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Climate Change Hastens Invasional Interference Between Two Notorious Invasive Plants, Common Ragweed (*Ambrosia Artemisiifolia*) and Redroot Pigweed (*Amaranthus Retroflexus*), in China

Cai-yun Zhao

CRAES: Chinese Research Academy of Environmental Sciences

Xiang-jian Zhao

CRAES: Chinese Research Academy of Environmental Sciences

Junsheng Li (≥ 106632752@qq.com)

CRAES: Chinese Research Academy of Environmental Sciences

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Abstract

As multiple invaders co-occur in similar habitats, understanding the interactions between different invasive species is very important. Invasional meltdown and neutral and interference relationships have been reported. However, interspecific interactions may vary with environmental change due to the different responses of various invaders. To better understand the interaction of notorious invasive alien plants under global climate change, the growth characters of common ragweed (*Ambrosia artemisiifolia*) and redroot pigweed (*Amaranthus retroflexus*) were compared when they were planted in monoculture or mixed culture under four environmental treatments: elevated CO₂, enriched N, elevated CO₂ + enriched N and a control. The results showed that 1) the plant height, basal stem diameter, and shoot, root, and total biomass of common ragweed all consistently increased in response to the treatments, while the growth traits of redroot pigweed were all inhibited. A significant CO₂×N interaction was found only for the shoot and total biomass of common ragweed. 2) Invasional interference between these two notorious alien invasive plants was discovered. Common ragweed consistently displayed an obvious competitive advantage over redroot pigweed regardless of treatment. 3) Elevated CO₂ and enriched N obviously changed the seed mass frequency distribution of common ragweed: elevated CO₂ increased the proportion of small seeds, while enriched N increased the proportion of large seeds. We conclude that common ragweed can outcompete redroot pigweed; moreover, elevated CO₂ and N addition hasten this competitive advantage.

Introduction

Invasive plants often show high adaptability and phenotypic plasticity so that they can survive under altered environmental conditions (Davidson et al. 2011; Liu and van Kleunen 2017), but different invasive plants vary in their responses to environmental change, such as climate change (Dukes and Mooney 1999). Numerous case studies have demonstrated that invasive plants benefit from climate change (Dukes and Mooney 1999; Sorte et al. 2013; Liu et al. 2016; Mozdzer et al. 2016), especially N deposition and elevated CO₂. Elevated CO₂ can facilitate plant invasion by increasing plant photosynthesis, water use, growth rates, resource use efficiency, productivity, seed production and seed banks (Stewart and Potvin 1996; Smith et al. 2000; Weltzin et al. 2003; Ziska 2003; Dukes et al. 2011; Smith et al. 2013). N deposition can facilitate plant invasion by increasing N availability, plant-soil feedbacks, plant growth and competitive ability (Limpens et al. 2003; Zhang et al. 2010; He et al. 2011; Wan et al. 2019). In most research, these two factors are studied independently. Understanding how invasive plants respond to the interactive effect of elevated CO₂ and N deposition is important but still underappreciated. Plant growth and biomass accumulation can be enhanced by elevated CO₂, and the rates of these processes may be constrained by soil N availability (Luo et al. 2004; Feng et al. 2015). The invasion of *Eupatorium adenophorum* may be exacerbated by CO₂ enrichment and N deposition (Lei et al. 2012).

Successful invasion by one plant not only is related to its adaptability to the environment but also depends on its ability to compete with other plants, including other invaders. As biological invasions increase in frequency, most habitats are invaded by multiple invasive plants, so interactions between different invasive species become more important (Shea and Chesson 2002). Invasive species can interact with each other (Russell et al. 2014; Kuebbing and Nunez 2014). One alien invasive species can be facilitated by another species, which is described as invasional meltdown (Simberloff and Von Holle 1999). Most known cases of invasional meltdown involve plants and organisms at other trophic levels, and there are few examples involving plant-plant interactions (Simberloff 2006). Invasion by one species can be negatively impacted by the presence of another invader, known as invasional interference (Yang et al. 2011; Rauschert and Shea 2012), especially when they require similar niches (Rauschert and Shea 2016). In some cases, these negative relationships may result in an invasive species replacing another invasive species, known as "overinvasion", which is used to describe this phenomenon in an animal context (Russell et al. 2014). Many authors have noted that a decline in one nonnative species results in a rapid increase in another, which indicates that competition among invasive plants may be common (Kuebbing and Nunez 2014). Invasional interference and overinvasion are understudied in plants. For example, the replacement of *Spartina anglica* by *Spartina alterniflora* was deduced (Zhi et al. 2007) in China. It is also possible that the interactions are neutral, as supported by a meta-analysis on the interactions of invasive animals (Jackson 2015).

