environmental conditions is crucial for broadening ecological amplitude and enhancing invasiveness.

3.2 Phenotypic Plasticity Characteristics of *T. minuta*

Differences in phenotypic plasticity among invasive populations suggest potential for plasticity evolution, which may explain their advantages (Hiatt and Flory, 2020). While consensus on plasticity quantification remains elusive (Wang and Zhou, 2017), most *T. minuta* modules showed significant biomass differences across habitats. Its CV and PI values were comparable to those of the highly plastic congener *Taraxacum mongolicum* (Zhang et al., 2017) and invasive *Aster subulatus* (Pan et al., 2010), indicating strong phenotypic plasticity. During colonization, population establishment, latency, and dispersal, phenotypic plasticity in alien invaders often broadens ecological amplitude and enhances invasiveness through adaptive mechanisms (Gong et al., 2009). Thus, *T. minuta*' s plasticity likely increases its adaptability and tolerance to heterogeneous environments, augmenting invasion capacity. Moreover, flower-fruit modules showed the highest plasticity, further facilitating reproduction and providing conditions for dispersal into new habitats. Strong phenotypic plasticity may therefore be a key factor in its successful invasion.

3.3 Characteristics of Reproductive-Vegetative Module Ratio and Root-Shoot Ratio

The reproductive-vegetative module ratio ranked as wasteland > roadside > orchard > river beach > vegetable garden, indicating adjustability across habitats. The highest reproductive organ allocation (29.72%) and reproductive-vegetative ratio (42.28%) occurred in wastelands with relatively low soil C, N, and P content, suggesting strongest reproductive capacity under resource limitation. This likely reflects a strategy where, after ensuring sufficient investment in vegetative organs for survival, most remaining resources are allocated to reproduction to promote dispersal.

The root-shoot ratio directly reflects coordination of biomass allocation between below- and aboveground parts, crucial for total production and individual growth (Hui and Jackson, 2006; Enquist and Niklas, 2002). The highest root-shoot ratio in vegetable gardens may relate to moisture content, nitrogen, and soil aeration. With moisture content of 6.22%, vegetable gardens experienced drought stress and low nitrogen (0.59 g · kg^{1}), causing roots to prioritize water and nitrogen acquisition at the expense of shoot supply, thereby inhibiting aboveground growth and increasing the root-shoot ratio (Li, 2019; Zou et al., 2019). This also correlates with frequent tillage creating loose, well-aerated soil favorable for root growth. Similar adjustability in root-shoot ratios has been documented in *Setaria viridis* (Jia et al., 2014). The ability to optimally allocate water and nutrients while adjusting root and shoot biomass represents an effective survival strategy promoting ecological adaptability.

3.4 Relationships Among Modules of *T. minuta*

Although module biomass and allocation ratios varied across habitats, significant positive correlations ($P < 0.01$) existed among all modules and between each module and total biomass, with correlation coefficients exceeding 0.951. Similar relationships have been observed in invasive *Galinsoga parviflora* (Qi et al., 2006), *Conyza canadensis* (Pan et al., 2009), and *Gaura parviflora* (Liu et al., 2012), though with lower coefficients than in *T. minuta*. This indicates tighter integration among *T. minuta* modules, with structural and functional interdependence and constraint. The coordinated survival strategy enhances environmental adaptability and invasiveness.

In summary, biomass allocation across five habitats followed the pattern stem > flower-fruit > leaf > root, with highly significant positive correlations ($P < 0.01$) among modules and with total biomass, indicating relative stability and integrated coordination. Through plastic adjustment, *T. minuta* achieved optimal biomass accumulation along roadsides and maximum seed production in wastelands—habitats most vulnerable to invasion that require enhanced monitoring and management. High CV and PI values demonstrate substantial phenotypic plasticity. Overall, *T. minuta* optimizes module biomass allocation to adapt to heterogeneous environments, with high reproductive biomass and strong phenotypic plasticity enhancing environmental adaptability—likely key factors underlying its invasion success.

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