Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

Asymmetric inter-specific competition between invasive Phytolacca americana and its native congener

Yun-Shan Liu
Yunnan University
Li Chen
Yunnan University
Yue Zhou
Yunnan University
Feng Xiao
Yunnan University
Dan-Feng Liu
Yunnan University
Yi Wang (yiwang@ynu.edu.cn)
Yunnan University

Research Article

Keywords: invasive Phytolacca americana, inter-specific competition, competitive ability, energy allocation, trade-off

Posted Date: December 2nd, 2022

DOI: https://doi.org/10.21203/rs.3.rs-2324224/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Plant Ecology on February 6th, 2023. See the published version at https://doi.org/10.1007/s11258-023-01298-1.

Abstract

Interspecific competition is an essential factor affecting the invasiveness of alien plants. *Phytolacca americana*, one of the most destructive invasive plants in China, was introduced from North America into China in 1935. Its population expand, thereby causing the loss of the ecological niches of its native congener and a shrinking of *Phytolacca acinosa* population. In this study, we used the invasive plant *P. americana* and its native congener *P. acinosa* to assess their competitive interaction in response to different competition patterns and spray treatments in a pot experiment in a homogeneous garden at Yunnan University. The results indicate that an asymmetric competition occurred between *P. americana* and *P. acinosa* in inter-specific competition. Specifically, *P. americana* severely inhibits the growth and reproduction of *P. acinosa*, and it was superior to *P. acinosa* in terms of defense strategy on account of its stronger resistance against insects and bacteria. Our study provides some theoretical basis for assessing the invasive plant *P. americana*.

Introduction

In recent years, biological invasion has become one of the top five global environmental problems (Lodge et al. 2006; Ehrenfeld 2010; Lowry et al. 2013). It has been shown that many invasive plants tend to outperform native plants in inter-specific competition, but there are also some invasive plants that exhibit low or no differential competitive ability with native species (Bossdorf et al. 2004; Sheppard and Burns 2014). The traditional view of invasion ecology holds that when invasive plants are closely related to native plants and have similar ecological niches, they often fail to invade successfully because of the biological resistance of native plants (Divisek et al. 2018). However, *Phytolacca americana* is a special case that not only successfully invades but also poses a serious threat to its native congener *Phytolacca acinosa* (Wu et al. 2019). Therefore, it is essential for the conservation and restoration of native plants by exploring the effects of inter-specific competition between invasive and native plants and revealing the mechanisms by which invasive plants affect native plants.

Plant populations with similar ecological habits compete fiercely for the need for resources and the means to obtain them, especially in dense populations (Zhang 1992; Li et al. 1998; Du et al. 2004). Plant growth rate, individual size, the resistance to stress and the number of nutrient organs are all significantly affected by competition. For instance, the native plant *Taraxacum japonicum* has a reduced percentage of seed set owing to the presence of its invasive sibling *Taraxacum officinale*, which is due to *T. officinale* deprives the pollinators of *T. japonicum* (Kandori et al. 2009; Lee et al. 2021). The intense competition from invasive plants often leads to a decrease in the abundance and dominance of native plants, and in some cases, to the local extinction of native species (D'Antonio and Meyerson 2002; Callaway et al. 2005; Sax et al. 2007).

The defense strategy of plants varies with the environment. The EICA hypothesis suggests that invasive plants tend to shift more resources from defense to growth and reproduction in the absence or presence of a relatively small number of generalist natural enemies at the site of introduction, thereby increasing the competitiveness of invasive plants (Muller-Scharer et al. 2004; Barrett et al. 2008; Joshi et al. 2014). The increase of plant tolerance may be related to the change of plant resource allocation pattern. In the field, it has been observed that when *P. americana* are symbiotic with *P. acinosa*, *P. acinosa* are more vulnerable to be attacked by phytophagous insects (Yan et al. 2012a). Therefore, to test the EICA hypothesis, we explored the effect of the resistance of the invasive plant *P. americana*, and native *P. acinosa* in response to different spray treatments.

P. americana, native to southwestern North America, was first introduced to China for its medicinal and ornamental value (Xu et al. 2006), and has invaded more than 20 provinces in China because it leaves behind its coevolved natural enemies of their origin, thereby causing a serious threat to the survival of *P. acinosa*, a traditional Chinese herb, and even the tendency to replace it. Moreover, it will also cause significant economic losses and ecological hazards (Liu et al. 2017; Wu et al. 2019). Therefore, it was listed as a Class I malignant invasive plant in the *Invasive Species List of Yunnan Province (2019 Edition)*. Competition among plants is a universal phenomenon, manifested mainly in the competition for available resources and space between the above- and below-ground parts of plants (Purves and Law 2002). To date, little is currently known regarding the competitive interaction between invasive plant *P. americana* and its native congener *P. acinosa* (Zhang et al. 2016; Zhou et al. 2016; Schirmel 2020; Wang et al. 2021).

In this study, we used *P. americana* and *P. acinosa* to simulate the effects of different planting methods (namely intra-specific competition: *P. americana* + *P. americana*; *P. acinosa* + *P. acinosa*; inter-specific competition: *P. americana* + *P. acinosa*) and spray treatments (e.g. insecticide spray, fungicide spray, insecticide + fungicide spray) on the two in a pot experiment. We tested the following two hypotheses: (1) when the level of inter-specific interactions or pest infestation increased, *P. acinosa* chose to preferentially use resources for synthesizing defense-like substances and correspondingly reduce biomass accumulation; (2) the "growth-defense" trade-off of *P. americana* was weakly influenced by the exogenous environment, and its invasiveness might have a high degree of internal stability.

Materials And Methods

Collection of study species

Seeds of *P. americana* were collected in August 2019 on the campus of Yunnan University (24°83'N, 102°85'E), Kunming City, Yunnan Province, and seeds of *P. acinosa* were collected at the same time in Fuyuan County (25°27'N, 104°19'E), Qujing City, Yunnan Province. After harvesting the ripe berries, we washed off the pulp and washed the seeds, air-drying and storing them at 25°C.

Experimental Design

We conducted the experiments in a greenhouse at Yunnan University with suitable temperature and relative humidity (average temperature of 25°C and average relative humidity of 60%) for the growth of *P.*

americana and *P. acinosa*.

