**Priority effects and competition by a native species inhibit an invasive species and may assist restoration**

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**Abstract**
Selecting native species for restoration is often done without proper ecological background, particularly with regard to how native and invasive species interact. Here, we provide insights suggesting that such information may greatly enhance restoration success. The performance of the native vine, *Pueraria lobata*, and that of the invasive bitter vine, *Mikania micrantha*, were investigated in South China to test how priority effects (timing and rate of germination and seedling growth) and competition (phytochemical effects and competitive ability) impact invasive plant performance. We found that, in the absence of competition, the germination rate of *M. micrantha*, but not of *P. lobata*, was significantly affected by light availability. *P. lobata* seedlings also performed better than those of *M. micrantha* during early growth phases. Under competition, negative phytochemical effects of *P. lobata* on *M. micrantha* were strong and we found *M. micrantha* to have lower performance when grown with *P. lobata* compared to when grown by itself. Relative interaction indexes indicated that, under interspecific competition, *P. lobata* negatively affected (i.e., inhibited) *M. micrantha*, whereas *M. micrantha* positively affected (i.e., facilitated) *P. lobata*. Higher photosynthetic efficiency and soil nutrient utilization put *P. lobata* at a further advantage over *M. micrantha*. Field trails corroborated these experimental findings, showing little recruitment of *M. micrantha* in previously invaded and cleared field plots that were sown with *P. lobata*. Thus, *P. lobata* is a promising candidate for ecological restoration and for reducing impacts of *M. micrantha* in China. This research illustrates that careful species selection may improve restoration outcomes, a finding that may also apply to other invaded ecosystems and species.

**KEYWORDS**
biotic interactions, competitive exclusion, ecological restoration, *Mikania micrantha*, priority effect, *Pueraria lobata*
1 | INTRODUCTION

Invasive plants pose significant threats to biodiversity, ecosystem services, regional economies, and public health (Castro-Díez et al., 2016; Ricciardi et al., 2017; Simberloff, 2005). What makes some species invasive and others not remains an open question in ecology. This reflects the high context dependency of biological invasions. That is, species’ traits interact in complex ways with conditions in the new environment to determine the outcome of non-native species introductions. These uncertainties also suggest that habitat-specific approaches are needed to effectively manage invasive populations (Tang et al., 2013).

Competition-based biotic resistance has been touted as an important mechanism to explain plant invasion success (Byun & Lee, 2017; MacDougall et al., 2009). Species-rich communities will utilize resources more completely than species-poor communities (Dimitrakopoulos & Schmid, 2004; Scherer-Lorenzen et al., 2003), thereby limiting the resources available to new arrivals (Fargione et al., 2003; Hector et al., 2001). Under these circumstances, only highly competitive non-native species may establish and become invasive. Species-poor communities, for example, in recently disturbed habitats, may also repel invasive species if resident native species are strong competitors. Mwangi et al.’s (2007) found such resource “pre-emption” to resist invasion during the early stages of succession. These authors showed that native species capable of earlier establishment, and that had faster growth rates, than non-native species, pre-empted resources, thereby negatively affecting slower-growing non-native species (Mwangi et al., 2007). These observations question the supposed link between high species richness and biotic resistance and suggest that resource pre-emption, via priority effects and strong competition, may resist invasion, even in species-poor communities.

From a restoration viewpoint, biotic resistance and resource pre-emption also suggest that selecting native plants with low niche differentiation, but with higher competitive ability, from the most common invasive species, may enhance restoration success following the clearing of invasive species (Funk et al., 2008; Roberts et al., 2010; Young et al., 2005). However, native species used in restoration are often selected with limited ecological background, especially with regard to species interactions. Native species selection can also be difficult in habitats where no information is available on the original or “pristine” state of communities (Ostertag et al., 2015). In China, we observed the native leghuminous vine, Pueraria lobata (Willd) Ohwi, and its cultivar Pueraria lobata var. thomsonii Bentham Vaniot der Maesen (hereafter collectively referred to as Pueraria), to often co-occur with the highly invasive vine, Mikania micrantha H. B. K. (hereafter referred to as Mikania). We also observed Pueraria seedlings to be generally taller than Mikania seedlings in the field, presumably because Pueraria seeds germinate earlier than Mikania seeds. Pueraria is widely distributed from South-East Asia to Australia, and it has vigorous growth (up to 26 cm per day or 15 m per growing season), with new roots being produced wherever nodes make contact with soil (EPPO, 1997). Pueraria is also frequently used to improve soil because of its ability to fix nitrogen through rhizobium symbiosis (Li et al., 2015), making it a promising candidate for restoration.

Here, we tested how interactions between native Pueraria and invasive Mikania vines in China impact on the performance of each species. Specifically, we measured germination, seedling growth, phytochemical effects, and competitive interactions between these two vines. Our aim was to determine whether Pueraria can outperform Mikania through priority effects (via the timing of germination and seedling growth) and high competitiveness (via phytochemical effects and competitive ability), and therefore whether this is a promising species for ecological restoration in areas previously invaded by Mikania.

2 | MATERIALS AND METHODS

2.1 | Seed germination and seedling growth performance

2.1.1 | Seed collection and scarification

Seeds of Mikania were collected during the flowering and seeding period (around November to December 2016) from a nursery site at Guangdong Academy of Agricultural Sciences, Guangzhou, China. Seeds of P. lobata var. thomsonii were bought from a commercial company. Half of the Pueraria seeds were soaked in 10 ml of 98% H2SO4 for 15–20 min, followed by rinsing with distilled water. The other half of Pueraria seeds and all Mikania seeds were sterilized by submersion in 10% sodium hypochlorite solution for 3 min followed by washing with distilled water.

