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ORIGINAL ARTICLE

Giant Ragweed Invasion is Not Well Controlled by Biotic Resistance

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Abstract The effect of native plant restoration on invasion by giant ragweed (*Ambrosia trifida*), an invasive species, is currently unknown. We hypothesized that (1) functional group identity would be a good predictor of biotic resistance to *A. trifida*, and (2) mixtures of species would be more resistant to invasion than monocultures. Using seven functional traits, 37 native and non-native plants were divided into three functional groups that differed primarily in longevity and woodiness. We conducted a competition experiment using an additive competition design with *A. trifida* and monocultures or mixtures of 14 species. Biotic resistance was evaluated by calculating a relative competition index (RCI_{avg}) based on the average performance of *A. trifida* in treatments compared with that in control. In monocultures, RCI_{avg} of resident plants did not significantly differ among the three functional groups or within each functional group. The highest RCI_{avg} (40%) was observed for some fast-growing annuals (FG1) such as *Zea mays* and *Secale cereal*, which were strong competitors. RCI_{avg} of resident plants was not significantly greater in mixtures than in monocultures. Taken together, the results show that plant diversity did not control invasion by *A. trifida* and that giant ragweed invasion cannot be well controlled by biotic resistance.

Keywords: *Ambrosia trifida*, Biotic resistance, Ecological restoration, Functional group, Invasive plant management, Giant ragweed

Introduction

Ambrosia trifida, called giant ragweed, is a noxious weed that is native to North America (Bassett and Crompton 1982). Controlling *A. trifida* is extremely difficult, and it is listed as one of the most harmful ecosystem-disturbing plants in South Korea (Kil et al. 2004). *Ambrosia trifida* is spreading across the globe in ecological terms as a pioneer species. It is one of the most ecologically destructive weeds (Kong et al. 2007). Intensive invasion by *A. trifida* reduces plant species richness depending on the density of the aliens (Washitani 2001). When present, it dominates the community, produces most of the plant biomass, and suppresses all other species (Abul-Fatih and Bazzaz 1979). *Ambrosia trifida* is increasingly becoming a major problem in agriculture because it out-competes corn and reduces grain yield (Harrison et al. 2001). Damage from invasion is much greater for crop plants with shorter stature, and yield loss can reach approximately 70% (Brandes and Nitzsche 2006).

Invasive plants such as *A. trifida* are usually controlled by cutting, burning, and herbicide application (Kettenring and Adams 2011; Hazelton et al. 2014). Mowing *A. trifida* is not effective because it has a very dense root system and produces shoots in response to cutting (Milakovic et al. 2014). The related species *Ambrosia artemisiifolia var. elatior* has seeds that are very tolerant of fire, and more plants proliferate after a burn than after raking (Tix and Charvat 2005). Repeated application of herbicide is required to control such invasive plants (Derr 2008; Kaur et al. 2014). Kaur et al. (2014) have discussed the importance of glyphosate resistant giant ragweed. Susceptible giant ragweed can be controlled with a single herbicide application when the correct herbicide and time of application is applied. Herbicides are costly and lead to other environmental problem such as bioaccumulation. Management costs increase dramatically after invasive plants become established. The natural recovery of native plants are not guaranteed by eradication of invasive plants (Reid et al. 2009; Thomsen et al. 2012). Eradication methods create disturbances and bare ground, that facilitates reinvasion (Iannone III and Galatowitsch 2008).

Evidence is accumulating that sowing seeds of resident species on disturbed bare ground slows down invasive plant invasion (Kettenring and Adams 2011; Byun et al. 2013;

