Potential use of *Helianthus tuberosus* to suppress the invasive alien plant *Ageratina adenophora* under different shade levels

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**Abstract**

**Background:** An ecological approach for managing biological invasions in agroecosystems is the selection of alternative crop species to manage the infestation of invasive alien plants through competition. In the current study, plant growth, photosynthesis, and competitive ability of the crop *Helianthus tuberosus* L. (Jerusalem artichoke) and the invasive alien plant *Ageratina adenophora* (Spreng.) R. M. King and H. Rob were compared under varying shade levels by utilizing a de Wit replacement series method. We hypothesized that *H. tuberosus* had higher competitive ability than *A. adenophora* even under shaded conditions.

**Results:** The results showed the main stem, leafstalk length, leaf area, underground biomass, and aboveground biomass of *A. adenophora* were significantly lower compared to *H. tuberosus* in monoculture although *A. adenophora* had a greater number of branches that were longer on average. Under full sunlight, the total shoot length (stem + branch length), main stem length and branch length of *A. adenophora* were significantly suppressed (P < 0.05) by increasing proportions of *H. tuberosus*, and the same morphological variables of *H. tuberosus* were significantly higher with decreasing proportions of *H. tuberosus*. With increasing shade rates and plant ratios, the plant height, branch, leaf, and biomass of both plants were significantly suppressed, but to a greater degree in the case of *A. adenophora*. The net photosynthetic rate (Pn) of *H. tuberosus* and *A. adenophora* increased gradually from July to September, then decreased in October. The Pn of *H. tuberosus* was consistently higher than that of *A. adenophora*. Although the Pn for both species was significantly reduced with increasing shade rates and plant ratios, *A. adenophora* experienced greater inhibition than *H. tuberosus*. The relative yield (RY) of *A. adenophora* was significantly less than 1.0 (P < 0.05) in mixed culture under all shade levels, indicating that the intraspecific competition was less than interspecific competition. The RY of *H. tuberosus* was significantly less than 1.0 under 40–60% shade and greater than 1.0 (P < 0.05) under 0–20% shade in mixed culture, respectively, showing that intraspecific competition was higher than interspecific competition under low shade, but the converse was true under high shade. The relative yield total (RYT) of *A. adenophora* and *H. tuberosus* was less than 1.0 in mixed culture, indicating that there was competition between the two species.
Background

Jerusalem artichoke (Helianthus tuberosus L.), also known as sunchoke, is a perennial herbaceous plant from family Asteraceae [1]. Native to North America, this plant has become broadly distributed throughout the world and introduced into China via Europe [2]. As an important multifunctional crop, H. tuberosus has been widely utilized in agriculture and industry. This crop usually produces around 7 t and potentially up to 14 t ha\(^{-1}\) of carbohydrate [3]. Its aerial parts and tubers are used as high quality fodder for livestock [4]. Tubers of H. tuberosus contain abundant inulin, B vitamins, pantothenic acid, potassium, phosphorus, vitamin A, iron, and calcium, providing an excellent vegetable and food source for human diets [5, 6]. The crop is used for the production of paper pulp, fuelwood, methane acetone, butanol, ethanol, hydroxymethylfurfural, fodder yeast, beer, lactic acid, propionic acid, mannitol, and pectic substances in industry [1, 3, 4, 6, 7]. Moreover, it may be grown to stabilize unstable sand and terraces, to provide fire barriers in forests, or as a promising crop for planting in coastal marginal land in China [6, 8–10].

Helianthus tuberosus has strong tolerance and suitability to various environmental and climatic conditions allowing it to be easily grown in tropical, temperate, frigid, and even arid and semi-arid regions [8–10]. Recently this plant has been emerging as an important economic crop in China. Helianthus tuberosus is known to have a strong competitive advantage through its efficient use of sunlight, stress resistance and vegetative propagation ability in comparison to other plants [4]. This crop has been demonstrated to suppress growth and photosynthetic ability of several invasive plants such as Ambrosia trifida, Cenchrus pauciflorus, and Flaveria bidentis [11–13]. Furthermore, allelochemicals produced by H. tuberosus may interfere with the growth of other species, resulting in improved growth, development, and spread by H. tuberosus [14, 15]. Therefore, this crop exhibits great potential to provide ecological management of other invasive alien plants.

Previous observations in fields where H. tuberosus was grown in Yunnan Province, China, indicated that H. tuberosus appeared to compete strongly with the invasive alien plant Ageratina adenophora (Spreng.) R. M. King and H. Rob. Native to Mexico and Costa Rica in Central America, A. adenophora has been considered one of the most problematic invasive alien species globally [16, 17]. In China, this invasive plant was first introduced from Myanmar into the south Lincang of Yunnan Province in the 1940s, and is now widely distributed in southwest regions of the country [18, 19]. Ageratina adenophora has invaded a broad range of habitats, causing tremendous economic losses and negative environmental and biodiversity impacts [20, 21]. This weed is a heliophilic species, but it may still grow under low sunlight conditions [22]. Ageratina adenophora retained advantages over two native congeners across different light levels, showing its greatest advantage under light saturated conditions, with its relative performance decreasing at lower irradiance levels [23]. Moreover, plasticity in some of these physiological traits may play a role in invasion success for A. adenophora but varies in different environments making broad generalizations difficult [24]. Thus, there is an urgent need to explore more effective control methods for mitigating the damage caused by the invasion of A. adenophora, including crop plants that could reduce A. adenophora populations through competition even under shaded conditions.

Based on preliminary field observations of excellent inhibition of A. adenophora by H. tuberosus, the main objective of this study was to examine the competitive relationship between H. tuberosus and A. adenophora, by looking at plant growth and photosynthesis characteristics under different shade levels in order to provide a scientific basis for setting up an effective management method utilizing ecological control techniques for A. adenophora.