2.1.2 | Response of seed germination to light

Photosensitivity of seed germination has a significant effect on the survival and establishment of plants (Finch-Savage & Leubner-Metzger, 2006). It was previously reported that Mikania seeds do not germinate easily under dark conditions and that the soil seed bank of this species produces very few seedlings in the absence of light (Li et al., 2002). Whether seed germination of Pueraria is dependent on the light is not clear. We designed an experiment to test to what extent light influences the germination of Pueraria and Mikania seeds.

Fifty sterilized Mikania seeds and 50 sterilized as well as 50 H2SO4-treated seeds of Pueraria were put in a petri dish containing two layers of moist filter. Each seed type was replicated five times (n total = 30). Petri dishes were placed in incubators (RXZ Intelligent Type, Ningbo Jiangnan Instrument Factory, China) and subjected to one of two incubation conditions: (a) full illumination and darkness for 12 hr, at 30 and 27°C, day/night temperature, respectively; (b) darkness for 24 hr (30/27°C, day/night temperature). Humidity was maintained at 65% throughout the experiment. The number of germinated seeds was counted daily at 24 hr of intervals over a 14-day
period. We considered the emergence of radicles (>1 mm) from the seed coat as an indicator for successful germination. Finally, germination rate (GR) and germination index (GI) (Javaid & Tanveer, 2014) were calculated as follows:

$$\text{GR} = \frac{\text{Number of germinated seeds}}{\text{Total number of tested seeds}} \times 100\%$$

$$\text{GI} = \frac{\sum \left( \frac{\text{Gt}}{\text{Dt}} \right) \times \left( \text{Gt} - \text{Number of germinated seed on day t} \right)}{\text{Dt} - \text{day t}}.$$ 

2.1.3 Seedling growth

Fifty sterilized Mikania seeds and 50 sterilized as well as 50 H2SO4-treated seeds of Pueraria were evenly sown in a pot (diameter: 12–19 cm, height: 15 cm) filled with nutrient-rich soils. Each seed lot planting was replicated five times. Pots were covered with plastic film and kept in an artificial climate incubator (RXZ Intelligent, Ningbo Jiangnan Instrument Factory) set for full illumination and darkness for 12 hr each, and 30 and 27°C, day/night temperature, respectively, with 65% humidity. Once emerging seedlings broke the soil surface, the plastic film was removed and pots moved to the glasshouse located at the School of Life Sciences, South China Normal University. During the growth period, seedlings were thinned out to make sure that equal numbers of seedlings remained in all pots. Pots were watered every day and were randomized weekly. Plant height, number of leaves, and total biomass from five plants of each pot were measured every 15 days, and plants were harvested after 60 days of growth. Total biomass was calculated after drying plant material for at least 48 hr at 65°C in an oven.

2.1.4 Phytochemistry

Allelopathy is an important mechanism of interspecific competition between plants, whereby phytochemicals released by one species inhibit the growth of another species (Rice, 1984). In order to compare the allelopathic potential of Pueraria and Mikania, a bioassay of aqueous phytochemical extracts on seed germination was carried out in a reciprocal experiment. Fresh stems and leaves of both species were collected from the biological garden in South China Normal University (23°8′N, 113°20′E). These were soaked in distilled water at room temperature for 48 hr. Extracts were diluted to obtain high (0.05 g/ml) and low (0.025 g/ml) phytochemical concentrations, while distilled water was used in control treatments. Fifteen milliliters of aqueous plant extract was added to a petri dish containing 50 seeds of the target species and kept in an incubator (RXZ Intelligent, Ningbo Jiangnan Instrument Factory) set at full illumination and darkness for 12 hr at 30 and 27°C day/night temperature, respectively, and a constant humidity of 65%. Each treatment was replicated five times. Moisture for each petri dish was maintained by adding equal amounts of treatment-specific solution in subsequent days. Seedlings were photographed after 10 days to measure root length and seedling height using ImageJ software (ImageJ2x). Germination rate and germination indices were calculated as discussed above. The response index (RI) and synthetical effects (SE) provide more direct and accurate comparison for phytochemical effects between species (Williamson & Richardson, 1988). Response index was calculated as $R = \left( \frac{T}{C} \right) - 1$, and synthetical effects (SE) as the average value of RI (Ma et al., 2006), where T is the treatment value, C is the control value. When $T > C$, RI > 0, it indicates the promoting effect; when $T < C$, RI < 0, it indicates the inhibiting effect, and the absolute value of RI represents the allelopathy intensity.

2.2 Plant performance and interspecific competition

2.2.1 Experimental design

To assess the competitive interactions between Mikania and Pueraria, healthy seedlings of both species with identical growth and developmental stages were selected and transplanted in outdoor pots (18–28 cm in diameter, 21 cm in height). Surface soil (0–20 cm) in the biological garden of South China Normal University was collected and used as growth medium. The soil was broken up and mixed with appropriate amount of river sand and organic fertilizer to improve gas permeability and fertility. The soil was broken up and mixed with appropriate amount of river sand and organic fertilizer to improve gas permeability and fertility. The soil was broken up and mixed with appropriate amount of river sand and organic fertilizer to improve gas permeability and fertility. To assess the competitive interactions between Mikania and Pueraria, healthy seedlings of both species with identical growth and developmental stages were selected and transplanted in outdoor pots (18–28 cm in diameter, 21 cm in height). Surface soil (0–20 cm) in the biological garden of South China Normal University was collected and used as growth medium. Each treatment was replicated 15 times. All pots were put at a naturally lit experimental site in the biological garden, received equal amounts of nutrients and water, and were randomized every three days.