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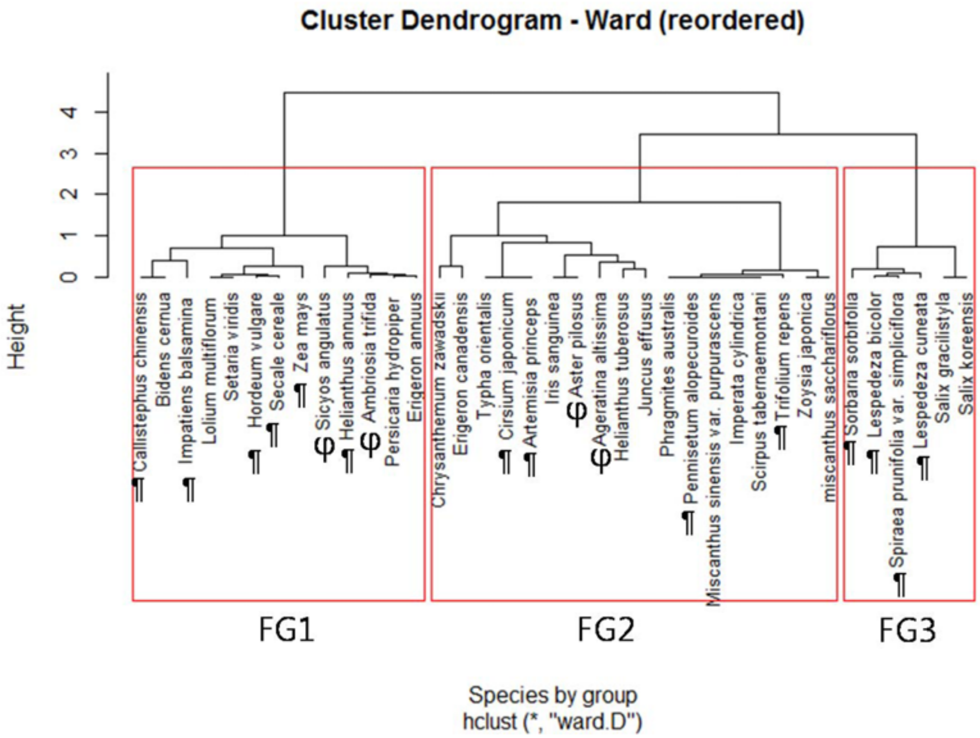

Fig. 1. Functional classification of species. ¶ denotes alternative resident plants; φ denotes major invasive plants in Seoul, South Korea. *Ambrosia trifida* was the target invasive plant in this experiment.

Byun et al. 2015; Byun et al. 2017). There have only been a few studies reporting the use of native plant restoration to counteract *A. trifida* invasion (Blumenthal et al. 2003; Lee et al. 2010), but there have been many studies reporting the use of native plant restoration to control other invasive plants such as *Phragmites australis* (Byun et al. 2013; Byun et al. 2015) and *Phalaris arundinacea* (Iannone III and Galatowitsch 2008; Reinhardt and Galatowitsch 2008). There is still a lack of information about using restoration of alternative plants to control invasion (Esler et al. 2010; Hazelton et al. 2014).

Our research focused on invasion when a site is disturbed, and when we want to limit the early establishment of a species such as *A. trifida*. Successful establishment of *A. trifida* may be influenced by biotic resistance, which is the ability of other plant species to limit invasion. We considered that some resident species or a combination of resident species would be more resistant to invasion than others. Following from our findings in *A. altissima* (Byun and Lee 2017), we hypothesized that certain functional groups would be most resistant to invasion, whereas species effects would be redundant within a functional group. Specifically, we framed our hypotheses around the limiting similarity hypothesis (Macarthur and Levins 1967) and hypothesized that resident plant communities that included the same functional group as *A. trifida* would be more resistant than communities that did not include the same functional group as *A. trifida*. We also hypothesized that there would be a diversity effect (Elton 1958), and that mixtures of species would be more resistant than monoculture species.

Results

Monoculture Treatments

In monoculture treatments, the relative competitive effects of native plants on *A. trifida* were not related to their functional group identity, and in other separate tests, the species identity effect within each functional group was also not significant (Fig. 2). The relative competitive indices (RCI_{avg}) of 14 resident plants on *A. trifida* were not significantly different among three FGs ($F_{2,37} = 2.21$, $P = 0.123$), and were not significantly different within each FG (FG1, $F_{5,10} = 2.58$, $P = 0.074$; FG2, $F_{3,6} = 0.60$, $P = 0.636$; FG3, $F_{3,6} = 0.675$, $P = 0.597$). RCI_{avg} of FG1 (annual plants) was the highest, followed by FG2 and FG3 (mean $RCI_{avg} = 0.207$, 0.114, and 0.097, respectively), although these differences were not statistically significant (Fig. 2). Most of native plants grew to a height far below that of *A. trifida*. Two species (*Zea mays* and *Secale cereale*) belonging to FG1 displayed effective control of *A. trifida* growth (approximately 40% less than control), although this was not statistically significant. Resident plant performance