Results

Plant growth

Plant growth of H. tuberosus and A. adenophora was significantly affected (P < 0.01) by the shade rates and density ratios (Tables 1, 2). In general, the main stem length of H. tuberosus was markedly longer than that of A. adenophora, but its branch length was less than that of A. adenophora. Under full sunlight conditions, the total shoot length (stem + branch length), main stem length and branch length of A. adenophora were significantly
suppressed (P<0.05) with increasing proportions of *H. tuberosus*. The main stem length and branch length of *A. adenophora* were reduced by 51.5% and 76.2% at the 2:1 *H. tuberosus: A. adenophora* ratio in mixed culture (Table 1). The main stem length (except 20% shade for *A. adenophora*) and branch length of *H. tuberosus* and *A. adenophora* were significantly suppressed with increasing shade rates in mono and mixed culture with *A. adenophora* generally more inhibited (Table 2). During the experiment, following the initial sprouting of *H. tuberosus* about one week after transplantation, its growth rate accelerated. Plant height of *H. tuberosus* exceeded that of *H. tuberosus* in mixed culture; and the branch number of *A. adenophora* was significantly suppressed (P < 0.05) with increasing proportions of *A. adenophora* in mixed culture; and the branch number of *A. adenophora* proportions of *A. adenophora* were significantly reduced with increasing shade rates in mono and mixed culture with *A. adenophora* generally more inhibited (Table 2). During the experiment, following the initial sprouting of *H. tuberosus* about one week after transplantation, its growth rate accelerated. Plant height of *H. tuberosus* exceeded that of *A. adenophora* within two weeks. The percent cover of *H. tuberosus* reached 75% at 50 days, and exceeded 95% within 60–65 days. By comparison, the percent cover of *A. adenophora* was only about 40% at 65 days, even in monoculture.

The branch number of *A. adenophora* was much higher than that of *H. tuberosus* in monoculture (Tables 1, 2). Under full sunlight conditions, the branch number of *A. adenophora* was significantly suppressed (P<0.05) with decreasing proportions of *A. adenophora*, and that of *H. tuberosus* was increased markedly with increasing proportions of *A. adenophora* in mixed culture; and the branch number of *A. adenophora* was inhibited by 65.0% at the 2:1 *H. tuberosus: A. adenophora* ratio in mixed culture (Table 1). The branch number of *H. tuberosus* and *A. adenophora* were significantly reduced with increasing shade rates, and the inhibition rates of *A. adenophora* were significantly higher (P<0.05) than those of *H. tuberosus* in monoculture (Tables 1, 2).

The leafstalk length and leaf area of *H. tuberosus* were much higher than those of *A. adenophora* in all treatments (Tables 1, 2). Under full sunlight conditions, the mean leafstalk length and leaf area of *H. tuberosus* were 5.80 cm and 64.57 cm², respectively, whereas those of *A. adenophora* were only 4.74 cm and 38.34 cm², respectively in monoculture. The leafstalk length

| Variables | Ratios (*H. tuberosus: A. adenophora*) |
|-----------|----------------------------------------|
|           | 4:0 | 2:1 | 1:1 | 1:2 | 0:4 |
| Total shoot length (cm) | 173.62 ± 3.59c | 181.74 ± 4.37b | 190.54 ± 4.51ab | 197.62 ± 4.26a | – |
| *H. tuberosus* | – | 61.67 ± 1.77d | 96.11 ± 1.46c | 140.58 ± 1.80b | 171.39 ± 2.26a |
| Main stem length (cm) | 138.06 ± 2.68c | 143.17 ± 3.76bc | 149.34 ± 3.60ab | 152.96 ± 3.27a | – |
| *H. tuberosus* | – | 41.06 ± 1.68d | 60.79 ± 1.55c | 75.22 ± 1.25b | 84.72 ± 1.93a |
| Total branch length (cm) | 35.56 ± 1.13d | 38.58 ± 1.09c | 41.19 ± 1.09b | 44.66 ± 1.04a | – |
| *H. tuberosus* | – | 20.61 ± 0.47d | 35.42 ± 0.50c | 65.36 ± 0.65b | 86.67 ± 0.96a |
| Branch number | 3.5 ± 0.4b | 4.0 ± 0.4b | 4.9 ± 0.5a | 5.1 ± 0.5a | – |
| *H. tuberosus* | – | 6.4 ± 0.5d | 9.4 ± 0.5c | 14.3 ± 0.6b | 18.3 ± 0.9a |
| Leafstalk length (cm) | 5.80 ± 0.02c | 5.95 ± 0.04b | 6.06 ± 0.03a | 6.10 ± 0.03a | – |
| *H. tuberosus* | – | 3.01 ± 0.02d | 3.45 ± 0.01c | 3.83 ± 0.01b | 4.74 ± 0.02a |
| Leaf area (cm²) | 64.57 ± 0.59c | 65.21 ± 0.71bc | 66.18 ± 0.74b | 67.93 ± 0.70a | – |
| *H. tuberosus* | – | 16.20 ± 0.15d | 20.25 ± 0.16c | 33.32 ± 0.36b | 38.34 ± 0.24a |
| Root biomass (g) | 236.97 ± 2.94c | 262.79 ± 4.60b | 264.76 ± 3.38b | 286.64 ± 3.20a | – |
| *H. tuberosus* | – | 2.74 ± 0.09d | 4.20 ± 0.24c | 8.25 ± 0.27b | 14.32 ± 0.30a |
| Aboveground biomass (g) | 95.16 ± 1.00c | 105.86 ± 2.03b | 106.75 ± 3.43b | 125.40 ± 3.98a | – |
| *H. tuberosus* | – | 11.24 ± 0.29d | 14.31 ± 0.29c | 16.29 ± 0.36b | 42.34 ± 1.43a |
| Total biomass (g) | 332.13 ± 3.79c | 368.64 ± 4.94b | 371.50 ± 5.04b | 411.84 ± 5.77a | – |
| *H. tuberosus* | – | 13.98 ± 0.20d | 18.51 ± 0.24c | 24.54 ± 0.41b | 56.64 ± 1.21a |