The types of interactions among plants depend on environmental, species and individual features (Callaway and Walker, 1997). A series of studies have compared responses to climate change between invasive plants and native plants (Dukes and Mooney 1999; Liu et al. 2016) or naturalized alien plants and native plants (Sorte et al., 2013). However, different invasive plants are seldom compared in altered environments. Competitive ability varies with changes in environmental conditions; for example, an increased competitive advantage of invasive species has been attributed to higher N availability (Quinn et al., 2007). Variations in the environment can influence the intensity of competitive interactions (James and Richards 2007) and competitive relationships of plants because competing species respond differently to environmental change (Miller et al. 2007; Mamolos 2006). Moreover, competition relationships and elevated CO₂ and N deposition often occur at the same time, and how these factors impact invasive species still needs to be determined.

To study the relationship of two notorious invasive plants, *Ambrosia artemisiifolia* (common ragweed) and *Amaranthus retroflexus* (redroot pigweed), and the impacts of elevated CO₂ and N deposition on their relationship, we planted these two plants in monoculture and mixed culture under different environmental treatments, namely, elevated CO₂, N deposition, elevated CO₂ + N deposition and a control. The growth characters, biomass and relative yield of the two invasive species were all measured, and we also examined the seed production of common ragweed under competition and elevated CO₂ and N deposition. We aimed to answer the following questions: (1) Do these two invasive alien plants respond to elevated CO₂, N deposition and competition in the same way? (2) Does climate change impact the relationship between two invasive alien plants? (3) How do elevated CO₂, N deposition and competition affect the reproduction of common ragweed?

Materials And Methods Plant materials

Two notorious invasive species were selected: *Ambrosia artemisiifolia* (common ragweed) and *Amaranthus retroflexus* (redroot pigweed), both of which are native to North America. *Ambrosia artemisiifolia*, which is an annual weed in crop fields, usually forms dense monospecific stands and produces a considerable amount of pollen (Gentili et al. 2018), and this weed is one of the most problematic aero-allergens (Ziska and Caulfield 2000). It was introduced into China in the 1930s and has since spread in twenty provinces (Liu et al. 2016). *Amaranthus retroflexus* occurs in various habitats, including agricultural and ruderal habitats (Valerio et al. 2011; Yang et al. 2011). It has a dramatic impact on ecosystems and native species (Rezaie and Yarnia 2009; Wang et al. 2017) and is regarded as the third most notorious weed in the world (Yang et al. 2011; Ma et al. 2012). *Amaranthus retroflexus* has expanded its distribution in large areas since its introduction to China in approximately 1905 (Qin et al. 2018). Seeds of common ragweed and redroot pigweed were collected from Mentougou District in Beijing (100 km from the experiment site) in October 2013.

Experimental design

The experiment was conducted in eight open-top chambers (OTCs: $2.2 \, \mathrm{m}$ in height with an octagonal ground surface area of $6.25 \, \mathrm{m}^2$) at the Experimental Base of the Chinese Research Academy of Environmental Sciences field laboratory located in Shunyi District, Beijing, China ($116.5875^{\circ}E$, $40.19^{\circ}N$), between June 5 and October 8, 2014. Four chambers each were randomly selected to be maintained at one of two CO_2 concentration levels: ambient CO_2 ($375 \, \mu l/L$) and elevated CO_2 ($700 \, \mu l/L$). Ten plastic pots ($32 \, \mathrm{cm}$ in diameter and $38 \, \mathrm{cm}$ in depth) were randomly arranged within each OTC in the following experimental design: $2 \, \mathrm{CO}_2$ levels $\times 2 \, \mathrm{N}$ levels $\times 5 \, \mathrm{competition}$ levels $\times 4 \, \mathrm{replicates}$. Thus, the experiment consisted of $80 \, \mathrm{pots}$ in total. During the growing season, the total N addition levels were 0 and 0. $80384 \, \mathrm{g \cdot pot}^{-1}$ ($10 \, \mathrm{g \cdot m}^{-2} \times 0.080384 \, \mathrm{m}^2 \cdot \mathrm{pot}^{-1}$). N was divided equally $8 \, \mathrm{times}$ and uniformly applied in the form of $\mathrm{NH_4NO_3}$ solution, and the control pots were sprayed with the same volume of water. Five competition levels were assigned as follows: 4A:0Am (where A and Am denote common ragweed and redroot pigweed, respectively), 1A:3Am, 2A:2Am, 3A:1Am and 0A:4Am. Four plants were planted in each plot under the different competition levels.