In August 2020, we planted the seeds of *P. americana* and *P. acinosa* in cavity trays in the greenhouse and watered them every 2–3 days. The seedlings were transferred to the pots (d = 9 cm) and watered them every 2–3 days when the seeds in the cavity trays had germinated and the fourth cotyledon had grown. The healthy seedlings up to 10 cm were selected and transferred to 35 cm diameter pots for one of the following three culture types: (1) two *P. americana* monoculture, (2) two *P. acinosa* monoculture, and (3) a mixed culture comprising one *P. americana* and one *P. acinosa* in a pot. At the same time, we sprayed the plants to assess their resistance with the following treatments: (1) spraying insecticide; (2) spraying fungicide; (3) spraying insecticide + fungicide; and (4) spraying water (Fig. 1). Specifically, the insecticide used was Esfenvalerate, which can be used against a broad spectrum of insects but does not negatively affect the plants themselves. The fungicide used was Benomyl. According to the application instructions, the dose of insecticide is 3 ml per plant and the dose of fungicide is 7 ml per plant. Both insecticide and fungicide were sprayed on the leaves and the control treatment was sprayed with 10 ml of water, with 12 replicates of each treatment. Spraying was done once every two weeks.

During the experiment, watering was done once every 2–3 days, and the position of the pots was changed randomly once a month. We harvested all the plant materials on January 17 and 18, 2021, and measured the plant height, basal diameter, and the number of leaves of each plant, determined the chlorophyll content of plant leaves with a portable chlorophyll meter and recorded the number of racemes and the fruits of *P. acinosa* and *P. americana*.

Competitive Ability Analyses

In order to investigate the competitive ability of the invasive plant *P. americana* and the native plant *P. acinosa*, we used the Relative Yield (RY, (Danieli-Silva et al. 2010)), the Relative Yield Total (RYT, (Fowler 1982)) and Competitive Balance Index (CBI, (Wilson 1988))to determine species competitive ability.

The equations were calculated as:

$$\mathrm{RY}_{\alpha} = \mathrm{Y}_{\alpha\beta}/\mathrm{Y}_{\alpha}$$

(Eq. 1)

$$\mathrm{RYT} = \mathrm{RY}_{\alpha}+\mathrm{RY}_{\beta}$$

(Eq. 2)

$$\mathrm{CBI} = \ln\left(\mathrm{RY}_{\alpha}/\mathrm{RY}_{\beta}\right)$$

(Eq. 3)

Where Y_{α} denotes the mean value of plant α biomass per plant in the same planting treatment and $Y_{\alpha\beta}$ denotes the mean value of plant α biomass per plant in the mixed planting treatment between the two species. When $RY_{\alpha} > 1$, it means that the interspecific competition between two species is less than the intraspecific competition of species α; when $RY_{\alpha} = l$, it means that the intraspecific competition of species α is equal to the interspecific competition between two species; when $RY_{\alpha} < l$, it means that the interspecific competition between two species is greater than the intraspecific competition of species α. When RYT > 1, it means that the invasive species and the native species are in a reciprocal symbiotic relationship; when RYT < 1, it means that the invasive species and the native species are in a competitive antagonistic relationship; when RYT = 1, it means that the two species need the same nutritional resources for survival, belonging to the contest competition. When CBI > 0, it indicates that the competitiveness of species α is greater than that of species β, moreover, and the larger the CBI, the stronger the competitiveness of species α is; and vice versa; when CBI = 0, it indicates that the competitiveness of species α and species β is equal.

Determination Of Chemical Substances

After the flowering period of the plants, the leaves of *P. acinosa* and *P. americana* were collected from the same parts under different treatment conditions, Further, we dried and ground at 60°C, and stored at -20°C for determing nutrients (starch and soluble sugars) and resistant substances (total phenols, total flavonoids, tannins, and lignin). The kits used for measuring the above six substances were: starch content kit (anthrone colorimetric method), soluble sugar content (SS) kit, total phenol (Tp) kit, total flavonoid (TF) kit, tannin (Tannin) content kit, lignin content (Lignin) kit (acetylation method), and all the kits were purchased from Suzhou Grace Biotechnology Co., Ltd., China.

Statistical analysis

The individual and interactive effects of the two competition types (inter-specific and intra-specific competition) as well as the three spray treatments (insecticide, fungicide, and insecticide + fungicide) on 16 studied traits of *P. americana* and *P. acinosa* were assessed using general linear models with SPSS software (IBM SPSS Statistics 25). The interaction effect had a significant effect on root-crown ratio, the number of racemes, soluble sugars, total phenols, tannins, and lignin content, whereas we detected no significant effect on the other traits ($P > 0.05$). In addition, we performed multiple comparison analysis (LSD test) for the above six traits. Some data were transformed appropriately to meet the assumptions of chi-square and normal distribution before analysis (Table S1). Plots were performed using Origin Pro 2021.

Results

Growth traits

The results of the homogeneous garden experiment showed that the interaction of planting methods and spraying treatments had significant effects ($P < 0.001$) on the root-crown ratio and soluble sugar content of the plants (Table S1). In addition, plant height, basal diameter, chlorophyll content, and the above-ground biomass were found to be significantly affected by the main effect of planting methods ($P < 0.001$) (Table S1). Specifically, compared with the monoculture, the fungicide spraying treatment significantly reduced the root-shoot ratio and soluble sugar content of *P. americana* in mixed culture. The groups sprayed with both insecticides and fungicides significantly increased the root-crown ratio and soluble sugar content of *P. acinosa* in mixed culture (Fig. 2a; Fig. 3f). Besides, the height, basal diameter, chlorophyll content, and the above-ground biomass of *P. americana* were higher in mixed culture than in monoculture in response to the spray treatments, while the opposite was true for *P. acinosa* (Fig. 4a-c, e). The findings indicated that the growth response of the two plants varies within and between species. However, no significant differences were detected between the number of leaves, total biomass, below-ground biomass, and the starch content of the plants (Fig. S1).

