

# Identity and Diversity of Invasive Plant Affecting the Growth of Native *Lactuca indica*

Rakhwe Kama, Qaiser Javed, Yanwen Bo, Muhammad A. Imran, Faten Zubair Filimban, Zhongyang Li, Xuhua Nong, Sekouna Diatta, Guangqian Ren, Sayed M Eldin, Rashid Iqbal, Iftikhar Ali,\* Javed Iqbal, and Jianfan Sun\*



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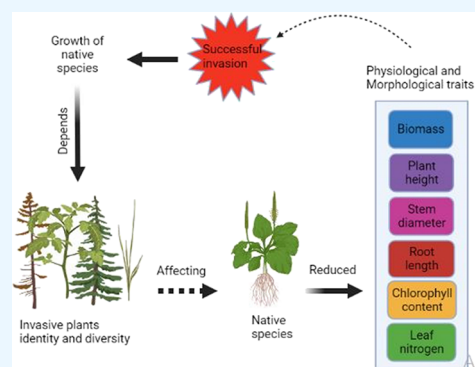
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**ABSTRACT:** Despite the significant number of studies that have recently focused on plant invasion and invasive plants' success, many uncertainties still exist on the effects of invasive plant identity and diversity on the native plant response under different levels of diversity. A mixed planting experiment was conducted using the native *Lactuca indica* (*L. indica*) and four invasive plants. The treatments consisted of 1, 2, 3, and 4 levels of invasive plants richness in different combinations in competition with the native *L. indica*. Here, the results showed that native plant response depends on the invasive plant identity and invasive plant diversity, which increases the native plant total biomass under 2–3 levels of invasive plant richness and decreases under high invasive plant density. This plant diversity effect was more significant in the native plant relative interaction index, which shows negative values except under a single invasion with *Solidago canadensis* and *Pilosa bidens*. The native plant leaf nitrogen level increased under four levels of invasive plant richness, which means more affected by invasive plant identity than invasive plant diversity. Finally, this study demonstrated that native plant response under invasion depends on the identity and diversity of invasive plants.



## 1. INTRODUCTION

In ecology, invasion is defined over a specific period on a geological or paleontological time scale. An invasion is characterized by the sustained increase in the range of a taxon, which can be one or more natural or anthropogenic populations. Plant invasions can considerably reduce the diversity and abundance of plant communities<sup>1,2</sup> and change soil microbial communities' activity, biomass, and structure, potentially affecting crucial ecosystem processes, such as organic matter decomposition and nutrient cycling.<sup>3–6</sup> The spread of invasive plants in natural habitats brings significant effects on native plants. For instance, native and invasive plants evolving in the same area interfere with each other's activities according to their age, size, and distance apart. These interactions directly affect native plants, characterizing invasive plants' dominance.<sup>7</sup> However, invasive species exhibited strong indirect interactions with the surrounding community by giving their disproportionately high biomass and abundance,<sup>8</sup> influencing the invasion success and impacts on native species.<sup>9</sup> Yet, the relative importance of direct and indirect interactions in modifying invasive species impacts remains unresolved. It is necessary to elucidate and understand the complexities underlying these interactions and the native plant response to invasive plant threats.

In native plant communities, invasive plants influence native plant growth; however, these effects may depend on the identity of the invasive plant and the type of invasion. For instance, previous studies showed that invasive species affect soil properties, leading to a considerable divergence in soil microbial characteristics over time,<sup>10</sup> which disturbs native plant growth. These effects may result from competition between native plants and their neighbor's invasive plants that alter the availability of nutrients, light, and space. In turn, plant nutritional quality influences the interaction between plants, especially the native plant response. However, whether the effects of an invasive plant on the native community depend on the native plant itself or the invasive plant's identity remains unresolved. Besides the identity of neighboring invasive plants, the diversity and abundance of the neighboring plants' community can also be an important factor that influence native and invasive plant interactions. For instance, it has been suggested that invasive plant diversity affects the expression of

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secondary metabolites in focal plants, and the secondary metabolites in the plant are affected by the diversity of the neighboring plants' community.<sup>11–13</sup> Several ecologists stated that the spread of invasive plants could be far from their natural range through successful colonization.<sup>14–16</sup> Invasive plants display different degrees of invasion in the invaded ecosystems.<sup>17–20</sup> At the same time, one invasive plant's successful colonization can construct such a niche in the invaded environments that could benefit another invasive plant for succeeding in the previously invaded ecosystems. One invasive plant colonization can trigger the probability of success of the upcoming invaders.<sup>18</sup> Hence, the co-invasion of two or more invasive plants is common in many ecosystems.<sup>17,21–23</sup> Thus, understanding and assessing the effects of the co-invasion of different invasive plants with different degrees of invasive plants richness on the native plant response could be significant in elucidating the mechanisms underlying invasive plants' success.