The seeds were treated at low temperature (-20°C) for two months and then stored at room temperature in paper bags. The seeds of the two species were sown on May 7, 2014, at a depth of 2 cm in two field plots and then watered to field capacity once to stimulate germination. After three weeks, uniformly strong and tall seedlings were transplanted into pots in the OTCs according to the experimental design. To ensure homogeneity of the growing conditions, the pots were filled with a homogeneous mixture of local soil (80%; collected at depth of $3 \sim 15$ cm from a weedy field neighboring the experiment base after the exclusion of topsoil) and vermiculite (20%). Before transplantation, the following soil nutrient contents were measured: organic carbon, 8.4 g·kg^{-1} ; total N, 0.73 g·kg^{-1} ; ammonium N, 10.77 mg·kg^{-1} ; and nitrate N, 6.53 mg·kg^{-1} IlOne week after transplantation, the elevated CO_2 and N enrichment treatments were initiated. Pots were watered weekly as needed throughout the experiment. In each OTC, pots were moved randomly every month. In the elevated CO_2 treatment, the achieved level was 695.00 ± 15.67 (mean \pm SD) ppm CO_2 (measured at 5-min intervals).

Measurements and calculations

The plant height, basal stem diameter and branch number per plant of common ragweed and redroot pigweed were measured. The shoots of each species in every pot were harvested from above the soil surface and stored in archival paper bags. Roots and soil were removed from the pots, and the roots of each species in every pot were collected and stored in archival paper bags. The shoots and roots were oven-dried at 80°C for 72 h. The shoot biomass and the root biomass of each species in each pot were measured, and the total biomass of each species was calculated per pot.

Relative yield (RY) is a measure of the relative competitive abilities of two species. RY values > 1 indicate that one species does better when competing against the other species than when competing against itself. High RY values indicate a high degree of competitiveness of one species relative to that of the other (Williams and McCarthy 2001). RY values are calculated using the equation below (Williams and McCarthy 2001; Weigelt and Jolliffe 2003).

$$RY_i = \frac{Y_{ij}}{p_i \times Y_i}$$

where Y_{ij} is the yield of species i in the presence of species j, p_i is the proportion at which species i was sown, and Y_i is the yield of species i in monoculture under the same CO_2 and N treatment as that for Y_{ij} .

To analyze the impact of elevated CO_2 and N addition on the reproduction of common ragweed, in each pot with common ragweed, seeds were collected by hand in October when the seeds were mature but had not yet begun to drop. The total seed number and the total seed weight were measured as seed yield. To examine the impacts of CO_2 and N on the size of seeds of *Ambrosia artemisiifolia*, a total of 100 seeds were selected randomly from each pot of monocultured *Ambrosia artemisiifolia*; each seed was weighed and placed in one of four mass classes (< 2 mg, 2–5 mg, 5–8 mg and > 8 mg) on the basis of individual seed mass. The percent ratio of each class per pot was calculated, from which the seed mass frequency distributions were determined.

Statistical analysis

Three-way ANOVA was used to test the effects of CO₂, N and competition on the growth performance and competitive ability of *Ambrosia artemisiifolia* and *Amaranthus retroflexus*. When competition level had a significant effect, significant differences between competition levels were tested using the Tukey honesty significant difference post-hoc analyses (HSD) (*P*<0.05). Two-way ANOVA was used to test the effects of CO₂ and N on the seed size of *Ambrosia artemisiifolia*. In all ANOVAs, data were log transformed where necessary to conform to the assumptions of normality and heteroscedasticity. All analyses were performed using IBM SPSS Statistics 19 (IBM, 2010).

Results

Effects of CO₂, N and competition on the growth characters of two invasive alien plants

The height, basal stem diameter and branch number of common ragweed were significantly increased by N addition when the species was grown in monoculture or with redroot pigweed, whereas only the height of redroot pigweed was increased by N addition (Fig. 1). Common ragweed benefitted more from the presence of redroot pigweed than vice versa. There were no distinct differences in height or basal stem diameter between the two alien plants when grown in monoculture; however, these characters were markedly decreased in redroot pigweed (P < 0.001) and increased in common ragweed when these two species were grown together. The basal stem diameter of common ragweed in the 1A:3Am competition treatment was larger than that in 3A:1Am (P < 0.001) and slightly larger than that in 2A:2Am (P = 0.02). Nonsignificant differences in the basal stem diameter of redroot pigweed were observed under different competition scenarios when the two alien plants were grown together. The branch number of common ragweed increased in response to competition (P < 0.001) and was not impacted by elevated CO_2 and N addition (Table 1). No change in branch number of redroot pigweed in response to competition was observed, even in the monoculture treatment. The interaction effects of different factors did not affect the growth characters of the two invasive plants.