Reproductive Traits

It was found that there was a significant interaction between planting methods and spray treatments on the number of plant racemes ($P < 0.05$) and the main effect of planting methods also significantly affected the weight of plant racemes ($P < 0.001$) (Table S1). Insecticide spraying and the treatment with both insecticides and fungicides significantly increased the racemes number of *P. americana* in mixed culture (Fig. 2b). In contrast, fungicide spraying and the treatment with both insecticide and fungicide significantly reduced the racemes number of *P. acinosa* under the mixed cultivation (Fig. 2b). Qverall, mixed cultivation has reduced the racemes weight of *P. acinosa*, whereas the racemes weight of *P. americana* has increased (Fig. 4d). It demonstrated that *P. americana* chose to devote more resources to reproductive output in inter-specific competition, which is consistent with our expected results.

Defensive Indicators

The experimental results showed that the interaction of planting methods and spray treatments had a significant effect on the content of total phenols, total flavonoids, lignin and tannins of the plants (Table S1). Specifically, the total phenol and tannin content of *P. acinosa* increased under the spraying treatment (compared with the control group), however, the content of defense substances was significantly lower in the mixed cultivated *P. acinosa* (Fig. 3a, c). Contrastingly, compared with the control group, the total flavonoid content of *P. americana* was significantly increased, and the content of the other three substances was detected no significant differences compared with the control group (Fig. 3b). In general, the content of defense substances was also significantly lower in the mixed cultivated *P. americana*.

Competitive Ability

The competitive ability of *P. americana* was stronger than that of *P. acinosa* with respect to the fungicide treatment (CBI > 0, P = 0.0037). As for the insecticide treatment and the blank treatment, the relative yield of *P. americana* was significantly higher than that of *P. acinosa*, indicating that the inter-specific competition of *P. americana* was less than the intra-specific competition. By contrast, the CBI was significantly greater than 0 in both groups, indicating that the competitive ability of *P. americana* was stronger than that of *P. acinosa* in the inter-specific competition (P = 0.0103; P = 0.0031). Additionally, RT, RYT, and CBI of *P. americana* as well as *P. acinosa* were detected no significant differences in the insecticide + fungicide treatment group, indicating that *P. americana* and *P. acinosa* were comparable in competitive ability, and they will compete for the same resources (Table 1).

Table 1
The competitive index under the treatments: spraying insecticide (I), fungicide (F), spraying insecticide and fungicide (I + F) at the same time, and the control treatment(C). RYM: Relative Yield Total of P. americana, RYT: Relative Yield Total, CBI: Competitive Balance Index.

Index	df	I		F		I + F		CK	
		F	P	F	P	F	P	F	P
RY_M	11	2.393	0.036*	1.969	0.075	2.084	0.061	2.442	0.033*
RYT	11	0.503	0.625	0.079	0.938	2.003	0.071	0.601	0.558
CBI	11	3.089	0.01*	3.668	0.004**	1.892	0.851	3.881	0.003**
* P < 0.05 ** P < 0.01									

Discussion

The growth and reproduction as well as defense strategies of plants are evolutionarily intertwined (Huot et al. 2014). For invasive plants, the enemy release hypothesis (ERH) and the evolution of increased competitive ability hypothesis (EICA) hold that invasive populations may have less resources for defense in that the natural enemies release and more resources are allocated for growth and reproduction (Muller-Scharer et al. 2004; Barrett et al. 2008; Joshi et al. 2014), resulting in a non-parallel skew in growth and defense between native and invasive populations (Blumenthal and Hufbauer 2007). For example, *Eupatorium odoratum* L. have evolved greater competitive ability after invasion by increasing the content of odoratin rather than by increasing individual size (Zheng et al. 2015). In this study, we compared the differences in inter-specific and intra-specific competition between the two *Phytolacca* plants in response to different spray treatments. We found that *P. americana* showed stronger competitiveness when competing with *P. acinosa*. In the presence of inter-specific competition, *P. americana* devoted more resources to growth and reproduction, while *P. acinosa* devoted more resources to defense.

The plant height, basal diameter and the biomass of *P. acinosa* were obviously suppressed by *P. americana*, indicating twice the root weight but lower above-ground biomass than *P. acinosa*. This demonstrates the different growth strategies of *P. americana* and *P. acinosa*, where *P. acinosa* prioritizes energy for the growth of the above-ground parts, while *P. americana* has a strong capture of resources in inter-specific competition and devotes more resources to root growth. This experimental result is consistent with that of Liu (2016). *P. americana*, a perennial herb with a large root to crown ratio that facilitates its uptake of soil water, is conducive to its access to more resources in a resource-limited environment, thus mitigating the competitive effects. Chlorophyll is a key element essential for photosynthesis, and chlorophyll content is positively correlated with plant yield. In our study, we found that the chlorophyll content of *P. acinosa* was suppressed by *P. americana*. Owing to the instability of chlorophyll, it will decompose under the stress of salt, alkali acid and oxidant (Gupta and Huang 2014; Shahid et al. 2020), and the results of Niu (2013) experiments showed that the chlorophyll content of soybean subjected to the salt and alkali stress decreased. Some studies found that the chemosensory effect of *P. americana* inhibited the germination and seedling growth of *Digitaria sanguinalis* (L) Scop. (Yan et al. 2012b), therefore, we speculate that the root secretion of *P. americana* may inhibit the formation of chlorophyll in the leaves of *P. americana*.

Invasive plants are usually characterized by high reproductive capacity (Davis et al. 2000; Grotkopp et al. 2002), and they always allocate more energy to the reproductive parts to facilitate their spread and reproduction. Zhou et al. (2013) explored the relationship between reproductive characteristics and the invasiveness of *P. americana*, concluding that *P. americana* is characterised by high fruit set, long seed life, both sexual and asexual reproduction. Our experimental results showed that the reproduction of *P. acinosa* is also significantly inhibited by *P. americana* compared with intra-specific competition. The racemes number and the racemes weight of *P. acinosa* were lower when it was mixed culture with *P. americana* than *P. acinosa* monoculture.

The secondary metabolites of plants are the result of adaptation to their environment over a long period of evolution (Chen and Guo 1999; Acamovic and Brooker 2005; Arbona et al. 2013; Pusztahelyi et al. 2015; Isah 2019). The findings showed that *P. americana* has a stronger anti-insect and antibacterial ability. Related studies have shown that the content of secondary metabolites in *P. americana* is higher than that of other species in the Phytolaccaceae family (Kim et al. 2005). However, in this study, the secretion of secondary metabolites was reduced in the three groups of spray-treated *P. americana* when competing with *P. acinosa* in that the spray treatments reduced the damage from outside insects and pathogens, thus altering the trade-offs in *P. americana* and devoting resources from defense to growth.