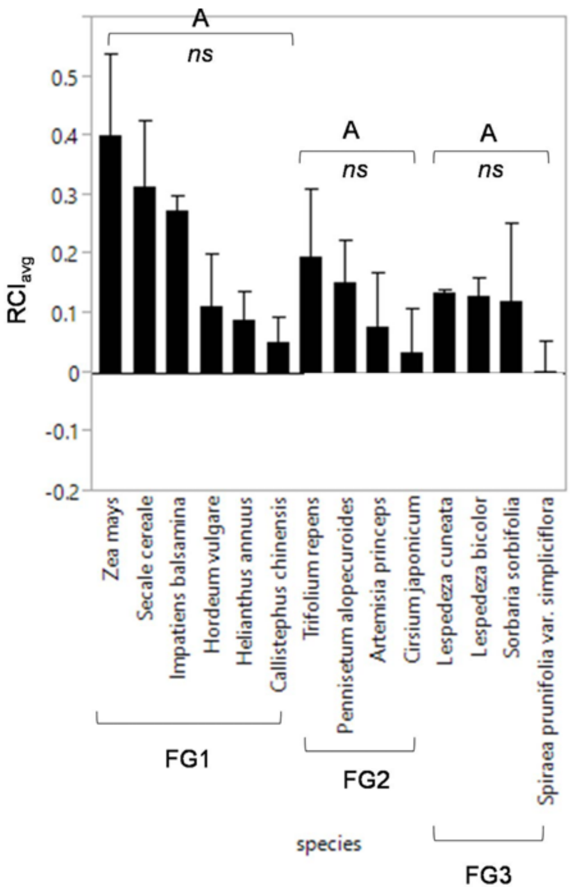

Fig. 2. Monoculture treatment for biotic resistance to *A. trifida* invasion. RCI_{avg} denotes the relative competition index of resident plant(s) as an indicator of biotic resistance. Each species was classified into one of three functional groups (FG1, FG2, and FG3). The same letter indicates no significant differences (functional group); *ns* denotes no significant differences between species within each functional group. Error bar denotes ± SE.

traits were significantly correlated with *A. trifida* in terms of biomass (Pearson coefficient, $r = -0.43$; $P < 0.001$) and plant cover ($r = -0.60$; $P < 0.001$), but not in terms of plant height ($r = -0.02$; $P = 0.852$) (Fig. 3).

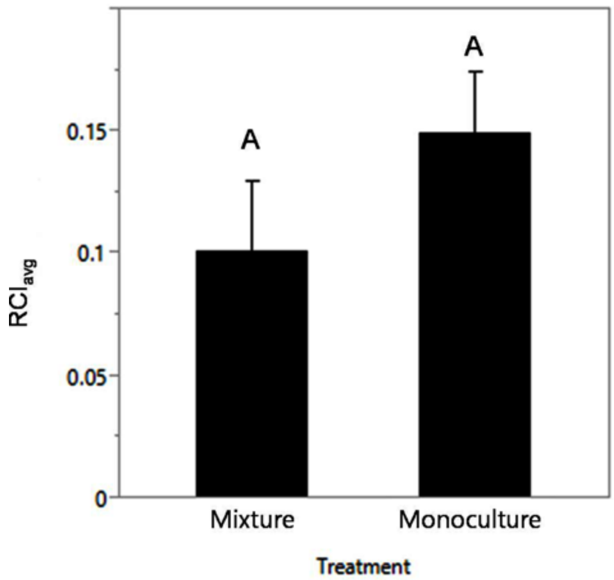

Fig. 4. Comparisons between monoculture and mixture treatments. RCI_{avg} denotes the relative competition index of resident plant(s) as an indicator of biotic resistance. The same letter indicates no significant differences. Error bar denotes ± SE.