Table 1 Results of three-way ANOVA for the basal stem diameter, height and branch number of the alien invasive plants common ragweed and redroot pigweed according to CO_2 , N and competition levels.

		bas	sal stem o	liameter		height				branch number			
		commor	1	redroot pigweed		common ragweed red		root	common ragweed		redroot pigweed		
		ragweed			pigweed			weed					
Effect	df	F	Р	F	Р	F	Р	F	Р	F	Р	F	Р
CO ₂	1	3.020	0.089	2.970	0.091	1.510	0.225	0.422	0.519	0.004	0.950		
N	1	33.395	0.000	3.707	0.060	16.006	0.000	21.267	0.000	0.076	0.784		
Competition	3	15.213	0.000	26.352	0.000	1.998	0.127	20.343	0.000	15.496	0.000		
CO ₂ ×N	1	0.104	0.749	0.044	0.836	3.533	0.066	0.766	0.386	2.003	0.163		
CO ₂ ×Competition	3	1.112	0.354	0.476	0.700	0.209	0.890	0.982	0.409	0.895	0.450		
N×Competition	3	1.182	0.326	1.429	0.246	0.412	0.745	0.748	0.529	2.174	0.103		
CO ₂ ×N×Competition	3	0.130	0.942	0.232	0.874	0.834	0.482	0.244	0.865	1.082	0.366		

Effects of CO₂, N and competition on the biomass of the two invasive alien plants

The three-way ANOVA results showed that N addition consistently resulted in significant increases in the shoot, root, and total biomass of common ragweed at all competition levels (P < 0.001) (Table 2; Fig. 2A, B, C). Elevated CO_2 increased the root biomass (P = 0.009) and the root-shoot ratio (P = 0.029) of common ragweed and inhibited the root biomass (P = 0.015) and the root-shoot ratio (P = 0.004) of redroot pigweed (Table 2). An interaction effect of elevated CO_2 and N addition was observed for the shoot biomass (P = 0.035) and total biomass (P = 0.042) of common ragweed. Competition notably decreased the shoot biomass and total biomass of redroot pigweed (P < 0.001) and differentially impacted the root biomass and the root-shoot ratio of these two invasive alien plants. The shoot biomass and total biomass of redroot pigweed under 3A:1Am were lower than those under 1A:3Am (P < 0.001), 2A:2Am (P < 0.05) and monoculture (P < 0.001). The root biomass of redroot pigweed under competition was lower than that under monoculture, with the root biomass under 3A:1Am lower than that under 1A:3Am (P = 0.006). The root-shoot ratio of redroot pigweed under 1A:3Am was lower than that under 3A:1Am (P = 0.034) and monoculture (P = 0.001). The root-shoot ratio of common ragweed under 1A:3Am was significantly lower than that under monoculture (P = 0.011).

Table 2
Results of three-way ANOVA for the shoot biomass, root biomass, root-shoot ratio and total biomass of two invasive alien plants according to CO₂, I

		shoot biomass				root biomass				root-shoot ratio				
		common		redroot		common		redroot		common		redroot		com
		ragweed		pigweed		ragweed		pigweed		ragv	veed	pigweed		ragv
Effect	df	F	Р	F	Р	F	Р	F	Р	F	Р	F	Р	F
CO ₂	1	1.575	0.216	0.007	0.934	7.389	0.009	6.430	0.015	5.083	0.029	9.332	0.004	2.39
N	1	115.273	0.000	1.463	0.232	80.287	0.000	0.012	0.912	2.393	0.128	0.368	0.547	120
Competition	3	0.713	0.549	91.511	0.000	5.508	0.002	53.507	0.000	4.341	0.009	4.107	0.011	1.02
CO ₂ ×N	1	4.715	0.035	0.533	0.469	1.425	0.238	0.050	0.823	2.196	0.145	0.085	0.773	4.36
CO ₂ ×Competition	3	0.091	0.965	0.445	0.722	0.699	0.557	0.560	0.644	0.678	0.570	1.305	0.284	0.12
N×Competition	3	0.130	0.942	0.464	0.709	1.472	0.234	0.171	0.916	1.073	0.369	0.177	0.912	0.22
CO ₂ ×N×Competition	3	0.125	0.945	0.030	0.993	0.127	0.944	0.351	0.789	0.247	0.863	0.706	0.553	0.11

Effects of CO₂, N and competition on the RY of two invasive alien plants

The RY of common ragweed was higher than that of redroot pigweed, and the largest RY value of common ragweed reached 4.72; in contrast, the largest RY of redroot pigweed was only 0.87. The RY of common ragweed was enhanced by elevated CO₂, N addition and competition (Table 3); moreover, the interactions of three factors and two factors also impacted the RY values of this invasive alien plant. By contrast, the RY values of redroot pigweed in all mixed cultures were significantly lower than expected. CO₂, N addition and competition all decreased the RY values of redroot pigweed, but the effect was significant only for N addition (Table 3, Fig. 3). These results showed that common ragweed had an obvious competitive advantage over redroot pigweed under control conditions; even one common ragweed plant could strongly inhibit three redroot pigweed plants.