Competitions among plants include inter-specific and intra-specific competition. among which inter-specific competition is usually asymmetric (Connell 1983; Young 2004). In contrast, exotic plants from similar habitats cause stronger impacts on native plants. Plant interactions affect the biomass allocation of plants (Blossey and Notzold 1995; Gaertner et al. 2009). For example, the invasive legume *Lespedeza. cuneata* (Dum. Cours.) G. Don has more biomass and root nodules when competing with the native plant *Lespedeza. virginica* (L.) Britton than with conspecifics (Hu et al. 2014). Some studies have stated that invasive plants are more dominant than native plants in situations where resources are limited or disturbed (Daehler 2003; Funk and Vitousek 2007). In this study, it is worth mentioning that *P. americana* gained competitive advantage by weakening intra-specific competition and enhancing inter-specific competition to successfully invade, and its mode of enhancing inter-species competition is mainly by allocating more resources to the subsurface (Svanback and Bolnick 2007). Additionally, *P. americana* has a well-developed root system and a strong ability to obtain resources. In competition with *P. acinosa*, it has a larger root-crown ratio, which means that its root system extends wider than that of *P. acinosa*. A larger surface area in contact with the soil contributes to absorbing more nutrients, thus forming an asymmetrical competition with *P. acinosa* (Freckleton and Watkinson 2001).

Conclusion

The study quantifies the effects of different competition methods and spray treatments on *P. americana* and *P. acinosa* with respect to the symbiosis of *P. americana* and *P. acinosa*, the strong capture of resources and the strong competitiveness of *P. americana* make *P. acinosa* to be crowded out, and the growth and reproduction are inhibited. In addition, *P. americana* has stronger insect and antimicrobial resistance. Hence, *P. americana* allocates more energy to growth, especially to the root growth, which facilitates the multi-year growth of *P. americana*. The effects invasive plants caused are not only on native plants in the invaded sites, but can pass along the food chain to the higher trophic levels. Noted that, the interactions between invasive plants and higher trophic levels are often overlooked. Future studies can be extended to the higher trophic levels, taking cascade effects into account to reveal the effects of invasive plants on native plants in more detail, and to provide some theoretical basis for the assessment of invasive plants.

Declarations

Author contributions YSL, LC, and YW planned and designed the research. YSL and LC collected the data. YSL and LC analyzed the data. YSL, YZ, FX, DFL and YW interpreted the results and wrote the manuscript. All authors contributed critically to the drafts.

Funding The study was supported by the National Key Research and Development Program of China (2022YFC2601100), National Natural Science Foundation of China (31870362 and U2102218) and Scientific Research Fund project of Yunnan Education Department (2022Y034).

The authors declare that there is no conflict of interest

References

1. Acamovic T, Brooker JD, 2005. Biochemistry of plant secondary metabolites and their effects in animals. Proc Nutr Soc, 64 (3): 403-412. https://doi.org/10.1079/pns2005449
2. Arbona V, Manzi M, de Ollas C, Gomez-Cadenas A, 2013. Metabolomics as a tool to investigate abiotic stress tolerance in plants. Int J Mol Sci, 14 (3): 4885-4911. https://doi.org/10.3390/ijms14034885

3. Barrett SCH, Colautti RI, Eckert CG, 2008. Plant reproductive systems and evolution during biological invasion. Molecular Ecology, 17 (1): 373-383. https://doi.org/10.1111/j.1365-294X.2007.03503.x
4. Blossey B, Notzold R, 1995. Evolution of increased competitive ability in invasive nonindigenous plants-a hypothesis. Journal of Ecology, 83 (5): 887-889. https://doi.org/10.2307/2261425
5. Blumenthal DM, Hufbauer RA, 2007. Increased plant size in exotic populations: a common-garden test with 14 invasive species. Ecology, 88 (11): 2758-2765. https://doi.org/10.1890/06-2115.1
6. Bossdorf O, Prati D, Auge H, Schmid B, 2004. Reduced competitive ability in an invasive plant. Ecology Letters, 7 (4): 346-353. https://doi.org/10.1111/j.1461-0248.2004.00583.x
7. Callaway RM, Ridenour WM, Laboski T, Weir T, Vivanco JM, 2005. Natural selection for resistance to the allelopathic effects of invasive plants. Journal of Ecology, 93 (3): 576-583. https://doi.org/10.1111/j.1365-2745.2005.00994.x
8. Chen XM, Guo SX, 1999. Research advances in plant disease resistive material. Chinese Bulletin of Botany (6): 658-664.
9. Connell JH, 1983. On the prevalence and relative importance of interspecific competition-evidence from field experiments. American Naturalist, 122 (5): 661-696. https://doi.org/10.1086/284165
10. D'Antonio C, Meyerson LA, 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. Restoration Ecology, 10 (4): 703-713. https://doi.org/10.1046/j.1526-100X.2002.01051.x
11. Daehler CC, 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. Annu Rev Ecol Evol Syst, 34 (1): 183-211. https://doi.org/10.1146/annurev.ecolsys.34.011802.132403
12. Danieli-Silva A, Uhlmann A, Vicente-Silva J, Sturmer SL, 2010. How mycorrhizal associations and plant density influence intra- and inter-specific competition in two tropical tree species: *Cabralea canjerana* (Vell.) Mart. and *Lafoensia pacari* A.St.-Hil. Plant and Soil, 330 (1-2): 185-193. https://doi.org/10.1007/s11104-009-0191-y
13. Davis MA, Grime JP, Thompson K, 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology, 88 (3): 528-534. https://doi.org/10.1046/j.1365-2745.2000.00473.x
14. Divisek J, Chytry M, Beckage B, Gotelli NJ, Lososova Z, Pysek P, Richardson DM, Molofsky J, 2018. Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. Nat Commun, 9 (1). https://doi.org/10.1038/s41467-018-06995-4
15. Du F, Liang ZS, Hu LJ, 2004. A review on plant competition. Chinese Journal of Ecology, 23 (4): 157-163.
16. Ehrenfeld JG, 2010. Annual Review of Ecology, Evolution, and Systematics. In: Futuyma, DJ, Shafer, HB, Simberloff, D (ed) Ecosystem consequences of biological invasions. Annual Reviews Inc., United States, pp 59-80.
17. Fowler N, 1982. Competition and coexistence in a north-carolina grassland: . mixtures of component species. Journal of Ecology, 70 (1): 77-92. https://doi.org/10.2307/2259865