Data are expressed as mean ± standard deviation. Different letters within the same row signify significant differences at P < 0.05.
Table 2  Morphological characteristics and biomass of *Helianthus tuberosus* and *Ageratina adenophora* competition under different shade levels

| Variables                        | Different shade rates | 60%   | 40%   | 20%   | 0%    |
|----------------------------------|-----------------------|-------|-------|-------|-------|
|                                  |                       | 40%   | 20%   | 0%    |       |
|                                  |                       | 40%   | 20%   | 0%    |       |
|                                  |                       | 40%   | 20%   | 0%    |       |
| Total shoot length (cm)          |                       |       |       |       |       |
| *H. tuberosus*                   |                       |       |       |       |       |
| 0:4                              | 95.51±1.43d           | 116.10±2.44c | 136.04±2.16b | 173.62±3.59a |
| 1:1                              | 93.71±1.85d           | 119.56±1.47c | 158.94±3.22b | 190.54±4.51a |
| A. adenophora                    |                       |       |       |       |       |
| 0:4                              | 45.67±0.53d           | 53.20±0.60c | 72.33±1.40b | 96.21±1.46a |
| 1:1                              | 73.26±1.65d           | 98.03±1.55c | 164.42±3.06b | 171.39±2.26a |
| Main stem length (cm)            |                       |       |       |       |       |
| *H. tuberosus*                   |                       |       |       |       |       |
| 0:4                              | 84.27±1.66d           | 99.23±2.32c | 108.31±2.04b | 138.06±2.68a |
| 1:1                              | 79.98±1.75d           | 94.11±1.41c | 126.48±3.35b | 149.34±3.60a |
| A. adenophora                    |                       |       |       |       |       |
| 0:4                              | 32.52±0.57d           | 37.96±0.64c | 50.28±0.97b | 60.79±1.55a |
| 1:1                              | 56.78±1.42d           | 67.31±1.13c | 111.06±2.08a | 84.72±1.93b |
| Total branch length (cm)         |                       |       |       |       |       |
| *H. tuberosus*                   |                       |       |       |       |       |
| 0:4                              | 11.24±0.31d           | 16.87±0.19c | 27.73±0.33b | 35.56±1.13a |
| 1:1                              | 13.72±0.18d           | 25.45±0.34c | 32.46±0.36b | 41.19±1.09a |
| A. adenophora                    |                       |       |       |       |       |
| 0:4                              | 13.16±0.46d           | 15.24±0.25c | 22.06±0.60b | 35.42±0.50a |
| 1:1                              | 16.49±0.27d           | 30.72±0.48c | 53.37±1.00b | 86.67±0.96a |
| Branch number                    |                       |       |       |       |       |
| *H. tuberosus*                   |                       |       |       |       |       |
| 0:4                              | 1.9±0.3b              | 2.1±0.3b  | 2.8±0.6a  | 3.5±0.4a  |
| 1:1                              | 2.5±0.4b              | 2.8±0.3b  | 3.4±0.5ab | 4.9±0.5a  |
| A. adenophora                    |                       |       |       |       |       |
| 0:4                              | 3.4±0.3d              | 4.2±0.5c  | 6.1±0.3b  | 9.4±0.5a  |
| 1:1                              | 4.5±0.4d              | 7.4±0.5c  | 13.4±0.5b | 18.3±0.9a |
| Leafstalk length (cm)            |                       |       |       |       |       |
| *H. tuberosus*                   |                       |       |       |       |       |
| 0:4                              | 5.36±0.02c            | 5.50±0.04b | 5.78±0.02a | 5.80±0.02a |
| 1:1                              | 5.04±0.03d            | 5.37±0.01c | 5.82±0.02b | 6.06±0.03a |
| A. adenophora                    |                       |       |       |       |       |
| 0:4                              | 3.19±0.02d            | 3.31±0.02c | 3.37±0.01b | 3.45±0.01a |
| 1:1                              | 3.94±0.02d            | 4.04±0.02c | 4.47±0.01b | 4.74±0.02a |
| Leaf area (cm²)                  |                       |       |       |       |       |
| *H. tuberosus*                   |                       |       |       |       |       |
| 0:4                              | 52.26±0.13d           | 55.11±0.12c | 60.11±0.17b | 64.57±0.59a |
| 1:1                              | 51.88±0.13d           | 56.36±0.21c | 61.75±0.19b | 66.18±0.74a |
| A. adenophora                    |                       |       |       |       |       |
| 0:4                              | 16.21±0.21d           | 17.13±0.15c | 19.19±0.13b | 20.25±0.16a |
| 1:1                              | 26.23±0.20d           | 30.28±0.14c | 35.22±0.20b | 38.34±0.24a |
| Root biomass (g)                 |                       |       |       |       |       |
| *H. tuberosus*                   |                       |       |       |       |       |
| 0:4                              | 95.31±2.04d           | 155.03±2.75c | 200.62±3.68b | 236.97±2.94a |
| 1:1                              | 95.51±1.89d           | 144.01±1.66c | 205.97±2.50b | 264.76±3.38a |
and leaf area of *A. adenophora* progressively declined (*P* < 0.05) with increasing proportions of *H. tuberosus*, and those of *H. tuberosus* were significantly increased with increasing proportions of *A. adenophora* in mixed culture. The leafstalk length and leaf area of *A. adenophora* were reduced by 36.5% and 57.7% at the 2:1 *H. tuberosus: A. adenophora* ratio in mixed culture, respectively (Table 1). The leafstalk length and leaf area of *H. tuberosus* and *A. adenophora* were significantly reduced with increasing shade rates in mono and mixed culture, and both shade and plant competition inhibited these parameters more for *A. adenophora* (Table 2).