2.2.2 Gas exchange and chlorophyll fluorescence

After 120 days of growth, three mature leaves of the same orientation (middle and upper leaves) from five plants of each treatment were selected and gas exchange and chlorophyll fluorescence measured. The net photosynthetic rate (Pn) and transpiration rate (Tr) were measured using a portable infrared gas analyzer Li-6400 (LI-COR, Inc.) at a photosynthetic photon flux density (PPFD) of 800 μmol m−2 s−1. At the same time, the maximum photochemical efficiency (Fv/Fm), the effective quantum yield (Yield), and the electron transport rate (ETR) were measured at actual light intensity using a portable pulse-modulated fluorometer (PAM-2100, Walz, Effeltrich). Finally, water use efficiency (WUE = Pn/Tr) and Rubisco content (Rubisco [g/m²] = ETR × 0.014) were estimated (Evans & Poorter, 2001).

2.2.3 Growth performance, competition, and soil nitrogen

Plant height, root length, number of branches, and biomass were determined for all five replicates at days 60, 90, and 120 following
planted. Plant height and root length were measured with a measure tape (accuracy of 1 mm), and the number of branches was counted. Biomass was dried in oven until constant weight at 65°C before being weighed.

We calculated the relative interaction index (RII) (Armas et al., 2004; Domènech & Vilà, 2008; Li et al., 2015) to estimate the intensity of competition as $\text{RII} = \frac{Bw - Bo}{Bw + Bo}$, where $Bw$ is the individual biomass of the target plant when growing with another plant (i.e., under interspecific competition), and $Bo$ is the individual biomass of the target plant when growing by itself (i.e., under intraspecific competition) after 120 days. RII has value range from $-1$ to $+1$, with negative values indicating competition (i.e., growth of the target species is reduced) while positive values indicate facilitation (i.e., growth of the target species is promoted).

Interspecific competition may change soil nutrient levels. Since Pueraria is a legume, it can elevate soil nitrogen availability through symbiosis with nitrogen-fixing rhizobium. This may also result in changes in soil microbial biomass nitrogen. We compared soil nitrogen and the soil microbial biomass nitrogen between Pueraria and Mikania. For each species, plants from five pots (grown in monoculture) were excavated and rhizosphere soils collected after 120 days of growth. Total nitrogen content of these soils was determined using the Kjeldahl method (air-dried soil passed through a 0.15-mm sieve), while levels of nitrogen were measured in fresh soil (passed through a 1-mm sieve) by continuous flow analyzer (Proxima, Alliance Instruments). Soil microbial biomass nitrogen was measured using a chloroform fumigation method (Jenkinson & Powlson, 1976).

### 2.3 Field experiment

An experimental site was identified in a Mikania infested area in University Town, Guangzhou, China (lat. 23°3′N, long. 113°23′E). The region has a subtropical monsoonal climate with an annual mean temperature of 21-24°C and annual average precipitation of ca. 1,800 mm. The coverage of Mikania at the site was about 85%. Soil at the site contained 3.49 g/kg of soil organic matter (SOM), 0.28 g/kg of total nitrogen (TN), 1.91 mg/kg of NO$_3$–N, 5.65 mg/kg of NO$_2$–N, 1.35 g/kg of total phosphorus (TP), 74.81 mg/kg of available phosphorus (AP), 5.51 mg/kg of microbial biomass nitrogen (MBN), and had a pH of 4.79.

Twenty-four 2 m × 2 m plots, separated by at least 50 cm, were established at the study site. All above-ground vegetation and most roots were removed in 12 plots to mimic Mikania control and removal. The remaining 12 plots were left untouched. Four sowing densities of Pueraria (0, 100, 200, and 400 grains/m$^2$) were each replicated in three cleared and three uncleared plots. All seeds were treated with H$_2$SO$_4$ and sown after radicle emergence. Pueraria and Mikania plants in each plot were harvested six months after sowing and fresh above-ground biomass (stem + leaf material) determined for each species. Samples were also oven-dried to determine dry weight.

### 2.4 Statistical analysis

All statistical analyses were performed using SPSS 18.0 software (SPSS Inc.). Plant performance variables, gas exchange parameters, the fluorescence variables, and soil nitrogen indices between were compared between treatments using one-way ANOVAs, followed by Duncan post hoc tests at $p < .05$. For germination rates and germination index analyses, significant differences under light and dark conditions were determined using t tests for two independent samples. We used linear regression to assess the response of total biomass and seedling height to planting time. Moreover, for total biomass and seedling height, significant differences between Pueraria and Mikania were determined using t tests for two independent samples in each stage throughout the growth period. General linear models were used to assess the effects of time and plant species as well as their interaction on total biomass and plant height during seedling growth period, and the effects of Mikania removal and sowing density of Pueraria seeds, as well as their interaction, on Mikania and Pueraria biomass under field conditions. The SigmaPlot 12.0 software was used to visualize data.

### 3 Results

#### 3.1 Response of seed germination to light seedling growth

The germination rate of Pueraria seeds was significantly lower than for Mikania seeds, especially under light conditions (Table 1). However, sulfuric acid treatment significantly improved both the

| Species/Index | Germination rate (%) | Germination index |
|---------------|----------------------|-------------------|
|               | Light | Dark | Sig. | Light | Dark | Sig. |
| Mikania seeds | 60.00 ± 0.07b | 40.00 ± 0.12b | * | 6.86 ± 0.74b | 3.52 ± 1.17c | * |
| Pueraria seeds | 32.67 ± 0.03c | 32.67 ± 0.01b | ns | 7.26 ± 0.76b | 6.83 ± 0.91b | ns |
| Pueraria seeds treated by H$_2$SO$_4$ | 78.67 ± 0.01a | 82.00 ± 0.02a | ns | 34.63 ± 0.43a | 38.89 ± 0.84a | ns |

Note: Data with different letters for the same column indicate significant difference (one-way ANOVA, followed by Duncan test, $p < .05$); "$p < .05$,
ns-no significance between light and dark, followed by t test of two independent samples.
germination rate and germination index of Pueraria seeds. Pueraria seeds (treated by $\text{H}_2\text{SO}_4$) germinated between 5.05 and 11.05 times faster than those of Mikania. The germination of Pueraria seeds was not affected by the light. Conversely, the germination rate and germination speed of Mikania were lower under the dark than under light conditions (Table 1).