18. Freckleton RP, Watkinson AR, 2001. Asymmetric competition between plant species. Functional Ecology, 15 (5): 615-623. https://doi.org/10.1046/j.0269-8463.2001.00558.x
19. Funk JL, Vitousek PM, 2007. Resource-use efficiency and plant invasion in low-resource systems. Nature, 446 (7139): 1079-1081. https://doi.org/10.1038/nature05719
20. Gaertner M, Den Breeyen A, Hui C, Richardson DM, 2009. Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. Prog Phys Geogr, 33 (3): 319-338.https://doi.org/10.1177/030913330 9341607
21. Grotkopp E, Rejmanek M, Rost TL, 2002. Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. American Naturalist, 159 (4): 396-419. https://doi.org/10.1086/338995
22. Gupta B, Huang BR, 2014. Mechanism of salinity tolerance in plants: physiological, biochemical, and molecular characterization. Int J Genomics, 2014: 1-18. https://doi.org/10.1155/2014/701596
23. Hu LZ, Busby RR, Gebhart DL, Yannarell AC, 2014. Invasive *Lespedeza cuneata* and native *Lespedeza virginica* experience asymmetrical benefits from rhizobial symbionts. Plant and Soil, 384 (1-2): 315-325. https://doi.org/10.1007/s11104-014-2213-7
24. Huot B, Yao J, Montgomery BL, He SY, 2014. Growth-defense tradeoffs in plants: a balancing act to optimize fitness. Mol Plant, 7 (8): 1267-1287. https://doi.org/10.1093/mp/ssu049
25. Isah T, 2019. Stress and defense responses in plant secondary metabolites production. Biol Res, 52: 39. https://doi.org/10.1186/s40659-019-0246-3
26. Joshi S, Gruntman M, Bilton M, Seifan M, Tielborger K, 2014. A comprehensive test of evolutionarily increased competitive ability in a highly invasive plant species. Annals of Botany, 114 (8): 1761-1768. https://doi.org/10.1093/aob/mcu199
27. Kandori I, Hirao T, Matsunaga S, Kurosaki T, 2009. An invasive dandelion unilaterally reduces the reproduction of a native congener through competition for pollination. Oecologia, 159 (3): 559-569. https://doi.org/10.1007/s00442-008-1250-4
28. Kim YO, Johnson JD, Lee EJ, 2005. Phytotoxic effects and chemical analysis of leaf extracts from three *Phytolaccaceae* species in South Korea. Journal of Chemical Ecology, 31 (5): 1175-1186. https://doi.org/10.1007/s10886-005-4255-z
29. Lee S, Woo S, Kim E, 2021. Differential effect of inter- and intraspecific competition on the performance of invasive and native *Taraxacum* species. Plant Spec Biol, 36 (2): 187-197. https://doi.org/10.1111/1442-1984.12301
30. Li B, Chen JK, Watkinson AR, 1998. A literature review on plant competition. Chinese Bulletin of Botany, 15 (4): 20-31.
31. Liu H, Xie XH, He P, He L, 2017. Study on the invasion mechanism of *Phytolacca Americana*. Journal of Green Science and Technology (7): 1-6. https://doi.org/10.16663/j.cnki.lskj.2017.07.002
32. Liu JH, 2016. Performance of invasive species and co-occurring native species under nutrient variability and competition. Master, Huazhong Agricultural University.

33. Lodge DM, Williams S, MacIsaac HJ, Hayes KR, Leung B, Reichard S, Mack RN, Moyle PB, Smith M, Andow DA, Carlton JT, McMichael A, 2006. Biological invasions: recommendations for US policy and management. Ecological Applications, 16 (6): 2035-2054. https://doi.org/10.1890/1051-0761(2006)016[2035:birfup]2.0.co;2
34. Lowry E, Rollinson EJ, Laybourn AJ, Scott TE, Aiello-Lammens ME, Gray SM, Mickley J, Gurevitch J, 2013. Biological invasions: a field synopsis, systematic review, and database of the literature. Ecol Evol, 3 (1): 182-196. https://doi.org/10.1002/ece3.431
35. Muller-Scharer H, Schaffner U, Steinger T, 2004. Evolution in invasive plants: Implications for biological control. Trends in Ecology & Evolution, 19 (8): 417-422. https://doi.org/10.1016/j.tree.2004.05.010
36. Niu L, 2013. The responses of structural evolvement and physiological in *Glycine* under salt stress and alkali stress. Doctor, Northeast Normal University.
37. Purves DW, Law R, 2002. Experimental derivation of functions relating growth of *Arabidopsis thaliana* to neighbour size and distance. Journal of Ecology, 90 (5): 882-894. https://doi.org/10.1046/j.1365-2745.2002.00718.x
38. Pusztahelyi T, Holb IJ, Pocsi I, 2015. Secondary metabolites in fungus-plant interactions. Front Plant Sci, 6. https://doi.org/10.3389/fpls.2015.00573
39. Sax DF, Stachowicz JJ, Brown JH, Bruno JF, Dawson MN, Gaines SD, Grosberg RK, HastingS A, Holt RD, Mayfield MM, O'Connor MI, Rice WR, 2007. Ecological and evolutionary insights from species invasions. Trends in Ecology & Evolution, 22 (9): 465-471. https://doi.org/10.1016/j.tree.2007.06.009
40. Schirmel J, 2020. Differential effects of American pokeweed (*Phytolacca americana*) invasion on ground-dwelling forest arthropods in southwest Germany. Biological Invasions, 22 (4): 1289-1298. https://doi.org/10.1007/s10530-019-02180-w
41. Shahid MA, Sarkhosh A, Khan N, Balal RM, Ali S, Rossi L, Gomez C, Mattson N, Nasim W, Garcia-Sanchez F, 2020. Insights into the physiological and biochemical impacts of salt stress on plant growth and development. Agronomy-Basel, 10 (7): 938. https://doi.org/10.3390/agronomy10070938
42. Sheppard CS, Burns BR, 2014. Effects of interspecific alien versus intraspecific native competition on growth of native woody plants. Plant Ecology, 215 (12): 1527-1538. https://doi.org/10.1007/s11258-014-0411-2
43. Svanback R, Bolnick DI, 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proc R Soc B-Biol Sci, 274 (1611): 839-844. https://doi.org/10.1098/rspb.2006.0198
44. Wang SS, Jia HD, Zhang ZF, Hu LX, Chen GH, 2021. Competitive effects between invasive plant *Phytolacca Americana* and three forage species. Acta agrestia sinica, 29 (1): 95-102.
45. Wilson JB, 1988. Shoot competition and root competition. Journal of Applied Ecology, 25 (1): 279-296. https://doi.org/10.2307/2403626
46. Wu RR, Liu LD, Zhang L, Hou YP, Wang LJ, 2019. Pollination ecology of the invasive plant species pokeweed. Chinese Journal of Ecology, 38 (8): 2420-2425. 10.13292/j.1000-4890.201908.030