Mixture Treatments

There were no significant differences in the suppression of *A. trifida* by mixtures of resident plants and that of monocultures. RCI_{avg} was similar for mixtures and monoculture treatments ($F_{1,62} = 1.508$; $P = 0.223$) (Fig. 4). Above-ground biomass of resident species was also similar for mixture and monoculture treatments ($F_{1,62} = 0.711$; $P = 0.402$).

Discussion

Functional Groups and Biotic Resistance

We found that functional group identity did not determine

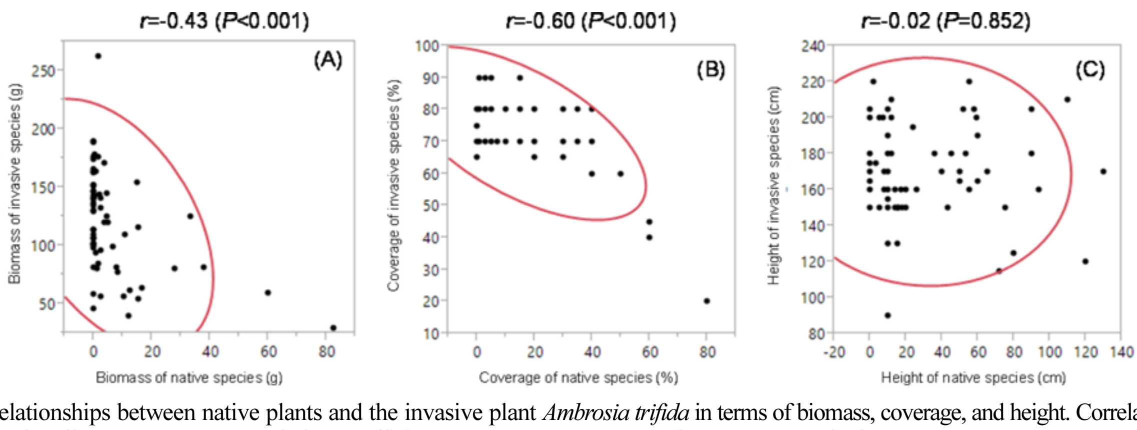

Fig. 3. Relationships between native plants and the invasive plant *Ambrosia trifida* in terms of biomass, coverage, and height. Correlation was significant for all cases (Pearson correlation coefficient were -0.536, -0.792, and -0.383, respectively).

biotic resistance to invasion by *A. trifida* (Fig. 2). And biotic resistance of species identity was not significantly different because all biotic resistance of almost plants was below 40% ($RCI_{avg} < 0.4$). One possible explanation is that biotic resistance of almost all of the species was not strong enough to suppress invasion by *A. trifida.* Another explanation is that sample size (n = 3 per species) was insufficient to estimate species-level variance. Statistical power could have been improved by ensuring better replication within species. In addition, seed density of resident plants might be not high enough to suppress *A. trifida*. Propagule pressure of invasive plants and seed density of resident plants are very important to have biotic resistance more effective (Byun et al. 2015). We used 500 pure live seeds per species for monoculture experiment. Problem was that seeding rate was 1:1 native versus *A. trifida*. To have biotic resistance effective, one need to increase native seeds versus *A. trifida* like 3:1 or more. In addition, timing of germination of *A. trifida* was much faster than other plants in eye obervation. It is probably because we treated seeds of *A. trifida* in cold and wet condition while other plants' seeds were only cold treated. We had to moisten to seeds of *A. trifida* before sowing seeds because their seeds did not germinate in pretest of germination before adding water. According to Page and Nurse (2015), dormancy of seeds of *A. trifida* needs to be alleviated by moisting. Lastly, tall stature and erect stem growth of *A. trifida* have competitive advantage by suppressing understory or coexisting plants through shading and space occupation (Dhileepan 2012; Bajwa et al. 2016).

By trend (not significance), the most resistant species, such as *Zea mays* and *Secale cereal,* belonged to the FG1 group (annuals). Although *A. trifida* also belongs to FG1, there was no statistical support for limiting similarity (Macarthur and Levins 1967) in this study. High density corn (such as *Zea mays*) is reported to compete effectively with and suppress giant ragweed with no impact on yield (Page and Nurse 2015).