Table 3
Results of three-way ANOVA for the relative yield of two invasive alien plants according to CO₂, N and competition levels.

		common	ragweed	redroot pigweed		
Effect	df	F	Р	F	Р	
CO ₂	1	8.201	0.007	1.184	0.284	
N	1	7.665	0.009	5.093	0.030	
Competition	2	11.594	0.000	0.625	0.541	
CO ₂ ×N	1	7.980	0.008	1.593	0.215	
CO ₂ ×Competition	2	5.855	0.006	0.558	0.577	
N×Competition	2	5.905	0.006	1.540	0.228	
CO ₂ ×N×Competition	2	5.651	0.007	1.381	0.264	

Effects of CO₂, N and competition on the reproductive characters of common ragweed

N addition increased the seed yield (P < 0.001; Table 4; Fig. 4A) and decreased the seed mean weight (P = 0.003) of common ragweed. The seed number, seed total weight and seed mean weight were not significantly altered by elevated CO_2 , competition or their interaction. To examine the impacts of elevated CO_2 and N addition, seeds collected from monoculture were grouped into four mass levels. The results showed that climate change obviously changed the seed mass frequency distributions. Elevated N and CO_2 enhanced the degree of seed size variation, and higher proportions of larger seeds (mass > 8 mg) and smaller seeds (mass < 2 mg) were produced. Elevated N significantly increased the proportion of larger seeds from 3.29 ± 1.12 in the ambient N pots to 6.04 ± 1.33 in the enriched N pots (P < 0.001; Fig. 5) and decreased the proportion of smaller seeds from 3.34 ± 1.24 to 1.58 ± 0.80 (P = 0.014; Table 3). Elevated CO_2 increased the proportion of smaller seeds to 12.53 ± 5.64 (P = 0.001; Fig. 5). There was no significant N× CO_2 interaction effect on any of the abovementioned indices.

Table 4
Results of three-way ANOVA for the seed number, seed total weight, and seed mean weight of common ragweed according to CO₂, N and competition levels.

		Seed number		Seed tot	al weight	Seed mean weight		
Effect	df	F	Р	F	Р	F	Р	
CO ₂	1	0.281	0.598	1.319	0.256	0.145	0.705	
N	1	15.462	0.000	1.292	0.261	9.536	0.003	
Competition	3	2.416	0.078	2.222	0.098	0.276	0.842	
CO ₂ ×N	1	1.726	0.195	1.040	0.313	0.001	0.976	
CO ₂ ×Competition	3	0.841	0.478	0.375	0.772	0.434	0.729	
N×Competition	3	0.456	0.714	0.964	0.418	0.624	0.603	
CO ₂ ×N×Competition	3	1.255	0.300	1.017	0.393	1.346	0.271	

Discussion

Negative interaction between common ragweed and redroot pigweed

In this experiment, common ragweed was clearly the superior competitor under the different treatment levels, which implied a negative interaction between these two notorious alien invasive species. Negative relationships between alien invasive species are common at broader taxonomic levels, such as in insects (Braks et al, 2004), mammals (Bailey 1993; Russell et al. 2014) and plants (Williams and Buxton, 1995; Kuebbing and Nunez 2014). Competition between two alien invasive species can occur with one species limiting the material, substance, or space of the other when they live in the same habitat or require the same scarce resource (Belote and Weltzin 2006; Griffen et al. 2008). In most cases, the alien invasive species belong to the same genus; however, in some cases, they are phylogenetically dissimilar (Kuebbing and Nunez, 2014). For example, the removal of water hyacinth, which increased the invasion of alligator weed, indicated that competition can occur between phylogenetically dissimilar species (Wundrow et al., 2012). Thus, phylogenetic relatedness is not always necessary for predicting interactions between invaders (Cahill et al., 2008).