**TABLE 2** Results of general linear models assessing the effects of time and plant species as well as their interaction on total biomass and plant height during seedling growth period

| Independent variables | Total biomass | Plant height |
|-----------------------|---------------|--------------|
| Time                  | $df$ | $F$ | $p$ | $df$ | $F$ | $p$ |
| Time                  | 4    | 68.98 | .000 | 4    | 430.37 | .000 |
| Plant species         | 1    | 142.03 | .000 | 1    | 336.48 | .000 |
| Time * Plant species  | 4    | 31.22 | .000 | 4    | 21.66 | .000 |

**FIGURE 1** Changes in seedling growth of Mikania and Pueraria over time (average $\pm$ SD, $n = 5$). P – Pueraria seedlings; sP – Pueraria seedlings germinated from sulfuric acid-treated seeds; M – Mikania seedlings. Red dotted lines indicate the equivalent level of the performance between Mikania and Pueraria seedling.
Results from general linear models showed that growing time, plant species, and their interaction had a significant effect on total biomass and plant height. The effects of growing time and plant species on plant height were much greater than on total biomass, whereas their interaction on plant height was lower than on total biomass (Table 2). Both H$_2$SO$_4$-treated and sterilized Pueraria seeds broke the soil surface about a week earlier than Mikania seeds. Mikania seedlings were small and slim at day 15, while Pueraria seedlings of the same age were taller and stronger. Pueraria seedlings from H$_2$SO$_4$-treated seeds were the best in appearance at day 15 compared to all other seedlings (Figure 1a). The size of Mikania seedlings was only similar to 15-day-old Pueraria seedlings after 45 days of growth. Pueraria started to form tendrils after 60 days but not Mikania (Figure 1a). There were no significant differences in total biomass, number of leaves, and plant height between Pueraria seedlings, irrespective of scarification treatment, and both seed types performed better than Mikania (Figure 1b–d). Total biomass and plant height of 45-day-old Mikania seedlings were equivalent to that of Pueraria at 15 days (Figure 1b,d). Furthermore, linear regression analysis and t test for two independent samples indicated that the growth rate of Pueraria seedlings was significantly higher than that of Mikania seedlings in each stage throughout the growth period.

### 3.2 | Phytochemistry

Aqueous phytochemical extracts of Pueraria inhibited the germination and seedling growth of Mikania, irrespective of concentration (Table 3). This potential allelopathic effect was stronger for extracts from Pueraria stems than extracts from leaves. The overall synthetical effect value of Pueraria on Mikania was $-1.39$.

Aqueous extracts of Mikania leaves and stems with lower concentration had inhibitory effects on the seed germination and seedling growth of Pueraria; however, its stem aqueous extract with high concentration promoted seed germination of Pueraria (Table 4). The overall synthetical effect value of Mikania on Pueraria was $-0.64$. The allelopathic inhibition of Pueraria on Mikania is therefore stronger than that of Mikania on Pueraria.

### 3.3 | Plant performance and interspecific competition

Mikania had slow growth during the first month. For the next 2–4 months, Pueraria showed much higher performance than Mikania under interspecific competition, irrespective of planting arrangement (Figure 2).

#### 3.3.1 | Mikania growth performance

In early and mid-growth stages (60 days and 90 days, respectively), there was no significant difference in root length of Mikania plants between treatments (Table 5). In later growth stages (i.e., 120 days), root length in higher mixed ratios of Pueraria to Mikania, that is, 1M3P and 2M2P, was significantly lower than for the 3M1P ratio or when grown by itself (4M) (Table 5). This was similar for plant height between 60 and 90 days of growth.

### Tables

| Phytochemicals | Leaves | Stems |
|----------------|--------|-------|
| Pueraria       |        |       |
| Phytochemicals | 0.025 g/ml | 0.05 g/ml | 0.025 g/ml | 0.05 g/ml | Overall |
| RI (germination rate) | -0.05 | -0.03 | -0.09 | -0.22 |
| RI (germination index) | -0.07 | -0.04 | -0.06 | -0.13 |
| RI (root length) | -0.34 | -0.27 | -0.43 | -0.68 |
| RI (height) | 0.20 | 0.22 | 0.24 | 0.36 |
| Synthetical effects | -0.26 | -0.12 | -0.34 | -0.67 | -1.39 |

| Phytochemicals | Leaves | Stems |
|----------------|--------|-------|
| Mikania        |        |       |
| Phytochemicals | 0.025 g/ml | 0.05 g/ml | 0.025 g/ml | 0.05 g/ml | Overall |
| RI (germination rate) | 0.02 | 0.00 | -0.06 | 0.11 |
| RI (germination index) | -0.16 | -0.08 | -0.12 | 0.12 |
| RI (root length) | -0.17 | -0.29 | -0.13 | -0.17 |
| RI (height) | 0.09 | 0.02 | 0.12 | 0.06 |
| Synthetical effects | -0.22 | -0.35 | -0.19 | 0.12 | -0.64 |
being significantly lower in all the three competition treatments, that is, 3M1P, 2M2P, and 1M3P, compared to when grown by itself (4M) (Table 5). In the competition experiment, as the ratio of *Pueraria* to *Mikania* increased, *Mikania* plant height decreased significantly following 120 days of growth (Table 5). *Mikania* did not branch after the first 60 days of growth, and there were no significant differences in the number of branches between treatments until 90 days of growth. Branch numbers of *Mikania* also declined gradually as the ratio of *Pueraria* to *Mikania* increased at day 120 (Table 5).