The total biomass of *H. tuberosus* was much greater than that of *A. adenophora* in all treatments (Table 1). Under full sunlight conditions, the underground biomass and aboveground biomass of *A. adenophora* were significantly suppressed (*P* < 0.05) with decreasing proportions of *A. adenophora*, whereas the biomass of *H. tuberosus* was markedly increased with increasing proportions of *A. adenophora* in mixed culture. The underground biomass and aboveground biomass of *A. adenophora* were reduced by 80.9% and 73.5% at the 2:1 *H. tuberosus: A. adenophora* ratio in mixed culture, respectively (Table 1). Under shaded conditions, the underground biomass and aboveground biomass of *H. tuberosus* and *A. adenophora* were significantly reduced with increasing shade rates, inhibiting *A. adenophora* were higher than those of more than *H. tuberosus* in mono and mixed culture (Table 2).

**Photosynthesis**

The photosynthetic rate (Pn) of both *H. tuberosus* and *A. adenophora* increased gradually from July to September, then decreased in October in all treatments. The Pn of *H. tuberosus* from July to October was higher than that of *A. adenophora* (Tables 3, 4). Under shaded conditions, the Pn of *H. tuberosus* was significantly higher than that of *A. adenophora*, and there were few differences within treatments for each plant species in July. During August and subsequent months, the Pn of *A. adenophora* was suppressed significantly (*P* < 0.05) with increasing proportions of *H. tuberosus*, whereas the Pn of *H. tuberosus* increased slightly with decreasing proportions of *A. adenophora* in mixed culture (Table 3). Under shaded conditions, the Pn of *H. tuberosus* and *A. adenophora* significantly declined with increasing shade rates, with the inhibition rates of *A. adenophora* higher than those of *H. tuberosus*, showing that shade and plant competition suppressed *A. adenophora* more (Table 4).

**Competitive interactions**

The relative yield (RY) of *H. tuberosus* and *A. adenophora* in different ratios showed that the two plants compete strongly (Tables 5, 6). Under full sunlight, the RY of *H. tuberosus* was significantly higher than 1.0, and the RY of *A. adenophora* was significantly less than 1.0 (*P* < 0.05) in mixed culture, indicating that the intraspecific competition was higher than interspecific competition for *H. tuberosus*, but the intraspecific competition was less than

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**Table 2 (continued)**

| Variables          | Different shade rates | 60% | 40% | 20% | 0% |
|--------------------|-----------------------|-----|-----|-----|----|
| A. adenophora      |                       |     |     |     |    |
| *H. tuberosus: A. adenophora* = 1:1 | 1.38 ± 0.03d | 2.25 ± 0.09c | 2.75 ± 0.09b | 4.20 ± 0.24a |
| *H. tuberosus: A. adenophora* = 0:4 | 3.22 ± 0.16d | 4.67 ± 0.21c | 9.68 ± 0.49b | 14.32 ± 0.30a |
| Aboveground biomass (g) |                       |     |     |     |    |
| H. tuberosus       |                       |     |     |     |    |
| *H. tuberosus: A. adenophora* = 4:0 | 67.78 ± 1.46d | 72.30 ± 1.77c | 90.90 ± 1.26b | 95.16 ± 1.00a |
| *H. tuberosus: A. adenophora* = 1:1 | 64.61 ± 1.09d | 73.97 ± 1.03c | 91.13 ± 1.89b | 106.75 ± 3.43a |
| A. adenophora      |                       |     |     |     |    |
| *H. tuberosus: A. adenophora* = 1:1 | 3.33 ± 0.26d | 5.55 ± 0.36c | 8.96 ± 0.35b | 14.31 ± 0.29a |
| *H. tuberosus: A. adenophora* = 0:4 | 7.30 ± 0.16d | 13.63 ± 0.49c | 21.94 ± 0.62b | 42.34 ± 1.43a |
| Total biomass (g)  |                       |     |     |     |    |
| H. tuberosus       |                       |     |     |     |    |
| *H. tuberosus: A. adenophora* = 4:0 | 163.08 ± 2.86d | 227.33 ± 2.58c | 291.52 ± 4.52b | 332.13 ± 3.79a |
| *H. tuberosus: A. adenophora* = 1:1 | 160.12 ± 1.43d | 217.98 ± 2.49c | 297.70 ± 1.68b | 371.50 ± 5.94a |
| A. adenophora      |                       |     |     |     |    |
| *H. tuberosus: A. adenophora* = 1:1 | 4.71 ± 0.25d | 7.79 ± 0.33c | 11.72 ± 0.44b | 18.51 ± 0.24a |
| *H. tuberosus: A. adenophora* = 0:4 | 10.53 ± 0.17d | 18.29 ± 0.41c | 31.61 ± 0.84b | 56.64 ± 1.21a |

Data are expressed as mean ± standard deviation. Different letters within the same row signify significant differences at *P* < 0.05.
Table 3  Net photosynthetic rate (Pn) of Helianthus tuberosus and Ageratina adenophora competition under full sunlight