Previous studies analyzed functional groups based on plant traits such as growth form, root structure, or plant height (Pokorny et al. 2005; Sheley and James 2010; Byun et al. 2013), and identified a significant role for functional group in biotic resistance, with one exception (Von Holle and Simberloff 2004). On other hand, our study found that functional groups did not differ with respect to their ability to suppress *A. trifida*.

A study investigating the control of *A. trifida* by plant restoration reported that *Salix koreensis* effectively controlled *A. trifida* within three growing seasons (Lee et al. 2010), although only one species was tested. Diversity index increased after the introduction of willow compared with that of the control site. Willow can restore riparian areas that have been placed by *A. trifida*. Selective removal of *A. trifida* from field plots early in the growing season is reported to increase biomass, density, and diversity of the remaining species (Abul-Fatih and Bazzaz 1979) and weed emergence time has been shown to influence weed competitiveness in an experiment with *A. trifida* (Hock et al. 2006). A study targeting a related weed species (*Ambrosia artemisiifolia*) reported that seeding prairie species resulted in dense cover of prairie species and reduced the stem numbers of *A. artemisiifolia* by increasing the strength of competitive effects and reducing available resources (Blumenthal et al. 2003). Seeding mixtures of grassland species can successfully suppress *A. artemisiifolia* in the early establishment on bare ground soil (Gentili et al. 2015).

The present study showed that biomass and plant coverage are important for controlling *A. trifida* invasion (Fig. 3). The biomass of resident communities is one of the best indicators for competitive ability on invasive species (Gaudet and Keddy 1988) and level of biotic resistance to invasion (Lulow 2006). Higher biomass of resident species suggests that fewer resources are available for invaders, which leads to stronger biotic resistance (Davis et al. 2000). Native plant height was not correlated with that of *A. trifida* in our experiment (Fig. 3). In this study, *A. trifida* stems extended very fast and quickly covered other species during early development. The height of most native plants was far below that of *A. trifida*. It is possible that *A. trifida* has competitive advantage because it extent shoots very fast and early in the spring season.

Effect of Diversity on Biotic Resistance

Our results failed to reveal a diversity-resistance relationship (Fig. 4). These results suggest that mixture treatments do not provide greater resistance to *A. trifida* invasion than monoculture treatments. This result is not consistent with previous community-scale experimental studies on multiple invaders (Stachowicz and Byrnes 2006; Frankow-Lindberg et al. 2009; Schamp and Aarssen 2010; Byun, et al. 2013; Zhu et al. 2015). The effectiveness of biotic resistance depends on the seed sowing density and propagule pressure (Byun et al. 2015). This may be the reason why we did not detect a diversity effect in this study. Sowing density was approximately only 500 pure live seeds/m^2 in our experiment, and the seedling rate was 1:1 natives versus *A. trifida*. For example, we found a diversity effect when we tested the same functional group against invasion by *Ageratina altissima* using a sowing density of 3:1 (Byun and Lee 2017). In our experiment, the effectiveness of most resistant species such as *Zea mays* was only about 0.4 RCI_{avg}; statistically, it was very difficult to detect significant differences among species and FGs. Follow-up experiments using a higher sowing density of natives versus *A. trifida* are required (e.g., 3:1) to detect differences between the biotic resistances of the species. It is also possible that the results would have been different in a natural field setting.

Implications for Management

Under field conditions, invasion success is determined by the interplay between biotic resistance, abiotic constraints, and propagule pressure (Perelman et al. 2007; Catford et al. 2009). Although our experiment did not test all these factors, our approach revealed that biotic resistance was not crucial under normal conditions for the control of *A. trifida*. *Ambrosia trifida* often flourishes in specific habitats such as the floodplain of a large river (Washitani 2001). *Ambrosia trifida* is an upland plant because its seeds cannot survive in inundated stream channels or in poorly drained high marsh due to lack of seedling tolerance to water-logged soil and shading by other species (Sickels and Simpson 1985). Prolonged drawdown condition facilitates *A. trifida* seedling establishment (Sickels and Simpson 1985). These conditions provide optimal windows of opportunity for *A. trifida*. Based on our results, we suggest that some FG1 species such as *Zea mays* and *Secale cereale* might be useful for the restoration of plant cover and the suppression of *A. trifida* invasion. However, *Zea mays* and *Secale cereale* are agricultural crop species and not native species. If none-agricultural plant cover must be restored, we suggest to use either *Impatiens balsamina* or *Trifolium repens* which are also non-native plants. Most native plants (*Pennisetum alopecuroides*) do not efficiently control *A. trifida* invasion. To be sure about suppression on *A. trfida*, follow-up monitoring and selective control of *A. trifida* establishment could be necessary for competitive exclusion.