**FIGURE 2** Changes in phenotypic characteristics under interspecific competition (average ± SD, n = 15). 4M – four *Mikania* seedlings planted by itself; 3M1P – three *Mikania* seedlings planted with one *Pueraria* seedling; 2M2P – two *Mikania* seedlings planted with two *Pueraria* seedlings; 1M3P – one *Mikania* seedling planted with three *Pueraria* seedlings; 4P – four *Pueraria* seedlings planted by itself

**TABLE 5** Changes of *Mikania* growth index under interspecific competition (average ± SD, n = 5)

| Growth index | Time (days) | 4M         | 3M1P       | 2M2P       | 1M3P       |
|--------------|-------------|------------|------------|------------|------------|
| Root length (cm) | 60         | 27.05 ± 3.92a | 25.11 ± 2.01a | 28.23 ± 2.57a | 25.90 ± 5.14a |
|               | 90         | 43.73 ± 4.02a | 45.38 ± 9.26a | 47.30 ± 9.90a | 52.53 ± 7.13a |
|               | 120        | 48.75 ± 9.43a | 39.76 ± 6.05b | 30.79 ± 3.72c | 26.32 ± 2.10c |
| Height (cm)   | 60         | 30.64 ± 6.49a | 18.24 ± 2.20b | 20.72 ± 2.40b | 17.26 ± 3.40b |
|               | 90         | 161.53 ± 27.53a | 114.82 ± 17.43b | 109.00 ± 14.01b | 83.53 ± 15.65c |
|               | 120        | 223.25 ± 25.52a | 199.92 ± 30.23b | 173.17 ± 38.60c | 102.10 ± 16.64d |
| Branches      | 60         | 0           | 0           | 0           | 0           |
|               | 90         | 4.3 ± 1.15a  | 3.3 ± 1.12a  | 3.0 ± 0.89a  | 2.7 ± 1.15a  |
|               | 120        | 8.4 ± 1.60a  | 7.3 ± 1.44ab | 6.6 ± 1.51b  | 4.2 ± 1.30c  |

Note: 4M – four *Mikania* seedlings planted by itself; 3M1P – three *Mikania* seedlings planted with one *Pueraria* seedling; 2M2P – two *Mikania* seedlings planted with two *Pueraria* seedlings; 1M3P – one *Mikania* seedling planted with three *Pueraria* seedlings. Means within the same row followed by different small letters indicate significant difference at p < .05 (Duncan test).
Total biomass, stem biomass, and root biomass of *Mikania* were significantly lower in all three competition treatments compared to when grown alone after 60 days of growth (Figure 3). These biomass fractions were significantly lower in the 2M2P and 1M3P than in the 4M and 3M1P planting arrangements after 90 days of growth (Figure 3). Stem biomass decreased gradually from 4M to 1M3P over the same period. Changes in the total biomass and leaf biomass significantly decreased in the order of: 1M3P < 2M2P < 3M1P < 4M, following 120 days of growth (Figure 3). Stem biomass and root biomass showed a similar trend (1M3P < 2M2P < 3M1P < 4M) as the mix ratio of *Pueraria* to *Mikania* increased (Figure 3).

### 3.3.2 *Pueraria* growth performance

In early growth stages (i.e., after 60 days), there was no significant difference in root length of *Pueraria* seedlings between planting arrangements (Table 6). In mid-growth stages (i.e., after 90 days), seedling root length in 1P3M was significantly higher than for the other treatments and in late growth stages (i.e., after 120 days of growth), and *Pueraria* root length gradually increased with an increase in *Mikania* to *Pueraria* planting ratios (Table 6). Variation in plant height followed a similar pattern (Table 6). Plant height of *Pueraria* in all the three competition treatments was higher than that of *Pueraria* grown...
by itself (4P) after 90 days of growth, and increased significantly as the ratios of Mikania to Pueraria increased after 120 days of growth (Table 6). The number of branches of Pueraria did not differ for the first 90 days and at 120 days between treatments, but they were higher in higher ratios of Mikania to Pueraria (1P3M and 2P2M) than in lower ratios (3P1M and 4P; Table 6).

We found no significant differences in the biomass production of Pueraria between treatments during early growth stages (i.e., after 60 days; Figure 4). In mid-growth stages (i.e., 90 days), Pueraria biomass started to increase gradually as the ratio of Mikania to Pueraria increased (Figure 4). After 120 days of growth, Pueraria grown with high-density Mikania (i.e., 1P3M) produced the most biomass (Figure 4).

3.3.3 | Relative interaction index (RII)

The relative interaction index of Mikania, when grown in the presence of Pueraria, was negative (RII<sub>3M1P</sub> = −0.253, RII<sub>2M2P</sub> = −0.379, RII<sub>1M3P</sub> = −0.625), indicating an inhibitory effect by Pueraria on Mikania growth (Figure 5a). Furthermore, the magnitude of these negative effects increased with increased ratios of Pueraria to Mikania. Mikania showed an opposite trend, positively effecting the growth of Pueraria (RII<sub>3P1M</sub> = 0.131, RII<sub>2P2M</sub> = 0.281, RII<sub>1P3M</sub> = 0.430). The magnitude of these positive effects increased as Mikania to Pueraria ratios increased in planting arrangements (Figure 5b).

3.3.4 | Gas exchange and chlorophyll fluorescence

The net photosynthetic rate (Pn) of Pueraria was significantly higher than that of Mikania when grown alone or under interspecific competition (Figure 6a). Competition did not affect the Pn of Pueraria but reduced the Pn of Mikania when the mix ratio of Pueraria to Mikania reached 3:1 (Figure 6a). Water use efficiency (WUE) showed a similar response with the WUE of Pueraria being significantly higher than that of Mikania under various planting arrangements (Figure 6b).