| Variables                      | Ratios (H. tuberosus: A. adenophora) |
|--------------------------------|--------------------------------------|
|                                | 4:0       | 2:1       | 1:1       | 1:2       | 0:4       |
| July                           |           |           |           |           |           |
| H. tuberosus (µmol CO₂ m⁻² s⁻¹) | 15.59 ± 0.06a | 15.65 ± 0.09a | 15.57 ± 0.10a | 15.69 ± 0.08a | –          |
| A. adenophora Pn (µmol CO₂ m⁻² s⁻¹) | –         | 9.06 ± 0.08b | 9.10 ± 0.06b | 9.17 ± 0.03ab | 9.27 ± 0.07a |
| August                         |           |           |           |           |           |
| H. tuberosus (µmol CO₂ m⁻² s⁻¹) | 18.42 ± 0.09c | 18.69 ± 0.07b | 18.84 ± 0.06a | 18.85 ± 0.03a | –          |
| A. adenophora Pn (µmol CO₂ m⁻² s⁻¹) | –         | 8.98 ± 0.05d | 10.10 ± 0.02c | 12.59 ± 0.04b | 13.26 ± 0.07a |
| September                      |           |           |           |           |           |
| H. tuberosus (µmol CO₂ m⁻² s⁻¹) | 20.11 ± 0.18d | 20.80 ± 0.11c | 21.49 ± 0.12b | 21.83 ± 0.09a | –          |
| A. adenophora Pn (µmol CO₂ m⁻² s⁻¹) | –         | 9.52 ± 0.12d | 11.46 ± 0.13c | 13.70 ± 0.13b | 15.51 ± 0.17a |
| October                        |           |           |           |           |           |
| H. tuberosus (µmol CO₂ m⁻² s⁻¹) | 18.39 ± 0.06c | 18.46 ± 0.07bc | 18.53 ± 0.07b | 18.71 ± 0.05a | –          |
| A. adenophora Pn (µmol CO₂ m⁻² s⁻¹) | –         | 9.28 ± 0.08d | 10.46 ± 0.05c | 12.64 ± 0.08b | 14.26 ± 0.06a |

Data are expressed as mean ± standard deviation. Different letters within the same row signify significant differences at P < 0.05

Table 4  Net photosynthetic rate (Pn) of Helianthus tuberosus and Ageratina adenophora competition under different shade levels

| Variables                      | Different shade rates |
|--------------------------------|-----------------------|
|                                | 60%       | 40%       | 20%       | 0%        |
| July                           |           |           |           |           |
| H. tuberosus (µmol CO₂ m⁻² s⁻¹) |           |           |           |           |
| H. tuberosus: A. adenophora = 4:0 | 8.67 ± 0.07d | 10.36 ± 0.09c | 13.51 ± 0.09b | 15.59 ± 0.06a |
| H. tuberosus: A. adenophora = 1:1 | 8.57 ± 0.10d | 10.34 ± 0.11c | 13.55 ± 0.11b | 15.57 ± 0.10a |
| A. adenophora (µmol CO₂ m⁻² s⁻¹) |           |           |           |           |
| H. tuberosus: A. adenophora = 1:1 | 5.05 ± 0.03d | 6.05 ± 0.02c | 8.80 ± 0.03b | 9.10 ± 0.06a |
| H. tuberosus: A. adenophora = 0:4 | 5.13 ± 0.07d | 6.21 ± 0.06c | 8.83 ± 0.08b | 9.27 ± 0.07a |
| August                         |           |           |           |           |
| H. tuberosus (µmol CO₂ m⁻² s⁻¹) |           |           |           |           |
| H. tuberosus: A. adenophora = 4:0 | 10.81 ± 0.05d | 13.11 ± 0.05c | 16.65 ± 0.09b | 18.42 ± 0.09a |
| H. tuberosus: A. adenophora = 1:1 | 10.67 ± 0.07d | 13.63 ± 0.06c | 16.88 ± 0.05b | 18.84 ± 0.06a |
| A. adenophora (µmol CO₂ m⁻² s⁻¹) |           |           |           |           |
| H. tuberosus: A. adenophora = 1:1 | 6.71 ± 0.03d | 7.27 ± 0.08c | 9.05 ± 0.01b | 10.10 ± 0.02a |
| H. tuberosus: A. adenophora = 0:4 | 7.43 ± 0.04d | 9.38 ± 0.04c | 11.21 ± 0.04b | 13.26 ± 0.07a |
| September                      |           |           |           |           |
| H. tuberosus (µmol CO₂ m⁻² s⁻¹) |           |           |           |           |
| H. tuberosus: A. adenophora = 4:0 | 11.64 ± 0.09d | 13.68 ± 0.08c | 17.62 ± 0.12b | 20.11 ± 0.18a |
| H. tuberosus: A. adenophora = 1:1 | 12.71 ± 0.05d | 15.64 ± 0.07c | 19.19 ± 0.13b | 21.49 ± 0.12a |
| A. adenophora (µmol CO₂ m⁻² s⁻¹) |           |           |           |           |
| H. tuberosus: A. adenophora = 1:1 | 8.14 ± 0.08d | 8.31 ± 0.07c | 10.06 ± 0.01b | 11.46 ± 0.13a |
| H. tuberosus: A. adenophora = 0:4 | 8.93 ± 0.03d | 10.47 ± 0.06c | 13.37 ± 0.07b | 15.51 ± 0.17a |
| October                        |           |           |           |           |
| H. tuberosus (µmol CO₂ m⁻² s⁻¹) |           |           |           |           |
| H. tuberosus: A. adenophora = 4:0 | 11.03 ± 0.03d | 12.85 ± 0.08c | 15.18 ± 0.07b | 18.39 ± 0.06a |
| H. tuberosus: A. adenophora = 1:1 | 11.70 ± 0.10d | 13.68 ± 0.09c | 15.80 ± 0.03b | 18.53 ± 0.07a |
| A. adenophora (µmol CO₂ m⁻² s⁻¹) |           |           |           |           |
| H. tuberosus: A. adenophora = 1:1 | 6.52 ± 0.04d | 7.55 ± 0.06c | 8.88 ± 0.05b | 10.46 ± 0.05a |
| H. tuberosus: A. adenophora = 0:4 | 8.24 ± 0.05d | 9.64 ± 0.06c | 11.99 ± 0.08b | 14.26 ± 0.06a |

Data are expressed as mean ± standard deviation. Different letters within the same row signify significant differences at P < 0.05
Ratios (H. tuberosus: A. adenophora) under different shade levels

Table 5

| Variables          | Ratios (H. tuberosus: A. adenophora) |
|--------------------|--------------------------------------|
|                    | 2:1        | 1:1        | 1:2        |
| H. tuberosus RYa   | 1.110 + 0.002b** | 1.119 + 0.013b** | 1.240 + 0.015a** |
| A. adenophora RYb  | 0.247 + 0.008c** | 0.327 + 0.010b** | 0.433 + 0.013a** |
| RYT                | 0.678 + 0.003c** | 0.723 + 0.009b** | 0.837 + 0.009a** |
| CBa index for H. tuberosus | 1.504 + 0.033a** | 1.231 + 0.033b** | 1.052 + 0.035c** |

Data are expressed as mean ± standard deviation. Different letters within the same row signify significant differences at P < 0.05. The t-test was used to compare each value with 1.0 and 0; * and ** indicate significant differences at 0.05 and 0.01 levels, respectively.