47. Xu HG, Qiang S, Han ZM, Guo JY, Huang ZG, Sun HY, He SP, Ding H, Wu HR, Wan FH, 2006. The status and causes of alien species invasion in China. Biodiversity and Conservation, 15 (9): 2893-2904. https://doi.org/10.1007/s10531-005-2575-5
48. Yan SL, Cui L, Xu S, Li ZR, Liao HM, 2012a. Anatomical studies on the vegetative organs of *Phytolacca acinosa* Roxb. and *Ph. americana* L. Journal of Mountain Agriculture and Biology, 31 (2): 124-128. https://doi.org/10.15958/j.cnki.sdnyswxb.2012.02.014
49. Yan XH, Zhang BL, Zhou B, Wang N, Yang JQ, 2012b. Allelopathic activity of the extract from *Phytolacca americana*-an invasive alien plant. Journal of Ecology and Rural Environment, 28 (2): 139-145.
50. Young KA, 2004. Asymmetric competition, habitat selection, and niche overlap in juvenile salmonids. Ecology, 85 (1): 134-149. https://doi.org/10.1890/02-0402
51. Zhang JZ, Bai XF, Hou YP, Dong ZY, Bu QM, 2016. Comparison on the competitiveness of the invaded pokeweed with its accompanying species in the coastal protection forest of Shandong Peninsula. Scientia Silvae Sinicae, 52 (3): 23-29.
52. Zhang YX, 1992. Competition, coexistence and coevolution among plant species. Journal of Biology (6): 1-2+5.
53. Zheng YL, Feng YL, Zhang LK, Callaway RM, Valiente-Banuet A, Luo DQ, Liao ZY, Lei YB, Barclay GF, Silva-Pereyra C, 2015. Integrating novel chemical weapons and evolutionarily increased competitive ability in success of a tropical invader. New Phytologist, 205 (3): 1350-1359. https://doi.org/10.1111/nph.13135
54. Zhou B, Yan XH, Xiao YA, Zhang ZG, Li XH, Yang JQ, 2013. Traits of reproductive biology associated with invasiveness in alien invasive plant *Phytolacca americana*. Ecology and Environmental Sciences, 22 (4): 567-574. https://doi.org/10.16258/j.cnki.1674-5906.2013.04.010
55. Zhou YL, Li LY, Gao JQ, Ding Y, 2016. Effects of interspecific competition on the growth of invasive and native species. Chinese Journal of Ecology, 35 (6): 1504-1510. https://doi.org/10.13292/j.1000-4890.201606.021