We focused on the relationship between two dissimilar invasive species that occupy similar niches. Common ragweed and redroot pigweed are both dominant invasive species included on the list published by the Ministry of Ecology and Environment of the People's Republic of China. The results of studies on interactions between invasive species are negative, which is not as commonly expected that a positive relationship will occur between dissimilar invasive species (Simberloff, 2006). These two invasive plants showed similar growth characters and biomass under monoculture (Figs. 1–2), but common ragweed showed a clear competition advantage in mixture culture (Figs. 1–3). The highest competitiveness was observed under 1*A*:3*Am*, where the RY of common ragweed increased to 350%, while that of redroot pigweed decreased to 20%. The growth characters of common ragweed, such as height and stem diameter, were also higher than those of redroot pigweed under interspecific competition, with the tall stature of the former species providing a strong advantage in the acquisition of light (Skálováet al. 2013). Rajcan et al. (2002) proved that both light quality and quantity influence the phenology of pigweed. The outcome of competition varies with the performance (Skálováet al. 2013) and resource availability (Lonsdale, 1999) of neighboring species. For example, Italian ryegrass has a competitive advantage over common ragweed (Leskovšek et al. 2012c), and redroot pigweed shows higher competitiveness than *Phaseolus vulgaris* L. (Amini et 2014). Competitiveness slightly decreased with an increasing density of common ragweed, which indicated inter- and intraspecific generality, as detected in other experiments (Kuebbing and Nunez 2014). Strong competitors often do better in the presence of interspecific competition than under intraspecific competition (Lambers et al. 2004; Golivets and Wallin 2018).

Climate change hastens the negative interaction

Alien species interactions will change in response to environmental alterations, such as climate change and N deposition (Tylianakis et al., 2008). Common ragweed benefited more than redroot pigweed from elevated CO₂ and N addition, which resulted in the enhanced competitive ability of common ragweed.

N addition exerted a similar effect on the height of both common ragweed and redroot pigweed but contrasting effects on their biomass. We found that N addition increased the shoot, root and total biomass of common ragweed but had no impact on these characters in redroot pigweed (Fig. 2). The level of responsiveness differs considerably between species under N addition (Blackshaw et al. 2003). These results are consistent with the findings of Leskovšek et al. (2012b) that the height and dry matter of common ragweed were increased by N addition in both greenhouse and field experiments. N addition stimulated the height of redroot pigweed, which was also observed in other experiments (Wang et al. 2017), and no discernible effect on biomass was observed. Biomass allocation in response to nutrients was also different between the two invasive alien species. Compared with monoculture, 1A:3Am and 2A:2Am decreased biomass allocation to the roots in common ragweed, and 3A:1Am increased it (Fig. 2). Results is dissimilar to previous study showed that biomass allocation of ragweed to the roots at N addition levels exhibited a low plasticity (Leskovšek et al, 2012a), and mainly because in our study inter- and intra- species competition are all considered. This result can be explained by resource-limitation theory, where plants allocate more biomass to roots in order to acquire more of the most limiting resource (Poorter and Nagel 2000; Liu et al. 2016). However, redroot pigweed allocated more biomass to the roots than to the shoots, as a clear decrease in shoot biomass and a slight decrease in root biomass were observed under competition (Fig. 2). The height disadvantage of redroot pigweed under competition results in a decrease in its light-capturing capacity (Wang et al., 2021), and root-foraging responses help it capture more nutrients (Keser et al. 2014, 2015). Decreased growth and physiological performance of redroot pigweed was also observed under competition (Wang et al., 2016). N addition

increased relative competition intensity measured according to most traits of common ragweed but decreased that for most traits of redroot pigweed when the two species were grown together. The negative interaction of these two species was amplified by N addition.

Elevated CO₂ increased the root biomass of common ragweed but decreased that of redroot pigweed. Most plants exhibit a positive growth response to elevated CO₂ due to increased photosynthesis and/or nutrient use efficiency when other factors (e.g., water and nutrients) are not limited (Kimball et al. 2002). Some research has also indicated that elevated CO₂ significantly increases shoot, root, and total plant biomass; plant height; and seed mass (Wayne et al. 2002; Rogers et al. 2006; Runion et al. 2014). Our results indicated that common ragweed gains a competitive advantage under N addition, so a positive relationship was observed between root biomass and elevated CO₂. Otherwise, we speculate that there is an obvious limit of available N for redroot pigweed growth in the experimental area, and the CO₂ effects on this weed are constrained by N limitation. We also observed that common ragweed grown in monoculture responded strongly to elevated CO₂, and when grown under competition with redroot pigweed, it responded to elevated CO₂ with a slight increase, whereas it exhibited a decrease under 1*A*:3*Am* of biomass. Invasive plant species show different responses to elevated CO₂ under monoculture and under competition, as also demonstrated in *Centaurea solstitialis* (Dukes 2002). Although elevated CO₂ often promotes invasion, it also commonly reduces N availability (Luo et al. 2004), which could indirectly limit CO₂ effects on invasion (Sorte et al. 2013), especially under N-limiting conditions such as those in our experiment. Blumenthal et al. (2016) also suggested that the lack of an elevated CO₂ effect on *Bromus tectorum* may be due to indirect effects of CO₂ on N limitation. Because most invasive plants are sensitive to N availability, the degree to which they are affected by CO₂ is constrained by N (Blumenthal et al. 2016), and this constraint could be intensified by progressive N limitation (Luo et al. 2004) or alleviated by N deposition (Köchy and Wilson 2002; Fenn et al. 2003).