Conclusions

The present study indicates that *A. trifida* is a very difficult invasive plant to control by biotic resistance alone. Therefore, plant restoration should be coupled with an intensive eradication method. Particularly, we suggest that different environmental conditions and a variety of functional groups should be tested for biotic resistance.

Materials and Methods

Species Selection and Functional Classification

Twenty-two resident species were selected based on expert recommendations, personal opinion, and commercial seed availability to test for biotic resistance to a typical invasive species in South Korea, *Ambrosia trifida*. These resident species are frequently found disturbed habitats. The TRY trait database (Kattge et al. 2011; Byun et al. 2013) was used to obtain functional traits of species, including specific leaf area, canopy height, life span, growth form, woodiness, relative growth rate, and dry leaf matter content. These functional traits are relevant for core plant traits related to dispersal, establishment, and persistence (Weiher et al. 1999), and for functional traits related to competitive ability and growth (Funk et al. 2008). To build a species-trait matrix, the median value of measured traits per species was measured for data consistency. Species were classified into three functional groups based on trait similarity. Using these functional traits, Gower's similarity coefficient among the species was calculated using the *gowdis* function in R (Gower 1971; Podani 1999). All traits were standardized and equally weighted in the calculation of the similarity coefficient. The 37 plants were classified into three functional groups by cluster analysis with the ward option using *hclust* functions in the R package (Fig. 1). The functional groups differed primarily by life span and woodiness: FG1 included annual plants, FG2 included perennial herbaceous plants, and FG3 included perennial woody plants. Detailed characteristics of each functional group are presented in Table 1. The same experiment design (classification of functional group) was used in our previous study (Byun and Lee 2017).

Experimental Design and Seed Preparation

A microcosm experiment was conducted in a greenhouse facility at the School of Biological Sciences at Seoul National University. This experiment simulated a situation where *A. trifida* seeds arrive on bare soil after biological disturbance. The pot size was 22 cm diameter and 30 cm height. The soil used in the experiments was fertile agricultural soil, and the pots were watered once per week. All pots received the same amount of water at each watering time. Pots remained wet for most of the week.

A. trifida seeds were collected at the roadside of an old field (Gwongi-do, Yoenchun-gun; 38 04 14.42 N, 127 08 10.90 E). Most of the native plant seeds were purchased from commercial seed suppliers. Seed viability among native plants was standardized by sowing the same number of live seeds per species to experimental

Table 1. Characteristics of functional group traits. SLA: specific leaf area, RGR: relative growth rate, LDMC: leaf dry matter content, FG: functional groups (Fig. 1)

Trait	FG1	FG2	FG3	Unit
Longevity	Annual	Perennial, biennial	Perennial	
Growth form	Herb, grass, forb	Herb, forb, sedge, grass	Shrub, tree	
Woodiness	Non-woody	Non-woody	Woody	
SLA	25.13 ± 4.10	26.95 ± 19.23	25.90 ± 11.12	$m^2\ kg^{-1}$
RGR	0.22 ± 0.05	0.17 ± 0.12		g/g/d
LDMC	3.57 ± 6.88	6.30 ± 10.31	8.23 ± 15.59	g/g
Height	140.3 ± 135.9	70.36 ± 55.16	156.5 ± 56.3	cm

units. To determine live seeds, germination tests were conducted. All seeds were cold-stratified at 3°C prior to the germination test according to standard methods (Lindig-Cisneros and Zedler 2001). *A. trifida* seeds were cold-wet-stratified according to the method of Page and Nurse (2015). Before the experiment, 100 seeds per species were placed in each of three Petri dishes containing filter papers (Whatman® No. 1) moistened with 6 mL of distilled water, and the dishes were placed under fluorescent lights. Any species with a germination rate below 3% was excluded. Among the 22 species, only 14 species had germination rates greater than 3%. Among 14 species, 6 species were none-native species and 8 species were native species. Live seeds (target number of seeds, divided by germination rate), not seedlings, were used for the pot experiments. In other words, the proportion of seeds that were viable was estimated, and then number of actual seeds that would result in the desired number of viable seeds was sowed.