Figures

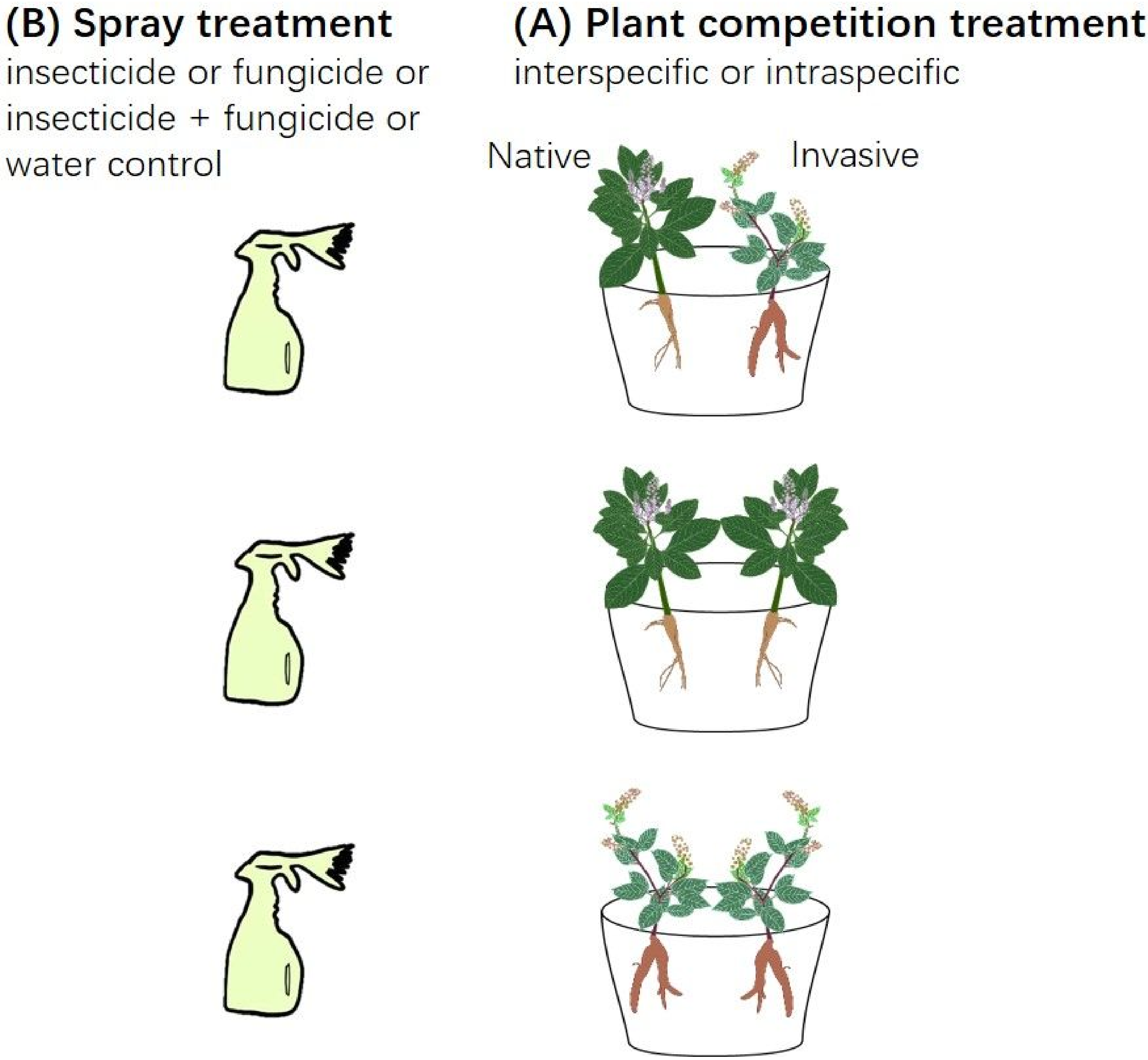

Figure 1

A summary of experimental design, (A) Plant competition treatment (inter-specific and intra-specific); (B) Spray treatment (insecticide, fungicide, insecticide + fungicide, and water control)

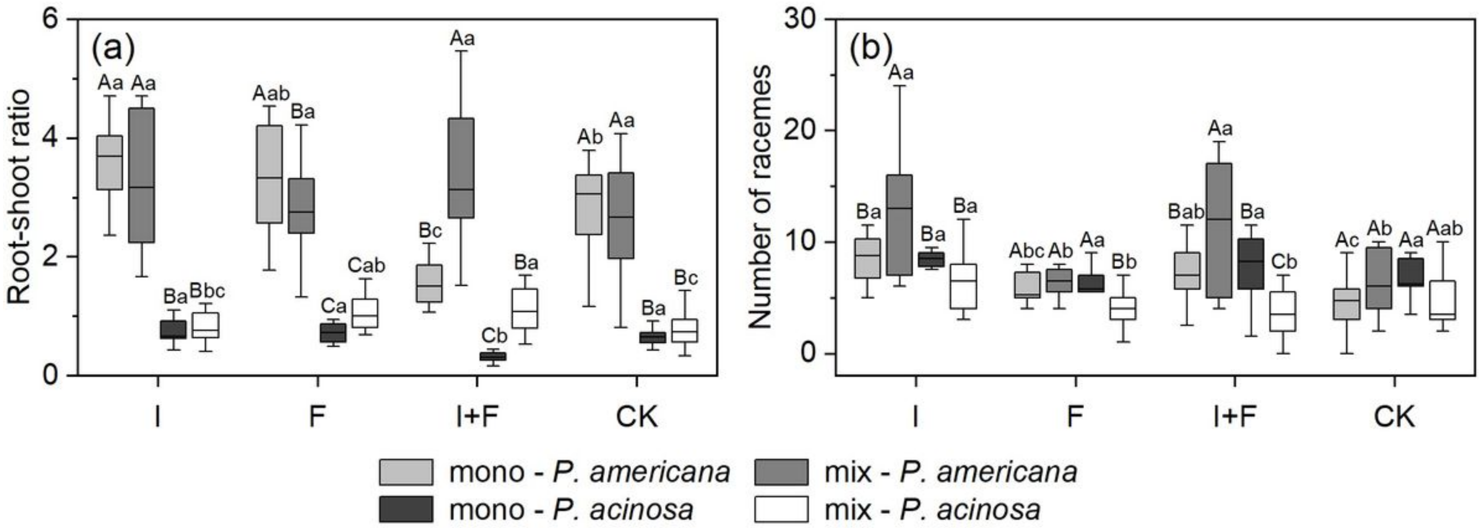

Figure 2

The root-shoot ratio (a) and the number of racemes (b) in *P. acinosa* and *P. americana* under different planting methods and spray treatments. Different lowercase letters indicate significant differences between different spraying treatments under each planting method (p<0.05) and different capital letters indicate significant differences between different planting methods under each spraying treatment (p<0.05)