N addition enhanced the reproductive ability of common ragweed

Effects of CO₂ and N on the seed yield of common ragweed have been reported (Wayne et al. 2002; Leskovšek et al. 2012b). However, their effects on the frequency distribution of seed mass are unclear, although this trait is as important as seed yield. We found that elevated CO₂ led to an increase in the proportion of smaller seeds; in contrast, N addition increased the proportion of larger seeds. Similarly, Hovenden et al. (2008) also found a higher frequency of small seeds of *Austrodanthonia caespitosa* under elevated CO₂ compared with a control. Research on the effect of N deposition on seed mass frequency distributions is lacking. Further, N addition increased the number and decreased the mean mass of common ragweed seeds in our experiment, disagreeing with the lack of N effects on the seed number and seed yield of common ragweed reported in other research (Leskovšek et al. 2012b).

Seed size/mass is highly influential in determining seed germinability, seedling establishment and seedling growth, particularly in competitive environments (Stanton 1984; Moles and Westoby 2004; Souza and Fagundes 2014). Therefore, alterations in mean seed mass (Flynn et al. 2005) or seed mass frequency distributions (Hovenden et al. 2008) caused by global change are of substantial importance. Large seeds usually have a higher germination potential (Mandal et al. 2010), improve seedling growth (Stanton 1984; Mandal et al. 2010; Anis et al. 2014), facilitate the interspecific competitive ability of seedlings (Eriksson 1999), and enhance the tolerance of seedlings emerging from greater burial depths (Mandal et al. 2010). By contrast, small seeds consume fewer plant resources (Venable 1992) and generally disperse farther than large seeds (Cappuccino et al. 2002), which is an important life-history trait of invasive alien plants (Rejmanek and Richardson 1996). We speculate that more large seeds in common ragweed may improve its interspecific competitive ability through rapid seedling growth during the early phase, while more small seeds would be beneficial for farther dispersal. Therefore, the intensified seed size variation resulting from elevated CO₂ and enriched N will promote the invasion of common ragweed. Of course, verifying this speculation will require more experiments to determine the exact relationships of seed size with seed germination, the seedling growth rate, interspecific competitive ability, and seed dispersal.

Conclusion

Common ragweed showed a higher competitive ability than redroot pigweed under interspecific competition, although no difference was observed under monoculture. The results revealed a negative interaction between these two notorious invasive species, which suggested invasional interference between them. In addition, elevated CO₂ and N addition increased the competitive ability of common ragweed but suppressed that of redroot pigweed, and simulated N deposition had a stronger effect than CO₂ on these two alien species. The results suggested that the competitive abilities of plants respond differently to climate change, N is a key factor in the invasion of these two species, and the role of elevated CO₂ may be impacted by insufficient N. Finally, N addition increased the proportion of smaller seeds of common ragweed, but elevated CO₂ increased the proportion of smaller seeds; thus, N should be beneficial for reproduction, and CO₂ favors the spread of common ragweed.

Declarations

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Availability of data

The data that supporting the results of this study can be accessed at https://figshare.com/s/4d7fb81abea5819e54c3.

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Figures

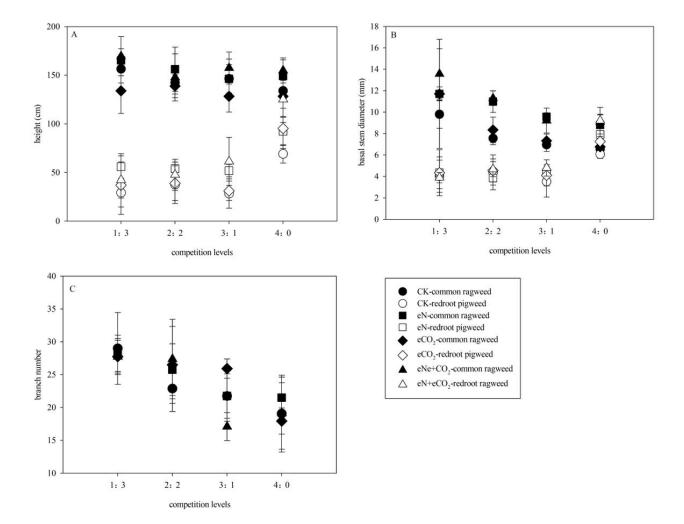


Figure 1

Effects of elevated CO2, N addition and competition level on the growth characters of two invasive alien plants. A. Height. B. Basal stem diameter. C. Branch number. On the horizontal axis, 1:3 refers to one common ragweed plant and three redroot pigweed plants, 2:2 refers to two common ragweed plants and two redroot pigweed plants, 3:1 refers to three common ragweed plants and one redroot pigweed plant, and 4:0 refers to four common ragweed plants or four redroot pigweed plants.