Competition Design

An additive competition design was used to test the competitive effect of resident species on *A. trifida* invasion (Keddy et al. 1994; Connolly et al. 2001; Byun et al. 2013). Each treatment pot was sown with seeds of *A. trifida* and native plants. The control pot was sown only with *A. trifida* seeds. For 14 monoculture treatments, one native species was used per pot. For eight mixture treatments, four randomly selected native species were used per pot. Three replicates of each of the four species and three replicates per treatment were performed. Three blocks were randomly allocated and a total of 69 pots were used. All species in monocultures or mixtures were sown in early March 2016 along with *A. trifida* seeds (treatments and control). The seeding density of native plant(s) and *A. trifida* was 20 pure live seeds per pot. Therefore, seeding rate was 1:1 native versus *A. trifida.* The sowing density was approximately 500 live seeds/m^2 for each species in monocultures and 125 live seeds/m^2 for each species in mixtures. A randomized complete block design were employed.

Data Measurement and Analysis

At the end of July 2016, the *A. trifida* plants were already very tall and in the predominant growth stage comparing to other resident plants. The number of shoots, above-ground biomass, plant height, and plant cover of *A. trifida* in each treatment pot and control pot were calculated as the main response variables (see below). Plant cover, plant height, and above-ground biomass of all the resident plants were also measured to correlate them with the response variables. The above-ground biomass (dry weight) was measured by harvesting the above-ground plant material, placing the material in an 80°C oven for 48 h, and then weighing the dry weight. Plant height was estimated for each species to the closest 0.5 cm. The relative competition index (RCI) was calculated to estimate the competitive effect of native plant(s) on *A. trifida* invasion using the following equation (Weigelt and Jolliffe 2003; Byun et al. 2013):

$$RCI_Y = \frac{Y_{control} - Y_{treatment}}{Y_{Control}} \qquad \text{(Eq. 1)}$$

where RCI is the relative competition index of a native plant on *A. trifida* either in monoculture or mixture for a given variable Y (number of shoots, above-ground biomass, plant height, or plant cover of *A. trifida*). $Y_{control}$ is the performance of *A. trifida* in the control, and $Y_{treatment}$ is the performance of *A. trifida* in the treatment. Because $RCI_{number\ of\ shoots}$, $RCI_{biomass}$, RCI_{height}, and $RCI_{plant\ cover}$ were highly correlated with each other, the arithmetic mean RCI_{avg} was calculated as the main response variable for all analyses. A value of 0 for RCI_{avg} suggests no competitive effect on *A. trifida*, a value of 1 suggests complete competitive exclusion of *A. trifida*, and negative RCI suggests facilitation of *A. trifida* establishment and growth by native plants.

A generalized linear mixed model was used to test for the effects of functional group identity and species identity on RCI_{avg} for monoculture treatments. The generalized linear mixed model (REML; *F*-test) was used to take into account the random block effect (Bolker et al. 2009). Normality of residuals and homoscedasticity were checked, and response variables were transformed (Log). First, the one way functional group effect on RCI_{avg} was tested in every pot except for the control pots. If a significant functional group effect was identified, the means of the functional groups were compared using a contrast test on each pair of functional groups because each functional group did not have an equal number of species. If a significant species identity effect was identified within each functional group, the differences were tested using Tukey's HSD multiple comparison for each functional group. Correlation tests were also performed on biomass, height, and coverage of *A. trifida* and native plants. All ANOVA tests and correlation analyses were conducted using JMP software (SAS Institute, Inc. Cary, NC, USA). Cluster analysis was conducted using R (http://www.r-project.org).

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Author's Contributions

CB and EL conceived the research; CB designed the research, performed the experiments, analyzed data, and wrote the manuscript; EL edited the manuscript. All the authors agreed on the contents of the paper and post no conflicting interest.

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