Table 6

| Variables          | Different shade rates |
|--------------------|-----------------------|
|                    | 60% | 40% | 20% | 0%  |
| H. tuberosus RYa   | 0.982 + 0.017c** | 0.959 + 0.017c** | 1.019 + 0.019b** | 1.119 + 0.013a** |
| A. adenophora RYb  | 0.447 + 0.021a** | 0.426 + 0.019a** | 0.371 + 0.017b** | 0.327 + 0.010c** |
| RYT                | 0.715 + 0.011a** | 0.692 + 0.013b** | 0.695 + 0.009b** | 0.723 + 0.009a** |
| CBa index for H. tuberosus | 0.787 + 0.057c** | 0.812 + 0.046c** | 1.012 + 0.056b** | 1.231 + 0.033a** |

Data are expressed as mean ± standard deviation. Different letters within the same row signify significant differences at P < 0.05. The t-test was used to compare each value with 1.0 and 0; * and ** indicate significant differences at 0.05 and 0.01 levels, respectively.

interspecific competition for A. adenophora; the relative yield total (RYT) of A. adenophora and H. tuberosus was less than 1.0 in mixed culture, indicating that there was competition between the two plants; the competitive balance index (CB) of H. tuberosus was greater than zero and the maximum CB index was 1.504 demonstrating a higher competitive ability than A. adenophora (Table 5). Under shaded conditions, the RY of H. tuberosus markedly declined with increasing shade rates in mixed culture, and the RY of A. adenophora was significantly increased with increasing shade rates. However, the CB of H. tuberosus was greater than zero, indicating a higher competitive ability than A. adenophora even under the highest shade level (60%) (Table 6). Overall, H. tuberosus exhibited greater competitive ability than A. adenophora under all shade levels (Table 6).

Discussion

The current study demonstrated that compared to A. adenophora, H. tuberosus possessed superior attributes in terms of plant height, leaf, biomass, and photosynthesis, and exhibited greater competitive ability than A. adenophora under all shade levels when the plants were grown together. Under interspecific competition, morphological characteristics (e.g., leaf shape) and biomass tend to be the most important parameters [25, 26]. Plant species with higher biomass, RY or CB index have stronger competitive ability and are more likely to replace neighboring plants [27, 28]. The underground biomass and above-ground biomass per H. tuberosus plant were significantly greater (P < 0.05) than those of A. adenophora in all treatments. Our finding that the RY of A. adenophora was significantly less than 1.0 in mixed culture under all shade levels, indicated that intraspecific competition was less than interspecific competition for A. adenophora.

The RY of H. tuberosus was significantly less than 1.0 under 40–60% and greater than 1.0 under 0–20% shade in mixed culture, respectively, showing that intraspecific competition was higher than interspecific competition under low shade rates, but the converse was true under high shade rates. Regardless of shade level, the RYT and CB for A. adenophora were significantly less than 1.0, demonstrating that H. tuberosus had greater competitive ability than A. adenophora. Thus, H. tuberosus can provide a promising replacement control candidate for A. adenophora.

The initial size of plant individuals and growth stages under all conditions can affect the competitiveness of a species during interspecific competition [26]. In this study, plant seedlings of A. adenophora with 4 leaves and 6–7 cm height and slices of H. tuberosus tubers with one bud were used to initiate the experiments, which provided A. adenophora with an obvious advantage in terms of initial plant height. However, this initial advantage of A. adenophora was not sustained during competition with H. tuberosus over the season. The lateral expansion rate of H. tuberosus seedlings was significantly higher than that of A. adenophora.
Previous studies observed that plant species with a competitive advantage over *A. adenophora* tended to have characteristics such as rapid growth rate, large leaf area and rapid canopy formation, e.g., *Paspalum wetsfetieni*, *Dolichos lablab*, *Imperata cylindrica*, and *Ipomoea batatas* [28–31]. The high carbohydrate content of *H. tuberosus* tubers, coupled with multiple regenerative strategies featuring vegetative expansion by an extensive rhizome system, and vegetative propagation from tubers, pieces of tubers and rhizomes, can lead to rapid population increases [4]. *Helianthus tuberosus* plants exhibit a rapid increase in plant height, number of leaves and tubers through one life cycle that enable *H. tuberosus* to outcompete most other plant species in arable land [4]. Meanwhile, the plant is also considered a serious weed in some areas because it competes vigorously with other plants in Europe and Canada [4, 15]. After *H. tuberosus* and *A. adenophora* were grown together over the course of a field season, the root biomass, main stem length, leafstalk length, and leaf area of *H. tuberosus* were markedly higher than those of *A. adenophora*, indicating *H. tuberosus* gains the competitive advantage via its strong underground roots and large aboveground individuals.