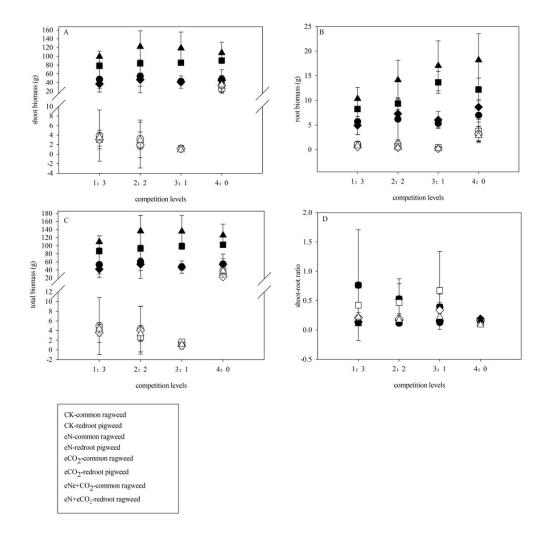


Figure 2

Effects of CO2, N and competition levels on the biomass of two invasive alien plants. A. Shoot biomass. B. Root biomass. C. Total biomass. D. Root-shoot ratio. On the horizontal axis, 1:3 refers to one common ragweed plant and three redroot pigweed plants, 2:2 refers to two common ragweed plants and two redroot pigweed plants, 3:1 refers to three common ragweed plants and one redroot pigweed plant, and 4:0 refers to four common ragweed plants or four redroot pigweed plants.

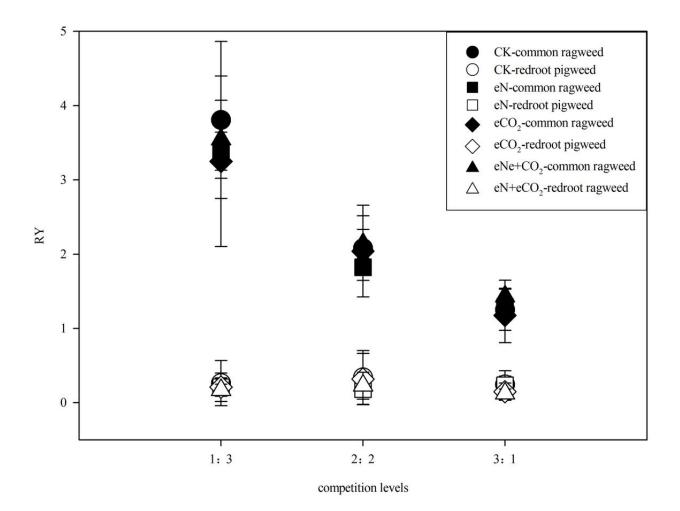


Figure 3

Effects of elevated CO2, N addition and competition level on the RY of two invasive alien plants.

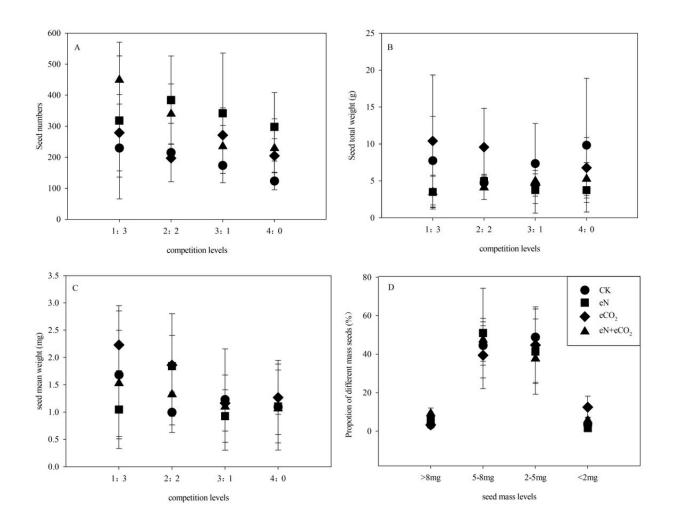


Figure 4

Effects of elevated CO2, N addition and competition level on the reproductive characters of common ragweed. A. Seed number. B. Seed total weight. C. Seed mean weight. On the horizontal axis in A-C, 1:3 refers to one common ragweed plant and three redroot pigweed plants, 2:2 refers to two common ragweed plants and two redroot pigweed plants, 3:1 refers to three common ragweed plants and one redroot pigweed plant, and 4:0 refers to four common ragweed plants. D. Proportions of different seed masses. The horizontal axis in D shows the different seed mass levels.

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Figure 5

Figure 5