When Mikania was grown alone or in lower mix ratios of Pueraria to Mikania (1:3), the maximal photochemical efficiency (Fv/Fm) of dark-relaxed Photosystem II (the photosystem that splits water to evolved oxygen) decreased significantly compared to that of Mikania grown with higher mix ratios of Pueraria to Mikania (2:2 and 3:1) (Table 7). However, the photochemical yield (Yield) of photosystem II of Mikania under illumination and the highest Pueraria to Mikania mix ratio (i.e., 3:1) was significantly lower than in other planting arrangements (Table 7). The electron transport rate (ETR) of Mikania, estimated by chlorophyll fluorescence, decreased significantly as the mix ratio of Pueraria to Mikania increased. Changes in Rubisco (the enzyme complex that fixes CO₂ in plant leaves) showed a similar trend (Table 7). However, Pueraria showed the opposite trend for chlorophyll fluorescence parameters. First, Fv/Fm of Pueraria was not affected by any of the competition treatments. Secondly, Yield, ETR, and Rubisco of Pueraria increased significantly as Mikania to Pueraria mix ratios increased (Table 7).

3.3.5 | Soil nitrogen characteristics

Following 120 days of growth, ammonium and microbial biomass nitrogen (MBN) were the highest in Pueraria soils among the three soils we analyzed, while nitrate nitrogen and total nitrogen were higher in Pueraria soils than in Mikania soils. There were no significant differences in nitrate nitrogen and total nitrogen between Pueraria soils and the initial soils (Table 8).

3.4 | Field experiment

Following clearing and sowing of Pueraria seeds in the field, we found that the regeneration of Mikania declined dramatically after six months (by −79.8%, −92.0% and −84.3%, at sowing densities of

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**TABLE 6  Changes in Pueraria growth index under interspecific competition (average ± SD, n = 5)**

| Growth index | Time (days) | 4P | 3P1M | 2P2M | 1P3M |
|--------------|-------------|----|------|------|------|
| Root length (cm) | 60          | 30.93 ± 6.79a | 32.58 ± 5.10a | 38.10 ± 7.86a | 41.97 ± 10.82a |
|                | 90          | 53.23 ± 9.81b | 47.77 ± 9.48b | 56.72 ± 13.45b | 67.00 ± 5.07a  |
|                | 120         | 54.54 ± 5.08b | 58.23 ± 8.02ab| 62.66 ± 10.24ab| 65.14 ± 8.57a  |
| Height (cm)    | 60          | 36.46 ± 6.03a | 41.07 ± 7.57a | 32.50 ± 7.83a | 38.10 ± 1.92a  |
|                | 90          | 110.26 ± 19.40b| 138.11 ± 13.08a| 138.40 ± 18.49a| 149.93 ± 11.68a|
|                | 120         | 195.00 ± 20.12c| 219.33 ± 19.20b| 244.08 ± 24.97a| 245.82 ± 41.79a|
| Branches       | 60          | 2.8 ± 0.39a   | 2.8 ± 0.44a   | 2.7 ± 0.52a    | 2.7 ± 0.58a    |
|                | 90          | 7.6 ± 1.98a   | 7.3 ± 1.80a   | 8.0 ± 1.26a    | 7.7 ± 1.15a    |
|                | 120         | 9.3 ± 1.74b   | 8.6 ± 1.59b   | 13.1 ± 2.64a   | 12.8 ± 2.05a   |

Note: 4P – four Pueraria planted by itself; 3P1M – three Pueraria seedlings planted with one Mikania seedling; 2P2M – two Pueraria seedlings planted with two Mikania seedlings; 1P3M – one Pueraria seedling planted with three Mikania seedlings; means within the same row followed by different small letters indicate significant difference at p < .05 (Duncan test).
100, 200, and 400 Pueraria seeds/m$^2$, respectively) compared to the control sites. Pueraria biomass increased significantly with increased sowing density (Figure 7a). Similar trends were observed when Pueraria seeds were sown in soils without the removal of Mikania. Although not as dramatic, the regeneration of Mikania significantly decreased by up to 55.0% when Pueraria was sown at a density of 400 seeds/m$^2$ (Figure 7b). Mikania regeneration was lowest in plots where Mikania was removed and when Pueraria sowing density was 200 seeds/m$^2$, while regeneration decreased significantly under a sowing density of 400 seeds/m$^2$ in plots without Mikania removal. Results from general linear models showed that removal, sowing density, and their interaction had a significant effect on above-ground biomass of both Mikania and Pueraria. The effect of Mikania removal treatments was higher than that of sowing density on biomass of both vine species, whereas the removal of Mikania had a lower impact on Mikania than Pueraria performance (Table 9).

4 | DISCUSSION

Understanding the ecological mechanisms that underlie the invasion success of non-native species has attracted much research attention, yet surprisingly little is known on how these processes may inform management and the restoration of invaded habitats. Using
native and invasive vines, we provide evidence to suggest that with careful selection of native species, based on intrinsic ecological and physiological attributes, enhanced ecological restoration outcomes may be achieved.

4.1 Differences between native and invasive species as modulated by abiotic conditions

Abiotic environmental conditions represent a significant barrier to the establishment success of, and subsequent invasion by, non-native species (Blackburn et al., 2011). We found the rate and speed of germination of scarified *Pueraria* seeds to be much higher than for *Mikania* seeds, independent of light exposure. *Pueraria* seedlings were also taller and stronger than *Mikania* during early growth, becoming more evident over time, as indicated by total biomass accumulation, number of leaves produced, and plant height. *Pueraria* seeds germinated one week earlier than *Mikania* seeds and the growth performance of *Mikania* seedlings lagged behind *Pueraria* seedlings for at least 1 month. Thus, abiotic conditions differentially affected the performance of these two vines and early emergence, fast germination, and seedling growth may lead to a priority effect of *Pueraria* on *Mikania*, and possibly to the pre-emption of resources. Early emergence is also expected to increase other components of plant fitness such as seedling growth (Verdu & Traveset, 2005). Others have previously found native species to similarly suppress the performance of invaders, suggesting that the ability of pioneer native species to rapidly colonize available habitat may suppress invasive species (Firn et al., 2010).

4.2 Interspecific competition between *Mikania* and *Pueraria*

Both our phytochemical and interspecific competition experiments supported the hypothesis of competitive exclusion of invasive *Mikania* by native *Pueraria*. Plants can affect their neighbors in numerous ways through the release of phytochemical compounds into the environment (He et al., 2012). For example, inhibitory allelopathic chemicals are widely reported as major contributors to enhanced interspecific competition (Bais et al., 2003; Callaway & Ridenour, 2004; Inderjit et al., 2008; Yuan et al., 2013). Our results showed that the total synthetical effects of *Pueraria* on *Mikania* were much higher than vice versa, indicating strong inhibitory effects of *Pueraria* on *Mikania*. A possible explanation for this could be the release of allelochemicals by *Pueraria* which enhance its competitive ability (i.e., interference competition) over *Mikania* by affecting the early growth performance of *Mikania*. Others have also found *Mikania* to be very sensitive to allelopathic chemicals produced by native plants (e.g., *Dicranopteris pedate*; Zhao et al., 2008).

The higher performance of *Pueraria* compared to *Mikania* that we observed for germination and seedling growth, as well as allelopathy, was also mirrored in plant performance under interspecific competition. That is, *Pueraria* negatively affected *Mikania* while *Mikania* had the opposite effect on *Pueraria*. Previous work also found sweet potato to have similar effects on *Mikania* (Shen et al., 2015). Both *Pueraria* and *Mikania* are perennial evergreen vines with large capacities for asexual propagation, and the two species share many morphological similarities, occupying virtually the same niche in agroforestry systems (Li et al., 2012; Lian et al., 2006). Our results provide some evidence for competitive exclusion of *Mikania* by *Pueraria*, suggesting that native species with similar traits, and with similar niche requirements to non-native species, may impede invasion (Emery, 2007; MacDougall et al., 2009). Tillering, branching, and plant height are important traits that facilitate competition in plants, and have been considered important for pre-empting resources during scramble competition (Jiang et al., 2008). The branch number and plant height of *Mikania* in the present study markedly decreased with higher planting ratios of *Pueraria* to *Mikania*. It is noteworthy that *Pueraria* is also a highly successful invasive species outside of its native range (Bentley & Mauricio, 2016; Kartzinel et al., 2015).

The apparent superior competitive ability of *Pueraria* could also be related to its photosynthetic characteristics. We found
Figure 6  Changes in net photosynthetic rate ($P_n$) and water use efficiency (WUE) under interspecific competition (average ± SD, $n = 9$). 4M – four Mikania seedlings planted by itself; 3M1P – three Mikania seedlings planted with one Pueraria seedling; 2M2P – two Mikania seedlings planted with two Pueraria seedlings; 1M3P – one Mikania seedling planted with three Pueraria seedlings; 4P – four Pueraria seedlings planted by itself. Different letters above the error bars indicate significant difference at $p < .05$ (Duncan test).

| Plant species | $Fv/Fm$   | Yield      | ETR ($\mu$mol m$^{-2}$ s$^{-1}$) | Rubisco (g/m$^2$) |
|---------------|-----------|------------|----------------------------------|-------------------|
| 1M 3P         | 0.807 ± 0.01a | 0.14 ± 0.03b | 44.96 ± 3.34d                   | 0.63 ± 0.05d      |
| 2M 2P         | 0.803 ± 0.01a | 0.23 ± 0.02a | 52.80 ± 2.37c                   | 0.74 ± 0.03c      |
| 3M 1P         | 0.784 ± 0.03b | 0.26 ± 0.01a | 66.24 ± 1.24b                   | 0.93 ± 0.02b      |
| 4M            | 0.799 ± 0.01b | 0.24 ± 0.01a | 86.42 ± 3.42a                   | 1.21 ± 0.05a      |
| 1P 3M         | 0.825 ± 0.02a | 0.43 ± 0.03a | 118.42 ± 0.79a                  | 1.66 ± 0.01a      |
| 2P 2M         | 0.831 ± 0.01a | 0.37 ± 0.02b | 71.84 ± 1.63b                   | 1.01 ± 0.02b      |
| 3P 1M         | 0.828 ± 0.01a | 0.23 ± 0.04c | 60.90 ± 1.24c                   | 0.85 ± 0.02c      |
| 4P            | 0.826 ± 0.01a | 0.19 ± 0.01d | 45.80 ± 2.74d                   | 0.64 ± 0.04d      |

Note: 1M3P – one Mikania seedling planted with three Pueraria seedlings; 2M2P – two Mikania seedlings planted with two Pueraria seedlings; 3M1P – three Mikania seedlings planted with one Pueraria seedling; 4M – four Mikania seedlings planted by itself; 1P3M – one Pueraria seedling planted with three Mikania seedlings; 2P2M – two Pueraria seedlings planted with two Mikania seedlings; 3P1M – three Pueraria seedlings planted with one Mikania seedling; 4P – four Pueraria seedlings planted by itself. Means within the same column (divided two groups, upper and lower parts as one independent group, respectively) followed by different small letters indicate significant difference at $p < .05$ (Duncan test).

Table 7  Changes in chlorophyll fluorescence parameters under interspecific competition (average ± SD, $n = 5$)

| Soil samples | $NH_4^+$-N (mg/kg) | MBN (mg/kg) | $NO_3^-$-N (mg/kg) | TN (g/kg) |
|--------------|--------------------|-------------|--------------------|-----------|
| Initial soil | 5.15 ± 0.81b       | 53.60 ± 13.70c | 8.58 ± 1.09a       | 0.93 ± 0.05a |
| Mikania soil | 4.75 ± 1.41b       | 95.60 ± 4.90b | 7.03 ± 1.06b       | 0.81 ± 0.08b |
| Pueraria soil| 27.15 ± 1.12a      | 141.50 ± 16.6a | 8.90 ± 1.35a       | 0.97 ± 0.06a |

Note: Data with different letters in the same column indicate significant difference at $p < .05$ (Duncan test).

Abbreviations: MBN, microbial biomass nitrogen; TN, total nitrogen.

Table 8  Soil nitrogen characteristics after Mikania and Pueraria, respectively, planted alone for 120 days in the pot experiment (average ± SD, $n = 3$)

| Soil samples | $NH_4^+$-N (mg/kg) | MBN (mg/kg) | $NO_3^-$-N (mg/kg) | TN (g/kg) |
|--------------|--------------------|-------------|--------------------|-----------|
| Initial soil | 5.15 ± 0.81b       | 53.60 ± 13.70c | 8.58 ± 1.09a       | 0.93 ± 0.05a |
| Mikania soil | 4.75 ± 1.41b       | 95.60 ± 4.90b | 7.03 ± 1.06b       | 0.81 ± 0.08b |
| Pueraria soil| 27.15 ± 1.12a      | 141.50 ± 16.6a | 8.90 ± 1.35a       | 0.97 ± 0.06a |

Note: Data with different letters in the same column indicate significant difference at $p < .05$ (Duncan test).
that gas exchange and chlorophyll fluorescence parameters give *Pueraria* an apparent advantage over *Mikania*. *Pueraria* produced much more leaf biomass per plant than *Mikania* under interspecific competition, which resulted in partial shading of the latter’s leaves. The lower growth irradiance to which *Mikania* leaves were exposed due to lower light availability under these conditions may also cause lower Rubisco and cytochrome *bf* content. The latter is often a rate-limiting bottleneck in electron flow from PSII to PSI (Anderson et al., 1988). Since *Mikania* is intrinsically heliophilic, with a high light compensation point of photosynthesis (1,002 μmol m⁻² s⁻¹) (Wen et al., 2000), it is capable of rapid growth under high light conditions. However, there is a sharp decline in this response under shaded conditions (Liao et al., 2003), making it be vulnerable to competition.

Our recent work also found *Mikania* invasion to lead to substantial losses of soil nitrogen (Liu et al., 2020), which provides a good opportunity for soil remediation by leguminous plants such as *Pueraria*. We found ammonium and microbial biomass nitrogen in *Pueraria* soils to be high at later growth stages (120 days). However, nitrate and total nitrogen did not change over the same time period in these soils. On the other hand, nitrate and total nitrogen were higher in *Pueraria* than *Mikania* soils. This may reflect the ability of *Pueraria* to fix atmospheric nitrogen through its association with rhizobium bacteria. This may provide *Pueraria* with a further competitive advantage over *Mikania* when competing for available nitrogen sources essential for rapid growth.

Our field data corroborated our potting experiments. We found that the removal of *Mikania* more severely impacted its performance than *Pueraria* sowing density, so management interventions require both the removal of *Mikania* biomass and active restoration. Similar competitive effects of *Pueraria* on other invasive vines have been observed, for example, we previously found the recruitment of invasive *Ipomoea cairica* to be severely hampered by *Pueraria* (Li et al., 2015).

## 5 | CONCLUSIONS

Through competitive exclusion, native species with superior fitness may limit the establishment and spread of non-native species. However, competitive exclusion is not widely applied

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**TABLE 9**: Results of general linear models assessing the effects of *Mikania* removal and sowing density as well as their interaction on *Mikania* biomass and *Pueraria* biomass in the field.

| Independent variables       | *Mikania* biomass | *Pueraria* biomass |
|-----------------------------|-------------------|--------------------|
|                             | df    | F     | p   | df    | F     | p   |
| *Mikania* removal           | 1     | 60.70 | <.001| 1     | 166.50| <.001|
| Sowing density              | 3     | 36.05 | <.001| 3     | 41.10 | <.001|
| *Mikania* removal * sowing density | 3     | 12.77 | <.001| 3     | 20.78 | <.001|
to control invasive plants (Byun & Lee, 2017). We found that plant traits such as seed germination, seedling growth speed, biomass accumulation, branching, plant height, photosynthetic efficiency, and the direction and magnitude of phytochemical effects, all played a significant role in the competitive exclusion of Mikania by Pueraria. Evidently, Pueraria can outperform Mikania, modulated by priority effects and strong competition. Although Pueraria is regarded as an invasive species elsewhere (Bentley & Mauricio, 2016; Kartzinel et al., 2015), it is a valuable native plant in China. The starch-rich roots of Pueraria are valued as a food source and for medicinal purposes. Thus, planting Pueraria is a promising approach to reduce the extent of Mikania invasion in tropical and subtropical agroforestry systems that are suitable for Pueraria cultivation, simultaneously providing weed management and economic benefits. Overall, this study provided promising strategies for species selection for restoration. Specifically, restoration will benefit from (a) the selection of highly competitive native species that have high niche overlap with invasive species, (b) the selection of native species that show strong priority effects (e.g., early emergence, rapid germination, and seedling growth), (c) selecting economically valuable native legumes that can improve restored soils through nitrogen fixation. Our study also provides a valuable framework that may be applied to other invaded ecosystems and species.

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CONFLICT OF INTEREST
None declared.

AUTHOR CONTRIBUTION
Hanxia Yu: Data curation (equal); Writing-review & editing (equal).
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Cui Wang: Investigation (equal). Johannes Le Roux: Writing-review & editing (equal). Chang Lian Peng: Writing-review & editing (equal). Weihua Li: Conceptualization (equal); Methodology (equal); Supervision (equal); Writing-original draft (equal); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT
All the data used in this manuscript are available from https://osf.io/vq9kw/.

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