The leaf is the main site of photosynthesis and leaf area provides a major index to measure growth condition and solar energy utilization efficiency of plants [32]. Greater specific leaf area may contribute to carbon assimilation due to higher leaf area production for a given investment in biomass [33]. *Helianthus tuberosus* and *A. adenophora* are heliophilic species, but may tolerate low sunlight conditions [22, 34]. Our study likewise demonstrated that *H. tuberosus* and *A. adenophora* can survive and grow under high shade rates (as high as 60%). The leafstalk length and leaf area of *H. tuberosus* were markedly greater than those of *A. adenophora* in all treatments. Under full sunlight, the leafstalk length and leaf area of *A. adenophora* progressively declined with increasing proportions of *H. tuberosus*, whereas those of *H. tuberosus* significantly increased with increasing proportions of *A. adenophora* in mixed culture. Similarly, previous studies also showed that the leaf area and Pn of some invasive species were greatly reduced with *I. batatas* competition [31, 35, 36]. The plant growth, biomass, leaf chlorophyll content, photosynthetic rate, transpiration rate, water use efficiency, and stomatal conductance of *A. trifida* were significantly decreased by *H. tuberosus* competition in mixed culture [11, 37]. The Pn of *H. tuberosus* from July to October was higher than that of *A. adenophora*, and the Pn of *A. adenophora* was significantly suppressed with increasing proportions of *H. tuberosus* in mixed culture from August to the end of the growing season. Under various shade levels, the Pn of *H. tuberosus* and *A. adenophora* significantly declined with increasing shade rates, and inhibition rates of *A. adenophora* were higher than those of *H. tuberosus*. Thus, larger leaf area and higher Pn of *H. tuberosus* during the growth period could be responsible for its higher growth rate, branching, and more biomass accumulation in competition with *A. adenophora*.

Competitive plants selected for replacement control should be easy to grow, have high economic value, and possess the ability to form a high canopy density within a short period of time [38]. Because *H. tuberosus* is a multifunctional crop with high ornamental, edible, medicinal, and economic value, it is readily accepted and promoted as an alternative crop [39]. Moreover, this crop is highly resistant to drought, cold temperatures, and saline soil conditions, enabling it to adapt to various climatic and environmental conditions invaded by *A. adenophora* [8, 9]. Our study found that *H. tuberosus* had a higher competitive ability than *A. adenophora* under all shade levels, showing that *H. tuberosus* could be widely used for ecological control in various habitats infected by *A. adenophora*, including shaded orchards and forest edges.

In addition, the competition process is also largely affected by the plant density and planting time [25]. Some studies reported that some replacement plants exhibited a higher CB index at intermediate replacement proportions than at low or high proportions [28, 40]. The plant growth and biomass of *A. trifida* were significantly decreased under different density ratios in mixed culture, and the intraspecific competition of *H. tuberosus* might be more intense than interspecific competition at plant density of 100 plants/m$^2$ [37]. Similarly, the current study found that the intraspecific competition was higher than interspecific competition for *H. tuberosus* at a plant density of 20 plants/m$^2$ under 0–20% shade. *Helianthus tuberosus* grows well in the presence of competitors, and the higher the population density, the sooner the maximum growth rate of each plant was attained [4]. Therefore, in order to optimize the competitive potential of an alternative crop species, a suitable plant density should be selected. Another important recommendation is to plant competitive crops such that they germinate earlier than the weed species of concern [41]. Abundant germplasm resources are available for *H. tuberosus*, and it is generally grown from pieces bearing 1–3 buds, 40–70 cm row spacing, 30–50 cm plant spacing, and two planting seasons (March–April and September–October). Thus, for replacement control of *A. adenophora*, rational schemes can be designed through row spacing, bud number, variety, and replacement period, in order to enhance the competitive ability of *H. tuberosus*. 
Conclusions
These results showed that as well as being used as a promising alternative crop to outcompete A. adenophora under optimal conditions, H. tuberosus may also be utilized even in shaded orchards and forest edges invaded by A. adenophora. In our experiments, H. tuberosus exhibited clear advantages over A. adenophora in morphological characteristics, and its competitive ability was significantly higher than that of A. adenophora under all shade levels. The H. tuberosus crop is a perennial plant with an extensive rhizome system that potentially contributes an even higher competitive advantage with increasing growth years if not harvested annually. Furthermore, as a crop, H. tuberosus has many favourable attributes such as nutritional value, ease of propagation, and a variety of medicinal and industrial uses, enabling it to be readily promoted to society as an alternative crop. Further studies of the competitive relationship between H. tuberosus and A. adenophora would be helpful in providing a stronger basis for utilizing H. tuberosus as a competitor, e.g., examining the effects of soil nutrients, enzyme activities and fertility levels.

Methods
Study site
The study site was located in Songming County (25° 05′−25° 28′ N; 102°40′−103° 20′ E), Kunming City, Yunnan Province, Southwest China. This area is characterized by a subtropical and temperate monsoon climate. Rainfall averages 1000–1300 mm per year and the annual mean temperature is 14.1 °C. Recently, A. adenophora has become widely distributed in orchard lands, wastelands, roadsites, forest edges, and other disturbed ecosystems in Songming County [42].

Study species
Helianthus tuberosus is widely grown as an important food and cash crop in temperate, tropical and subtropical regions in China. This crop mainly reproduces through asexual means and is usually propagated via tubers [6]. Since 2015, various H. tuberosus varieties in Yunnan Province have been collected and grown in the greenhouse of the Agricultural Environment and Resource Research Institute, Yunnan Academy of Agricultural Sciences, in Xiaojie Town, Songming County, utilizing a de Wit replacement series method [44]. Seeds of A. adenophora were propagated in the greenhouse starting on 20 April. On 23 June, the tubers of H. tuberosus sown in the greenhouse in 2018 were collected and cut into one-bud pieces. Then, seedlings were planted with consistently the same height (four leaves, 6–7 cm) of A. adenophora and one-bud pieces with uniform size of H. tuberosus were selected. Treatments of 60% (3 layers), 40% (2 layers), 20% (1 layer), and 0% (0 layer, full sunlight, CK) shade rates in this study were created by covering shade houses with different layers of black nylon shade netting. Five ratios of H. tuberosus and A. adenophora plants (4:0, 3:1, 2:1, 1:2, 1:3, 0:4) under full sunlight, and three ratios of H. tuberosus and A. adenophora plants (4:0, 1:1, 0:4) under three shade levels (60, 40 and 20%) were utilized, respectively, while maintaining a constant overall planting density of 20 plants/m² (0.25 m × 0.20 m space). All plots were arranged in a complete randomized design with 4 replicates utilizing 9 m² plots (3 m × 3 m). All plants were transplanted and distributed evenly within the plot. During the experiment, the plots were weeded and no synthetic fertilizers were used.

From July to October, net photosynthetic rate (Pn) measurements on leaves for H. tuberosus and A. adenophora were conducted mid-month using a Portable Photosynthesis System (LI-COR LI6400XT), between 8:00 am and 11:30 am, with a 6400-02 or -02B LED source and 1000 μmol m⁻² s⁻¹ photosynthetically active radiation under different sunlight conditions. During sampling, CO₂ concentration, air temperature and relative humidity (RH) in the chamber were under natural conditions. Measurements were made on a representative leaf randomly chosen on five to six randomly selected individuals of each species.

The experiment was terminated on 22 October 2019, 121 days after the initial transplanting. Twenty plants of each species were selected randomly and harvested from the interior of each plot. Total shoot length, main stem length, branch number, and leafstalk length, were measured with a ruler. Underground and aboveground biomass (fresh weight) were measured using an electronic balance. Leaves were clipped and passed through a leaf-area meter (Li-3000A; Li-Cor Corp.) to determine leaf area index.

Experiment design and data collection
The experiments were conducted during the April–October 2019 growing season at the Agricultural Environment and Resource Research Institute, Yunnan Academy of Agricultural Sciences, in Xiaojie Town, Songming County, utilizing a de Wit replacement series method [44]. Seeds of A. adenophora were propagated in the greenhouse starting on 20 April. On 23 June, the tubers of H. tuberosus sown in the greenhouse in 2018 were collected and cut into one-bud pieces. Then, seedlings were planted with consistently the same height (four leaves, 6–7 cm) of A. adenophora and one-bud pieces with uniform size of H. tuberosus were selected. Treatments of 60% (3 layers), 40% (2 layers), 20% (1 layer), and 0% (0 layer, full sunlight, CK) shade rates in this study were created by covering shade houses with different layers of black nylon shade netting. Five ratios of H. tuberosus and A. adenophora plants (4:0, 3:1, 2:1, 1:2, 1:3, 0:4) under full sunlight, and three ratios of H. tuberosus and A. adenophora plants (4:0, 1:1, 0:4) under three shade levels (60, 40 and 20%) were utilized, respectively, while maintaining a constant overall planting density of 20 plants/m² (0.25 m × 0.20 m space). All plots were arranged in a complete randomized design with 4 replicates utilizing 9 m² plots (3 m × 3 m). All plants were transplanted and distributed evenly within the plot. During the experiment, the plots were weeded and no synthetic fertilizers were used.

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Data analyses
The RY per plant, RYT and CB were calculated from final biomass for each species in each plot. Relative yield per plant of species a or b (i.e., species a and b represented H. tuberosus and A. adenophora in a mixed culture with species b or a was calculated as $R_Y^{a} = \frac{Y_{ab}}{Y_{a}}$ or $R_Y^{b} = \frac{Y_{ba}}{Y_{b}}$ [44]. Relative yield total was calculated as $RY_T = \frac{(R_Y^{a} + R_Y^{b})}{2}$ [45]. Competitive balance index was calculated as $CB_a = \ln \left(\frac{RY_a}{RY_b}\right)$ [46]. Where $Y_{ab}$ is the yield for species a growing with species b (g/individual), $Y_{ba}$ is the yield for species b growing with species a, $Y_{a}$ is the yield for species a growing in pure culture (g/individual), $Y_{b}$ is the yield for species b growing in pure culture. Values of $RY_{ab}$ measure the average performance of individuals in mixed cultures compared to that of individuals in pure cultures. An $RY_{ab}$ of 1.00 indicates species a and b are both equal in terms of intraspecific competition and interspecific competition. An $RY_{ab}$ greater than 1.00 means intraspecific competition of species a and b is higher than interspecific competition, and an $RY_{ab}$ of less than 1.00 implies intraspecific competition of species a and b is less than interspecific competition. Relative yield total is the weighted sum of relative yields for the mixed culture components. An RYT of 1.00 means that both species are competing for the same resources, and one is potentially capable of excluding the other; an RYT of greater than 1.00 means that the two species exploit different resources and therefore do not compete (e.g., due to different root depths); finally, an RYT of less than 1.00 implies that the two species are mutually antagonistic, with both having a detrimental effect on the other [45]. Values of $CB_{a}$ greater than 0 indicate that species a is more competitive than species b [46].

All morphological variables (total shoot length, branch number, leaf area, leafstalk length, and biomass), as well as photosynthetic rate (Pn) of H. tuberosus and A. adenophora plants were analyzed by analysis of variance (two-way ANOVA) using IBM SPSS 23.0 software (Armonk, New York, USA). If significant differences were detected with the ANOVA, Duncan’s multiple range tests were used to detect differences among treatments at a 5% level of significance. Relative yield and RYT from each mixed culture were compared to the value of 1.00 using one sample t-tests ($P = 0.05$), and values of RYT were tested for deviation from 1.0 and values of CB for deviation from 0 using a paired t-test.

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Authors’ contributions
SS and FZ conceived and designed the experiments; SS, GX, DL, SY, GJ, SL, AC, JR, LW, QT, SZ, and JY performed the experiments; SS and DRC analyzed the data and wrote the draft. All authors read and approved the final manuscript.

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Availability of data and materials
The data set supporting the results of this article is available in the Dryad Digital Repository https://doi.org/10.5061/dryad.s4m6w3m96c.

Declarations
Ethics approval and consent to participate
All aspects of the study comply with institutional, national, and international guidelines. All experiments were conducted on non-regulated organisms. The study site belongs to the Agricultural Environment and Resource Research Institute, Yunnan Academy of Agricultural Sciences and no permits were required to take samples.

Competing interests
The authors declare no conflict of interest.

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