Invasive species are well known to be superior to native plants in terms of competitive ability.<sup>24</sup> For example, preceding studies propose that invasive species might be more tolerant and resistant than native species, so they have better physiological and morphological performance<sup>25–27</sup> in the growing competition with local plants and local populations or native communities.<sup>24,28</sup> There have been varied approaches to determining the effects of an invasive plant on the native community, with most studies attempting to compare invaded vs non-invaded habitats. Still, little is known about the impact of invasive plant identity and diversity on the native plant response.

This study aims to determine the effects of invasive plant identity and diversity on the native plant *Lactuca indica* (*L. indica*) response under different invasion types and invasive plant richness. Based on the assumptions and raised questions, this study addressed the following hypotheses: (i) *L. indica* response depends on the identity of the invasive plant and would differ from one invasive plant to another, (ii) the invasive plant diversity has a positive impact on the native plant response (iii) the native plant response would be more positive under co-invasion with increasing invasive plant diversity than under single invasion.

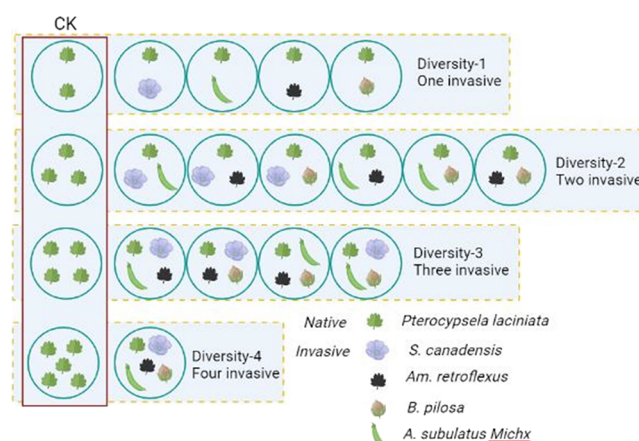
## 2. MATERIALS AND METHODS

**2.1. Study Species.** Four invasive plants, one of which *Amaranthus retroflexus* (*A. retroflexus*) from Amaranthaceae family, and the *Solidago canadensis* (*S. canadensis*) L, *Aster subulatus* (*A. subulatus*) Michx, and *Bidens pilosa* (*B. pilosa*) L. from Asteraceae. In particular, these invasive species can simultaneously invade the same plant community, such as wastelands and farmlands, in China.<sup>29,30</sup> Therefore, these four invasive species were selected because they usually co-exist with the native target plant *L. indica* to determine the effects of invasive plant identity and diversity on the native plant response under invasion. *L. indica* is a native plant in China and is mainly distributed in Shandong, Zhejiang, and Jiangxi Provinces.<sup>31</sup> *S. canadensis* and *B. pilosa* have become worldwide invasive herbs. They have had serious severe ecological consequences in some countries, especially *S. canadensis*, which presents a strong expansion range. It is considered a severe invasive weed because of its adverse effects on native ecosystems in many countries, especially in Europe and Asia,<sup>32</sup> and it is widely distributed in the eastern US and Canada.<sup>33</sup> *A. subulatus* Michx is mainly restricted to Eurasia. *A. retroflexus* is

an annual species growing to 0.9 m in flower from July to September, and the seeds ripen from August to October. It is a troublesome broadleaf weed in autumn crop fields in China. For instance, many farmers stated that *A. retroflexus* is very difficult to control at the recommended field rate in maize fields especially in Northeast China.<sup>34</sup>

**2.2. Seed Collection.** The seeds of *L. indica* and *B. pilosa* were collected from adult plants in Zhenjiang Jiangsu province near the roadside, respectively, in October and November 2018. The seed of *S. canadensis* and *A. subulatus* Michx were collected in November 2018 near Jiaoshan Mountain in Zhenjiang city, Jiangsu province. Due to low seed production in Zhenjiang city, seeds of *A. retroflexus* were purchased from an online plant market. After collection, the seeds were kept in plastic bags and stored in the laboratory until July 2019.

**2.3. Experimental Design.** The experiment was performed in the greenhouse through pots cultivation with a uniform size: height of 21 cm and top diameter of 18.5 cm. The soil used in this experiment was a mix of natural, nutrient, and sandy soil in a 1/3:1/3:1/3 ratio. In July 2019, seeds of *L. indica* and the four invasive plants were separately sown into a seedbed located in the greenhouse of the School of Environment and Safety Engineering, Jiangsu University, Zhenjiang, Jiangsu province, China. After 20 days, similar-sized and vigorous seedlings (approximately 10 cm tall) were transplanted into the pots. The seedlings of *L. indica* were grown under four conditions of invasive plants richness: single invasive, two invasive, three invasive, and four invasive plants in all the possible combinations (Figure 1). Each treatment



**Figure 1.** Schematic design of the experiment. A mixed planting experiment contains one native plant *Lactuca indica* as target species and four invasive plants with different treatment and richness. N = native *Lactuca indica*; I = invasive plant.

was replicated five times ( $19 \times 5 = 95$  pots in total). Data collection of the above-ground part was started after one month of transplantation. All plants were harvested at the end of August, and the above and below ground biomasses were weighed.

**2.4. Measurements.** **2.4.1. Growth and Physiological Parameter Measurements.** The considered parameters were plant height, stem diameter, root length shoot, and root biomass. Among the five replicates of each treatment, three plants showing the best growth rate were selected for the measurement of growth parameters. Plant height was measured with a tape and was recorded from the ground to the highest

leaf position. The stem diameter was measured with the Vernier caliper. The electronic balance determined to shoot and root biomass weight at the end of the experiments. Physiological parameters were collected every three days after one month of the transplanted seedling's growth; the considered parameters were leaf chlorophyll content (*Chl*) and leaf nitrogen level (*Ln*). The hand-held plant nutrient meter was used for their determination. Chlorophyll concentrations were calculated in BSPAD units based on absorbance at 650 and 940 nm. The root–shoot biomass ratios were determined by using the following equation.<sup>35</sup>

$$\text{Root – shoot biomass ratio} = \text{RB/SB} \quad (1)$$

Where RB is the dry weight of root biomass (g), and SB is the dry weight of shoot biomass (g).

**2.4.2. Relative Interaction Index.** Relative interaction index (RII) responses of the native target plant under mono and mixed culture were calculated based on the total dry weight of a plant. The RII is appropriate for evaluating positive or negative interactions among two species. Through RII, the performance of *L. indica* under different plant patterns depending on the invasive plant identity and diversity, as well as their combinations can be compared. The RII was calculated using the following equations.<sup>25,36</sup>

$$\text{RII} = (\text{Ax1x2} - \text{Ax1}) / (\text{Ax1x2} + \text{Ax1}) \quad (2)$$

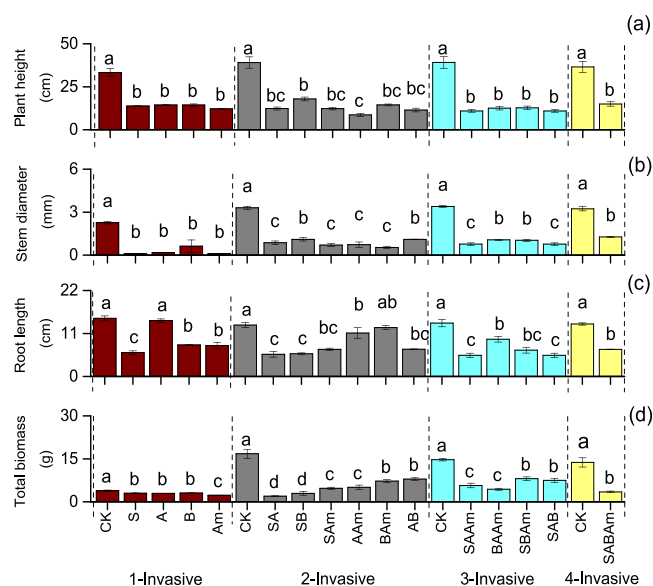
where *A* is the total dry weight of the native plant *L. indica*, while *x1* represents the native plant in control (CK) and *x2* represents the native plant in competition with the invasive plant.

**2.5. Statistical Analysis.** SPSS version 22:0 (SPSS Inc., IL, USA) was used for statistical analysis, and graphs were produced in OriginPro9. Differences in native plant height and root and shoot biomass grew in single invasion with different invasive plants and under co-invasion with a different combination, and invasive plant richness was tested using analysis of variance (ANOVA). To determine the changes in native plant parameters among different planting patterns followed by multiple comparison tests, i.e., Duncan's multiple-range and Tukey tests. Data were presented in means ± SE at *P* < 0.05.

### 3. RESULTS

#### 3.1. Effects of Invasive Plant Identity and Diversity on the Growth and Biomass Allocation of Native *L. indica*.

This study showed that the native plant height decreases under co-invasion compared to the single. This adverse effect of co-invasion on native plant growth depends on the invasive plant combinations (Figure 2). The most surprising aspect of the result is that the native *L. indica* response was positively more significant under three levels of invasive plant richness specifically when grown with *A. subulatus* Michx, *B. pilosa*, and *A. retroflexus*, as well as under *S. canadensis*, *A. subulatus* Michx, and *B. pilosa* combinations. Invasive plant diversity plays a positive role in native plant growth, possibly due to the complementary interactions between invasive plants that reduce the stress on native plant growth (Figure 2). Native *L. indica* growth characteristics were significantly affected by the invasive plant's presence. Invasive plant presence negatively affects native plant total biomass depending on the identity of the invasive plant and diversity, as well as their level of richness (Figure 2 and Table 1). Interestingly, this negative effect was more pronounced under *A. retroflexus* as compared to *S.*



**Figure 2.** Effects of invasive plant identity and diversity on *L. indica* growth characteristics, Mean + SE with different letters indicate a significant difference among mono and mixed culture treatments (at *P* < 0.05). (a) Plant height, (b) stem diameter, (c) root length, and (d) total biomass. CK = control, P = *L. indica*, S = *S. canadensis*, A = *A. subulatus* Michx, Am = *A. retroflexus* B = *B. pilosa*.

*canadensis*, *B. Pilosa*, and *A. subulatus* Michx. Contrast, the native plant root biomass was not significantly affected by plant invasion; moreover, it increased under invasion (Table 1). The native plant had greater total biomass under co-invasion (invasive plant diversity) than single invasion (invasive plant identity).

The native plant root–shoot and root–shoot biomass ratios significantly increased under single invasion and decreased with increasing plant diversity (Figure 2). This study showed a greater root–shoot ratio and root–shoot biomass ratio of the native plant under co-invasion with *S. canadensis* and *A. subulatus* Michx. However, it is important to mention that this response depends on the identity of the invasive community and its combination (Figure 2). Invasive plant diversity positively affects the native plant response, which decreases under high-level invasive plant density. The results suggest that the native plant's growth under invasion depends not only on the identity of the invasive plant but also on the invasive plant's combination and the level of richness (Table 1).

The results showed that invasive plant identity and diversity significantly affect native plant growth. Native plant root–shoot biomass ratio increased under invasion as compared to monoculture. This positive effect was more pronounced under single invasion than co-invasion with three different levels of invasion plant richness, which suggests that invasive plant identity plays a positive role in the native plant biomass ratio. Surprisingly, this positive effect increases under two levels of invasive plant richness with the native plant grown under co-invasion with *S. canadensis* and *A. subulatus* Michx and starts decreasing from three invasive plant richness (Figure 3).

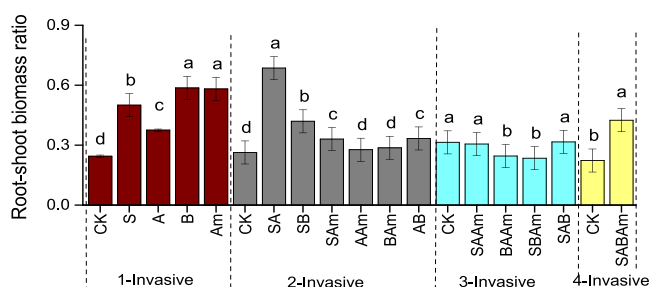
Significant differences were observed in the native plant *L. indica* root–shoot biomass ratio depending on the invasive plant identity and diversity and, more importantly, the level of invasive plant richness and their combination. Native plant biomass increases with invasive plant diversity at a specific level of invasive plant richness and decreases significantly under four

Table 1. Effects of Invasive Plant Identity on the Native Plant Growth Characteristics (Mean  $\pm$  SE) under Invasion<sup>a</sup>

invasive plant richness	growth and morphological traits of native species							
	plant height	stem diameter	root length	Chl content	leaf nitrogen	shoot biomass	root biomass	
1-Invasive	Ck	33.30 $\pm$ 1.68***	2.26 $\pm$ 0.08***	14.86 $\pm$ 0.64**	4.38 $\pm$ 2.53**	2.30 $\pm$ 0.06*	3.13 $\pm$ 0.15***	0.77 $\pm$ 0.09***
	P $\times$ S	13.80 $\pm$ 0.76***	0.10 $\pm$ 0.00***	6.13 $\pm$ 0.43**	7.50 $\pm$ 4.33**	1.86 $\pm$ 0.15*	2.00 $\pm$ 0.06***	1.00 $\pm$ 0.06***
	P $\times$ A	14.36 $\pm$ 0.34***	0.18 $\pm$ 0.02***	14.30 $\pm$ 0.44**	0.37 $\pm$ 0.22**	2.30 $\pm$ 0.12*	2.13 $\pm$ 0.12***	0.80 $\pm$ 0.10***
	P $\times$ Am	12.16 $\pm$ 0.98***	0.10 $\pm$ 0.00***	7.90 $\pm$ 0.83**	4.78 $\pm$ 2.76**	2.07 $\pm$ 0.33*	1.43 $\pm$ 0.09***	0.83 $\pm$ 0.07***
2-Invasive	P $\times$ B	14.40 $\pm$ 0.90***	.616 $\pm$ 0.44***	8.07 $\pm$ 0.16**	0.50 $\pm$ 0.29**	2.67 $\pm$ 0.13*	1.93 $\pm$ 0.07***	1.13 $\pm$ 0.12***
	Ck	39.10 $\pm$ 0.61***	3.30 $\pm$ 0.12***	13.13 $\pm$ 0.64***	31.50 $\pm$ 0.72**	2.53 $\pm$ 0.15**	44.93 $\pm$ 2.14***	11.83 $\pm$ 0.84***
	P $\times$ S $\times$ A	12.33 $\pm$ 1.34***	0.86 $\pm$ 0.12***	5.67 $\pm$ 0.73***	22.10 $\pm$ 0.15 ns	2.07 $\pm$ 0.09***	1.17 $\pm$ 0.12***	0.80 $\pm$ 0.06***
	P $\times$ S $\times$ Am	12.30 $\pm$ 1.37***	0.70 $\pm$ 0.12***	6.93 $\pm$ 0.32***	23.03 $\pm$ 1.61 ns	2.30 $\pm$ 0.17**	3.53 $\pm$ 0.26***	1.17 $\pm$ 0.12***
3-Invasive	P $\times$ SX Pb	17.90 $\pm$ 1.40***	1.10 $\pm$ 0.12***	5.80 $\pm$ 0.25***	25.27 $\pm$ 2.83*	2.13 $\pm$ 0.13**	2.07 $\pm$ 0.55***	0.87 $\pm$ 0.09***
	P $\times$ A $\times$ Am	15.30 $\pm$ 1.67***	0.73 $\pm$ 0.19***	8.60 $\pm$ 0.96***	26.00 $\pm$ 0.55*	2.37 $\pm$ 0.03**	3.97 $\pm$ 0.78***	1.10 $\pm$ 0.06***
	P $\times$ A $\times$ B $\times$ Am	11.47 $\pm$ 0.87***	1.10 $\pm$ 0.00***	6.97 $\pm$ 0.09***	21.73 $\pm$ 1.67 ns	2.07 $\pm$ 0.13**	6.17 $\pm$ 0.41***	1.77 $\pm$ 0.12***
	P $\times$ Am $\times$ B	14.43 $\pm$ 0.87***	0.53 $\pm$ 0.09***	12.50 $\pm$ 0.52***	20.60 $\pm$ 0.85 ns	2.07 $\pm$ 0.17**	5.40 $\pm$ 0.32***	1.80 $\pm$ 0.21 ns
4-Invasive	Ck	39.13 $\pm$ 0.61***	3.40 $\pm$ 0.06***	13.67 $\pm$ 0.95***	27.93 $\pm$ 1.99*	2.53 $\pm$ 0.15**	41.63 $\pm$ 1.31***	13.07 $\pm$ 1.12***
	P $\times$ S $\times$ A $\times$ Am	10.93 $\pm$ 1.51***	0.77 $\pm$ 0.09***	5.40 $\pm$ 0.55***	22.13 $\pm$ 2.17 ns	1.57 $\pm$ 0.42**	4.37 $\pm$ 0.73***	1.33 $\pm$ 0.34***
	P $\times$ A $\times$ AmXB	12.57 $\pm$ 1.51***	1.07 $\pm$ 0.03***	9.53 $\pm$ 0.74***	23.37 $\pm$ 1.99 ns	1.13 $\pm$ 0.15**	6.53 $\pm$ 0.84***	1.53 $\pm$ 0.30***
	P $\times$ SX AmXB	12.77 $\pm$ 0.82***	1.03 $\pm$ 0.07***	6.73 $\pm$ 0.74***	25.03 $\pm$ 0.55*	2.27 $\pm$ 0.09**	3.53 $\pm$ 0.26***	0.87 $\pm$ 0.09***
4-Invasive	P $\times$ S $\times$ A $\times$ B	8.00 $\pm$ 0.91***	0.90 $\pm$ 0.06***	5.50 $\pm$ 0.65***	22.13 $\pm$ 2.17 ns	1.57 $\pm$ 0.42**	4.50 $\pm$ 0.23***	2.10 $\pm$ 0.07***
	Ck	28.33 $\pm$ 7.69***	2.57 $\pm$ 0.70***	11.43 $\pm$ 2.61***	19.63 $\pm$ 4.61 ns	2.27 $\pm$ 0.15**	46.30 $\pm$ 22.15***	10.13 $\pm$ 4.59***
	P $\times$ S $\times$ A $\times$ B $\times$ Am	20.83 $\pm$ 8.44***	1.53 $\pm$ 0.84**	7.90 $\pm$ 2.23**	22.37 $\pm$ 5.38 ns	2.53 $\pm$ 0.07*	28.13 $\pm$ 21.44**	6.50 $\pm$ 5.25**

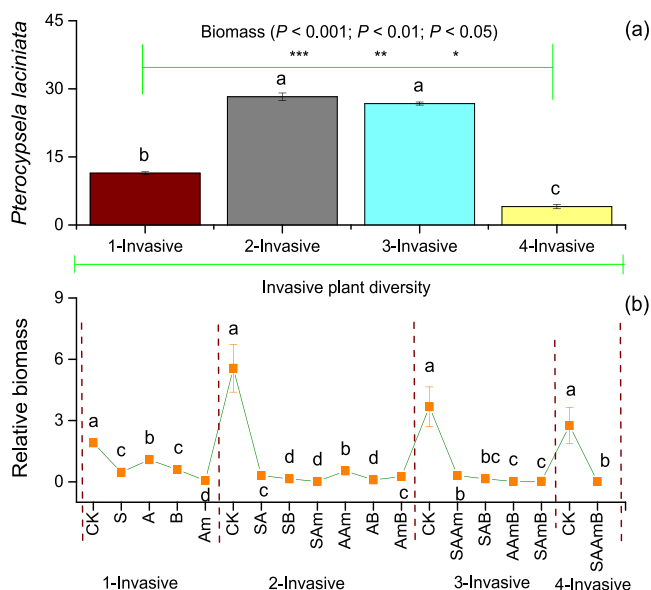
<sup>a</sup>Asterisks indicate significant effects based on the invasive plant identity and the native plant growth parameters. Asterisks indicate significant effect at \*\*\* $P$  < 0.001; \*\* $P$  < 0.01; and \* marginally significant effect at  $P$  < 0.05.





**Figure 3.** Effects of invasive plant identity and diversity on the native plant root–shoot biomass ratio. Mean + SE with different letters indicate a significant difference among mono and mixed culture treatments (at  $P < 0.05$ ). CK = control, P = *L. indica*, S = *S. canadensis*, A = *A. subulatus Michx*, Am = *Am. retroflexus* B = *B. pilosa*.

levels of invasive plant richness (Figure 4). This study showed that invasive plant diversity plays a significant role in native

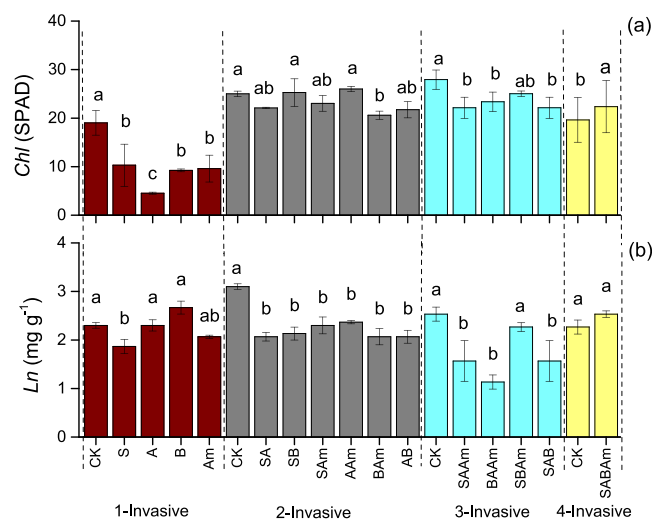


**Figure 4.** Effects of invasive plant diversity on the native species *Lactuca indica* biomass production (a); the effect of invasive plant identity and diversity on the native relative biomass (b). Mean + SE with different letters indicate a significant difference among different levels of invasive plants richness (at  $P < 0.05$ ). CK = control, P = *L. indica*, S = *S. canadensis*, A = *A. subulatus Michx*, Am = *Am. retroflexus* B = *B. pilosa*.

plant response depending on their level of richness and combinations. Figure 4 shows that the native plant's relative biomass depends clearly on invasive plant identity. However, this effect of invasive plant identity can be modified with increasing invasive plant diversity, suggesting that the native plant response depends on invasive plant identity and their diversity and level of richness.

**3.2. Effects of Invasive Plant Identity and Diversity on the Physiological Traits of Native *L. indica*.** The one-way ANOVA analysis of the native plant leaf chlorophyll content and nitrogen level showed significant differences depending on invasive plant identity and diversity and their level of richness and combinations (Table 1). The native plant chlorophyll content was negatively affected by invasive plant presence under a single invasion compared with the effects of an invasive plant on native plant nitrogen level. However, the native plant

leaf chlorophyll content increased with invasive plant diversity and abundance at the specific level of three invasive plant richness, in contrast to the nitrogen level (Figure 5).



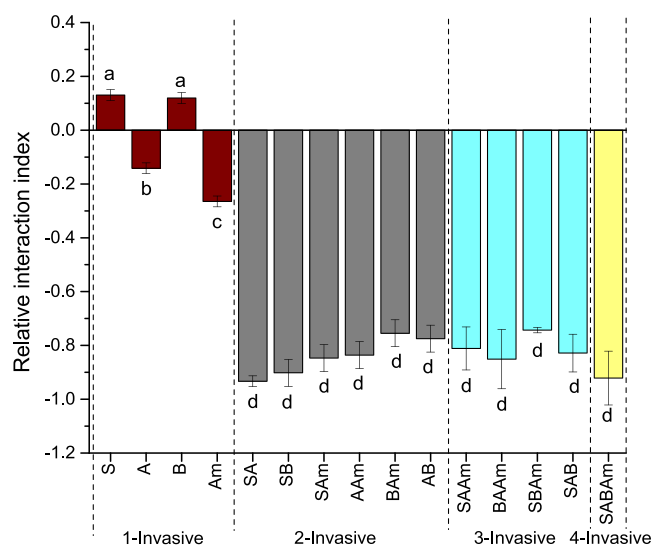
**Figure 5.** Effects of invasive plant identity and diversity on the native plant leaf chlorophyll content and nitrogen level. Mean + SE with different letters indicate a significant difference among mono and mixed culture treatments (at  $P < 0.05$ ). (a) Leaf chlorophyll (Chl), (b) leaf nitrogen (Ln). CK = control, P = *L. indica*, S = *S. canadensis*, A = *A. subulatus Michx*, Am = *Am. retroflexus* B = *B. pilosa*.

The native plant leaf nitrogen level increased under four levels of invasive plant richness while the leaf chlorophyll stabilized from three invasive plant richness. Invasive plant identity and diversity negatively impact the native plant's physiological parameters depending on the type of invasion and the level of invasive plant richness. However, positive effects of invasive plant diversity were observed in the native plant physiological parameters under four levels of invasive plant richness.

**3.3. Effects of Invasive Plant Identity and Diversity on the RII of Native *L. indica*.** Plant invasion negatively affects native plant growth. This situation is more significant in the RII, presenting negative values except under a single invasion with *S. canadensis* and *B. pilosa*. More importantly, this negative effect is more pronounced with invasive plant diversity and abundance (Figure 6). Significant differences were observed under single depending on the invasive plant identity, while no significant effects were observed depending on the invasive plant diversity.

## 4. DISCUSSION

Assessing invasive species' effects on the native population demands understanding the mechanisms underlying their interactions. Invasive species' success is mainly attributed to their release from natural controls regulating population growth within their native range.<sup>37,38</sup> It has been suggested that invasive plants are superior to native plants in terms of competitive ability, high reproductive potential, and predation strategies.<sup>39–41</sup> Invasive plants negatively affect the character of native plants, such as plant size and quality. However, these invasive plant effects might be positive depending on the type of invasion and the invasive plant's identity and diversity.<sup>42</sup> For instance, this study was conducted using the native plant *L. indica* and four invasive plants to determine the effects of



**Figure 6.** Effects of invasive identity and diversity on the native plant relative interaction index, Mean + SE with different letters indicate a significant difference among mono and mixed culture treatments (at  $P < 0.05$ ), CK = control, P = *L. indica*, S = *S. canadensis*, A = *A. subulatus* Michx, Am = *Am. retroflexus* B = *B. pilosa*.

invasive plant identity and diversity on native plant growth and physiological characteristics. It was found that the native plant response was dependent on the invasive plant identity as native plant roots were not well settled under *S. canadensis*, which is characterized by significant root biomass and its large leaves compared to *A. subulatus* Michx and *B. pilosa*. Invasive plant presence negatively affects native growth depending on the identity of the invasive plant. For instance, it was observed that the response of the native plant *L. indica* under invasion was different from one invasive to another (Table 1). Overall, this study confirmed that invasive plant negatively affects native plant growth and depends on the invasive plant's identity.

Invasive plant presence significantly affects the native plant's physiological parameters. However, these effects are dependent on invasive plant identity. For instance, this study showed the native plant leaf *Chl* content and *Ln* level showed significant differences depending on invasive plant identity (Table 1). The native plant *Chl* was negatively affected by invasive plant presence under a single invasion, contrastingly nitrogen level. This difference of invasive plant identity on the native plant differs from one invasive to another due to their differences with the soil microbial community.

Moreover, invasive plants alter the availability of nutrients, light, and space for the native plant.<sup>43–45</sup> More importantly, this study also suggests that increasing invasive plants' abundance and diversity positively affects the native plant response. However, this positive effect of invasive plant diversity decreases under high density (Table 1). It is also important to mention that changes might influence native and invasive plant interactions in plant nutritional quality,<sup>46,47</sup> and this phenomenon was observed in this study (Table 1). In addition, it was noted that invasive plant diversity positively affects native plant growth and native plant growth is mainly influenced by their co-existing invasive plant diversity.<sup>48,49</sup> Differences were noticed in the native plant root biomass under invasive plant presence and without presence. The native plant root biomass was lower under *S. canadensis* invasion due to its long and large roots, which inhibit the

native plant root development. However, the root biomass decreases under co-invasion and, more importantly, when the diversity and abundance of the invasive plant are increased (Table 1). This study suggests that invasive plant diversity positively affects native plants' response to invasion at a specific level of invasion plant richness.

It is well known that invasive plants are superior to native plants in terms of competitive ability and adaptation through their physiological and growth traits.<sup>50</sup> The native plant's physiological and growth parameters can be significantly impacted by the high level of invasive plant diversity and density.<sup>48</sup> For instance, the *Chl* and *Ln* of the native plant *L. indica* increase significantly under the high level of invasive plant diversity (Table 1). More importantly, the native plant response was more significant under invasive plant diversity than the single invasion but decreased under high invasive plant density (Figure 2). This study shows that the native plant response under invasion was positively impacted by increasing the invasive plant diversity (Figures 2 and 3). Increasing the invasive plant abundance affects the native plant response, which can be enhanced with the invasive plant diversity under the specific level of invasive plant richness.

It has been suggested that invasive plant richness can affect soil biota to increase their competitive effects, negatively affecting the native plant.<sup>51–53</sup> Thus, these studies suggest a mechanism by which invasive species diversity provides resistance to the native plant by enhancing its competitive ability. Many factors contribute to these effects of invasive plant diversity, including the structure or height of the neighboring vegetation, which directly affects the local plant's appearance and the size and composition of the soil that could subsequently spill over to the native plant physiological parameters. In this study, we observed that invasive plant diversity and abundance increase native plant growth under invasion. However, this positive impact was dependent on the invasive plant combinations. More importantly, the native plant growth parameters differed from one invasive plant combination to another, suggesting that the native plant response was strictly dependent on the invasive plant identity despite the positive effect of their diversity and abundance. Overall, the abundance and diversity of the invasive plant positively impact the native plant response at a specific level of richness. This positive effect becomes negative under high invasive plant density. This study showed significant differences in the native plant *L. indica* growth and physiological parameters depending on the invasive plant diversity and combination and the invasion type, except for the chlorophyll content, which showed no significant difference. Invasive plant diversity has a direct positive effect on the native plant response.

Although an essential number of studies on the effects of plant invasion on the native plant do not ideally provide much information about the native plant response, they provide insightful information about the native and invasive plant interaction and the mechanism underlying this interaction. Our experiment revealed that the native plant *L. indica* response depends on the invasive plants' identity, diversity, and abundance. Moreover, we observed a significant negative effect of the invasive plant on the native plant growth under *S. canadensis* invasion or in combination with another invasive plant. The influence of invasion on the native target plant *L. indica* depends on the invasive plant's identity and diversity. This study surprisingly shows that invasive plant diversity

increases native plant biomass. Moreover, invasive plant diversity positively affects the native plant response in a specific level of invasive plant richness since these positive effects reduce under high invasive plant density. More studies on the combination of invasive plants would significantly support invasive plant control and the reduction of native plant extinction.

## AUTHOR INFORMATION

### Corresponding Authors

**Iftikhar Ali** – Center for Plant Science and Biodiversity, University of Swat, Charbagh 19120, Pakistan; Department of Genetics and Development, Columbia University Irving Medical Center, New York, New York 10032, United States; [orcid.org/0000-0003-2319-2175](https://orcid.org/0000-0003-2319-2175); Email: [iftikharali@uswat.edu.pk](mailto:iftikharali@uswat.edu.pk)

**Jianfan Sun** – Institute of Environment and Ecology, School of the Environment and Safety Engineering, Jiangsu University, Zhenjiang 212013, China; Key Laboratory of Tropical Medicinal Resource Chemistry of Ministry of Education, Hainan Normal University, Haikou 571158, China; Email: [zxsfj@ujs.edu.cn](mailto:zxsfj@ujs.edu.cn)

### Authors

**Rakhwe Kama** – Institute of Environment and Ecology, School of the Environment and Safety Engineering, Jiangsu University, Zhenjiang 212013, China; Institute of Farmland Irrigation of CAAS, Xinxiang 453002, China

**Qaiser Javed** – Institute of Environment and Ecology, School of the Environment and Safety Engineering, Jiangsu University, Zhenjiang 212013, China; [orcid.org/0000-0003-2825-8217](https://orcid.org/0000-0003-2825-8217)

**Yanwen Bo** – Institute of Environment and Ecology, School of the Environment and Safety Engineering, Jiangsu University, Zhenjiang 212013, China

**Muhammad A. Imran** – Shenzhen International Graduate School, Tsinghua University, Shenzhen 518055, China

**Faten Zubair Filimban** – Division of Plant Sciences Department of Biology, King Abdulaziz University, Jeddah 21589, Saudi Arabia

**Zhongyang Li** – Institute of Farmland Irrigation of CAAS, Xinxiang 453002, China

**Xuhua Nong** – Key Laboratory of Tropical Medicinal Resource Chemistry of Ministry of Education, Hainan Normal University, Haikou 571158, China

**Sekouna Diatta** – Laboratory of Ecology, Faculty of Sciences and Technology, Cheikh Anta Diop University of Dakar, Dakar 50005, Senegal

**Guangqian Ren** – Institute of Environment and Ecology, School of the Environment and Safety Engineering, Jiangsu University, Zhenjiang 212013, China

**Sayed M Eldin** – Center of Research, Faculty of Engineering, Future University in Egypt, New Cairo 11835, Egypt

**Rashid Iqbal** – Department of Agronomy, Faculty of Agriculture and Environment, The Islamia University of Bahawalpur, Bahawalpur 63100, Pakistan

**Javed Iqbal** – Department of Botany, Bacha Khan University, Charsadda 24420 Khyber Pakhtunkhwa, Pakistan

Complete contact information is available at:

<https://pubs.acs.org/10.1021/acsomega.3c01139>

## Author Contributions

Conceptualization, R.K. and J.S.; methodology, Q.J.; software, Q.J., I.A., X.N., J.L., and M.A.I.; validation, Q.J., J.L., S.M.E., X.N., and Z.L.; formal analysis, R.K., I.A., and R.I.; investigation, Q.J., I.A., and R.K.; resources, J.S.; data curation, S.D.; writing—original draft preparation, I.A., R.K., and Q.J.; writing—review and editing, J.L., S.M.E., F.Z.F., Q.J., and G.R.; visualization, G.R.; supervision, F.Z.F. and Z.L.; project administration, J.S. and Y.B.; funding acquisition, S.M.E. and F.Z.F. All authors have read and agreed to the published version of the manuscript. R.K. and Q.J. contributed equally to this work.

## Notes

The authors declare no competing financial interest.

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