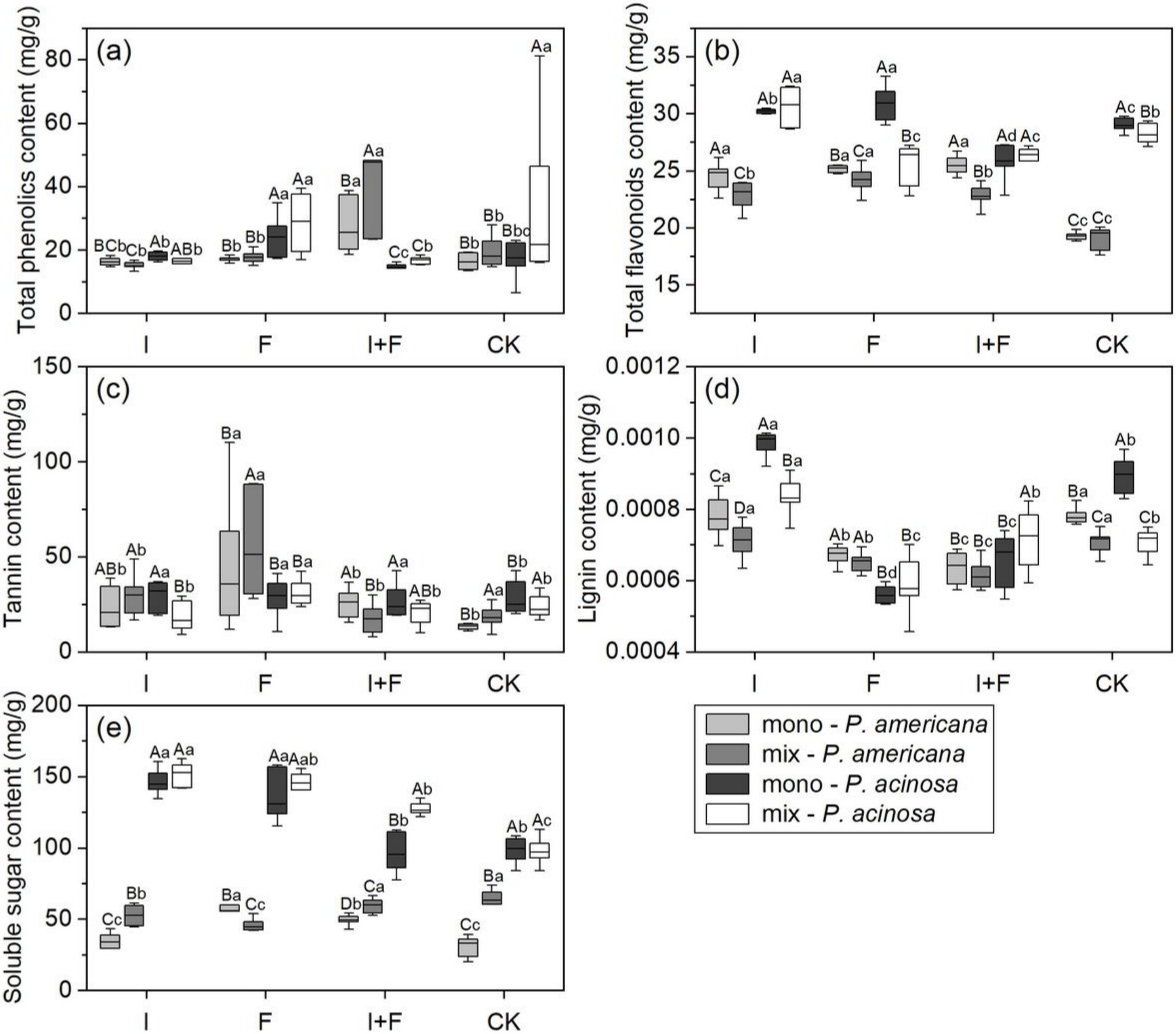

Figure 3

Total phenols (a), total flavonoids (b), tannins (c), lignin (d), and soluble sugars (e) content in *P. acinosa* and *P. americana* under different planting methods and spray treatments. Different lowercase letters indicate significant differences between different spraying treatments under each planting method ($p<0.05$) and different capital letters indicate significant differences between different planting methods under each spraying treatment ($p<0.05$)

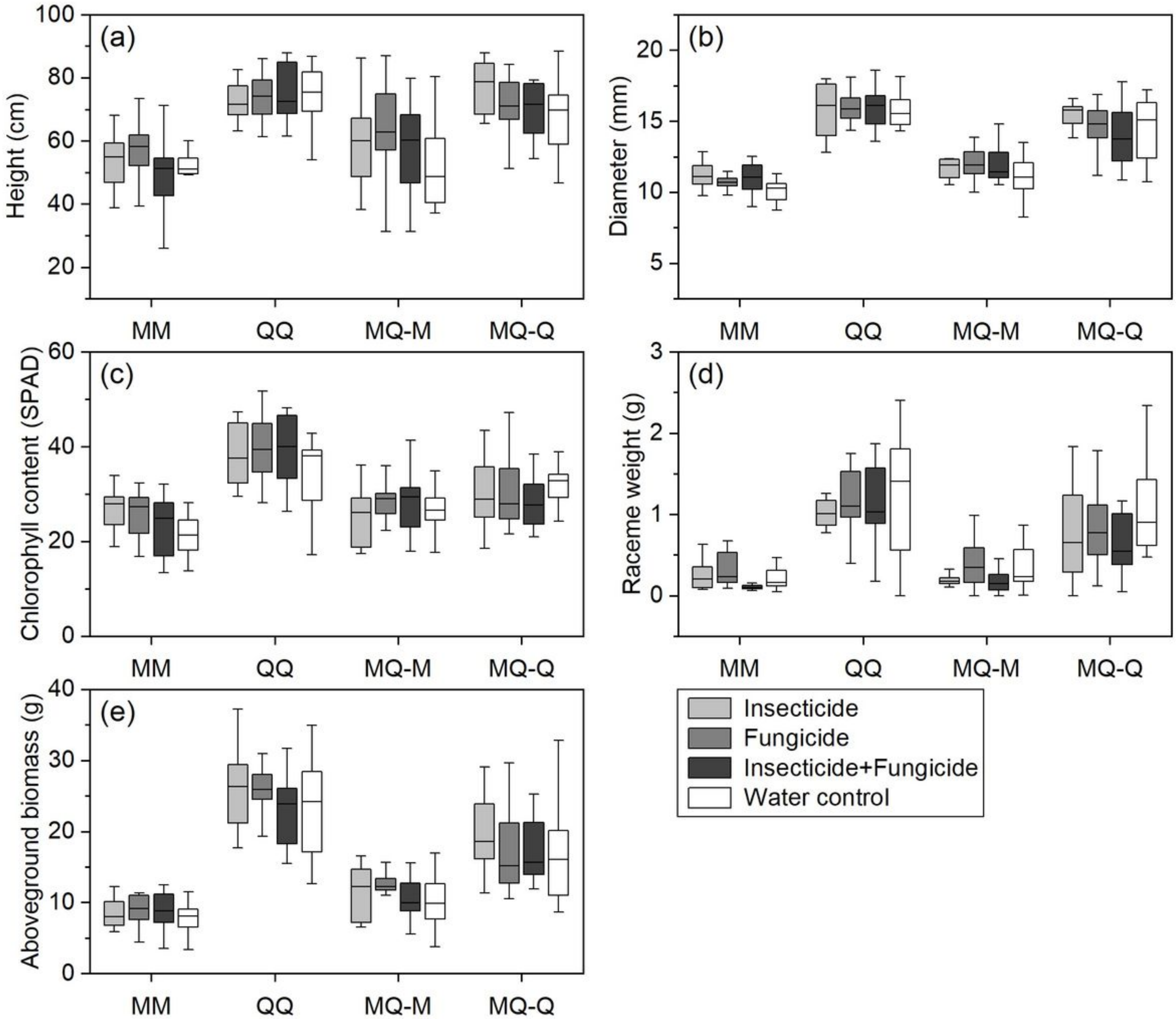

Figure 4

The differences in plant height (a), basal diameter (b), chlorophyll content (c), raceme weight (d), and above-ground biomass (e) between *P. acinosa* and *P. americana* under different planting methods and spray treatments

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryDataYunshanLiuLiChen.docx