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Effect of elevated atmospheric carbon dioxide on the allelopathic potential of common ragweed

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Abstract

Background: Allelopathy has been suggested as one potential mechanism facilitating the successful colonisation and expansion of invasive plants. The impacts of the ongoing elevation in atmospheric carbon dioxide (CO₂) on the production of allelochemicals by invasive species are of great importance because they play a potential role in promoting biological invasion at the global scale. Common ragweed (*Ambrosia artemisiifolia* var. *elatior*), one of the most notorious invasive exotic plant species, was used to assess changes in foliar mono- and sesquiterpene production in response to CO₂ elevation (389.12 ± 2.55 vs. 802.08 ± 2.69 ppm).

Results: The plant growth of common ragweed significantly increased in elevated CO₂. The major monoterpenes in the essential oil extracted from common ragweed leaves were β-myrcene, DL-limonene and 1,3,6-octatriene, and the major sesquiterpenes were β-caryophyllene and germacrene-D. The concentrations of 1,3,6-octatriene (258%) and β-caryophyllene (421%) significantly increased with CO₂ elevation.

Conclusions: These findings improve our understanding of how allelochemicals in common ragweed respond to CO₂ elevation.

Keywords: Allelopathy, *Ambrosia artemisiifolia* var. *elatior*, Monoterpene, Sesquiterpene, CO₂ elevation

Background

Invasive exotic plants are recognised as one of the biggest threats to native ecosystems because they outcompete native species and alter environmental conditions and resource availability (D'Antonio and Vitousek 1992). Native to North America, common ragweed (*Ambrosia artemisiifolia* var. *elatior* L.) is rapidly spreading across many parts of East Asia (Chen et al. 2007; Fang and Wan 2009; Kil et al. 2004; Miyawaki and Washitani 2004; Xu et al. 2006), Europe (Bullock et al. 2010; Essl et al. 2015; Smith et al. 2013) and Australia (Bass et al. 2000), where it becomes invasive and poses a threat to agroecosystems, native ecosystems and public health. In South Korea, common ragweed is designated as one of

the 14 most problematic invasive alien plants by the Act on the Conservation and Use of Biodiversity, the Ministry of Environment.

The allelopathic effect of plant terpenoids is of great ecological interest as many plant species enhance their competitiveness and fitness through allelopathy. The Novel Weapon hypothesis proposed by Callaway and Ridenour (2004) attributes the successful establishment and proliferation of some invasive exotic plants in introduced ranges to their allelochemicals (Callaway and Ridenour 2004). Although these chemicals are relatively ineffective against neighbours in the native range of the invasive species due to co-evolved tolerance, these substances can act as 'novel weapons' when encountered by adjacent plant species in invaded ranges (Callaway and Aschehoug 2000; Callaway and Ridenour 2004). Allelopathic effects of invasive plant terpenoids on the germination and growth of native and crop species in invaded ranges have been observed in numerous cases, demonstrating that allelopathy plays a potential role in the success of some invasive exotic plants (Barney et al. 2005;

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Cipollini and Dorning 2008; Ens et al. 2009a; Ens et al. 2009b; Kong et al. 2007; Maharjan et al. 2010; Orr et al. 2005; Prati and Bossdorf 2004; Sun et al. 2006; Tefera 2002; Wang et al. 2010; Yamamoto 1995; Zhao et al. 2009). Most volatile and reactive terpenes such as mono- and sesquiterpenes are usually stored in leaves, and these compounds induce allelopathic effects on neighbouring plants through leaf volatilisation or leachates.

Allelopathy has been suggested as a possible mechanism underlying the successful introduction and establishment of invasive exotic plant species in new habitats because allelochemicals released from an invader are often evolutionarily novel to a recipient native community (Callaway and Ridenour 2004; Hierro and Callaway 2003). Volatile oils of common ragweed are allelochemicals released into the environment through leaf volatilisation or leachates that can affect the growth and other functions of nearby flora (Beres et al. 2002; Chalchat et al. 2004; Fischer and Quijano 1985; Pajević et al. 2010). Vidotto et al. (2013) demonstrated that leaf residues of common ragweed inhibit early growth of crop species including tomato and lettuce, as well as germination of weed species such as large crabgrass (*Digitaria sanguinalis*). Choi et al. (2010) reported that an extract from common ragweed leaves inhibits germination and seedling growth of various weed species including barnyard grass (*Echinochloa crus-galli*), large crabgrass (*D. sanguinalis*) and Asian flatsedge (*Cyperus microiria*). A bioassay study showed that the allelopathic effect of common ragweed leaf extract was stronger than that of flower and achene extracts (Kazinczi et al. 2008a, 2008b). By contrast, Kazinczi et al. 2008a, 2008b demonstrated that leaf extracts of sunflower (*Helianthus annuus*), field bindweed (*Convolvulus arvensis*) and velvetleaf (*Abutilon theophrasti*) promoted rather than inhibited germination and growth of common ragweed, and found that common ragweed could utilise these extracts as a source of nutrients. Additionally, no autotoxicity of common ragweed extracts was observed in their studies (Kazinczi et al. 2008a, 2008b). Therefore, allelopathic effects may provide common ragweed with a competitive advantage over the neighbouring plant community and may play a role in facilitating its successful invasion and proliferation in newly invaded habitats.

Global mean atmospheric carbon dioxide (CO₂) has increased by 29% since preindustrial times and is anticipated to reach 600 to 1000 ppm by the year 2100 (Pachauri et al. 2014). Rising CO₂ mixing ratio in the atmosphere is responsible for climate change and has widespread impacts on terrestrial biology. Due to its threats to native ecosystems and public health, specific attention has been given to determine the role of rising atmospheric CO₂ mixing ratio with respect to the distribution, growth and pollen production of common ragweed

(Bullock et al. 2010; Essl et al. 2015; Hamaoui-Laguel et al. 2015; Rogers et al. 2006; Smith et al. 2013; Ziska and Caulfield 2000). However, no information is currently available concerning the impact of rising CO₂ mixing ratio on the allelopathic potential of this species. Elevated atmospheric CO₂ mixing ratio increases carbon (C) supply and thus leads to high C/N ratios in plant tissues, eventually making conditions favourable for the production of C-based secondary compounds (Bazin et al. 2002; Berenbaum 1995; Bryant et al. 1983; Coley et al. 1985; Coviella et al. 2002; Peñuelas and Estiarte 1998; Raisanen et al. 2008; Stamp 2003). However, the effects of elevated atmospheric CO₂ mixing ratio on the production of allelochemicals affecting the invasiveness of plants have not been widely studied (Applebee et al. 1999; Lindroth 1996).

Understanding the physiology and ecology of common ragweed in response to environmental change is of great importance because this species poses a major threat to public health, native ecosystems and agroecology in many parts of the world. Previous studies showed that global environmental changes such as elevated CO₂ mixing ratio and global warming can promote the growth and allergenic pollen production of common ragweed (Hirose et al. 1996; Ziska et al. 2007; Ziska and Caulfield 2000).

Carbon-based substances such as mono- and sesquiterpenes are the prominent components of volatile allelochemicals derived from common ragweed leaves (Chalchat et al. 2004). Therefore, we hypothesised that elevated CO₂ mixing ratio concentrations would increase foliar mono- and sesquiterpene production in this species.

Materials and methods

Growth chamber

Growth chambers (140 × 74 × 1200 cm³, DS-51GLP, Dasol Science, Republic of Korea) with different target CO₂ mixing ratio concentrations (400 and 800 ppm) were used for CO₂ mixing ratio manipulation experiments. Chambers were programmed with an alternating day/night temperature regime of 28/22 °C, a 14/10 h day/night photoperiod and relative humidity of 60%. The light intensity was 148.5 PPFD (μmol/m²/s), and the dawn and dusk transitions lasted 1 h. The CO₂ mixing ratio concentration in the chamber was lowered by incoming air from the laboratory in which the CO₂ mixing ratio concentration was higher than 430 ppm; therefore, CO₂ mixing ratio absorbent (SODASORB, Grace Dares Packaging Technologies, USA) was applied to achieve the target ambient CO₂ mixing ratio concentration. To minimise any absorbent-specific effects, the same amount of CO₂ absorbent was also applied for the target elevated CO₂ mixing ratio condition. The CO₂ mixing ratio conditions for both the ambient (389.12 ± 2.55 ppm) and elevated (802.08 ± 2.69 ppm) atmospheres during the

experimental period (60 days) were maintained by applying 500 g of absorbent and replacing it every 5 days.

Seed collection and plant propagation

Common ragweed involucre achenes (hereafter referred to as seeds) were extracted from soil samples collected along agriculture field edges infested with the species in Heungeop-ri, Heungeop-myeon, Wonju-si, Gangwon-do, South Korea (latitude 37.18° N, longitude 127.54° E) in April 2009. We had to moisten the seeds of common ragweed before sowing seeds because their seeds are highly dormant (Baskin and Baskin 1980). Common ragweed seeds need cold-wet stratification period lasting for 2–4 weeks. A total of 100 randomly chosen seeds were placed on two layers of Whatman No. 2 filter paper (Whatman International Ltd.) moistened with 5 mL of distilled water in four Petri dishes (25 seeds per dish). Dishes were placed in the growth chamber under ambient CO₂ mixing ratio conditions. Following the 7-day germination period, 48 seedlings of similar height (3–5 cm) were planted into twelve 3-L pots (four seedlings per pot) filled with a standard potting mixture containing peat moss, decomposed organic soil, sand, vermiculate and perlite at a ratio of 2:2:2:1:1 (v/v). Pots were randomly assigned to the two growth chambers (six pots per chamber). Four plants in each pot were thinned to one plant per pot at the six to eight leaf stage in order to ensure uniformity among the plants. In this way, shading effect on neighbouring plant was prevented. The selected plants were grown for 60 days, and pots were randomly rearranged within the chamber weekly to minimise location-specific effects. Shading by neighbouring plants was not observed during the experiments. The entire experiment was repeated 12 times.

Growth analysis

After 60 days of growth, growth analysis was performed.

Allelochemical extraction and analysis

After 60 days of growth, all leaves were separated from the stem and ~3 g of fresh leaves from each plant was manually ground at room temperature with sea sand (15–20 mesh) and 40 mL of n-pentane. Each sample was then spiked with 1 mL of 0.1% tetradecane as an internal standard. The resulting extract was filtered through a Whatman No. 40 filter paper cone (Whatman International Ltd.) with sodium sulphate and concentrated by evaporation with a gentle stream of nitrogen gas. Extracts were stored in sealed vials at –20 °C until chemical analysis.

Gas chromatography/mass spectrometry (GC/MS) analysis was performed using an Agilent 6890 Plus gas chromatograph equipped with a 5973-N quadrupole mass selective detector (Palo Alto, CA, USA). Using a

DB-5 MS capillary column (30 m × 0.25 mm i.d., 0.25 µm film thickness, 5% diphenyl:95% dimethylsiloxane phase, J&W Scientific, Folsom, CA, USA), the GC oven was maintained at 60 °C for 2 min then elevated to 310 °C in increments of 5 °C/min and maintained at that temperature for 2 min. The sample was injected at a split ratio of 1:10. The temperature of the GC injection port and the MS interface was 250 °C and 280 °C, respectively. The mass selective detector was run in electron impact (EI) mode with an electron energy of 70 eV. The mass spectrometer was operated in full scan mode between 50 and 700 amu. The Wiley7n spectra database was used for compound identification.

The internal standard yielded a peak with a retention time ranging from 19.26 to 19.46 min. The identity of each compound was confirmed by determining the retention time and comparing with mass spectral data in publicly available databases (≥90% representing a positive identification). To investigate the effects of CO₂ mixing ratio on the number of mono- and sesquiterpenes produced, the detection frequency with which each individual compound was observed in each treatment was measured. The area of the internal standard peak and those of mono- and sesquiterpenes in the GC chromatograms were calculated, and their ratios were then used to measure the concentrations of the analytes.

Statistical analysis

Data collected from chemical analyses were averaged for each treatment. One-way analysis of variance (ANOVA) was used to investigate the effects of CO₂ mixing ratio on allelochemical content. All analyses in the present study were conducted with JMP version 8 (SAS Institute Inc., Cary, NC, USA 2008).

Results

Growth of common ragweed (number of leaves, aboveground height, fresh weight) significantly increased in elevated CO₂ compared to ambient CO₂ condition (Table 1). The retention time and detection frequency of individual mono- and sesquiterpenes are shown in Table 2. The major mono- and sesquiterpenes (those most abundant and present in all extract samples) included three monoterpenes (β-myrcene, DL-limonene

Table 1 Growth of common ragweed (number of leaves, aboveground height, fresh weight) in ambient CO₂ treatment and elevated CO₂ treatment

	CO ₂ treatment		P value
	Ambient	Elevated	
No. of leaves	35.5 ± 3.5	45.0 ± 1.8	0.02577
Aboveground height (mm)	246.3 ± 10.3	345.8 ± 26.5	0.00205
Fresh weight (g)	4.6 ± 0.3	6.1 ± 0.5	0.02276

Table 2 Retention time, relative frequency and relative abundance of identified mono- and sesquiterpenes in essential oil from *A. artemisiifolia* var. *elatior* leaves

Monoterpenes			Sesquiterpenes		
Compounds	R.T.	D.F. (%)	Compounds	R.T.	D.F. (%)
2-Hexenal	4.56	88	Bicycloelemene	17.51	21
Santolina triene	5.57	63	δ -Elemene	17.59	46
α -Pinene	6.40	96	α -Copaene	18.69	38
Camphene	6.82	4	β -Bourbonene	18.92	13
Sabinene	7.39	29	β -Elemene	19.04	38
β -Pinene	7.54	83	β -Caryophyllene	19.88	100
β -Myrcene	7.78	100	γ -Elemene	20.06	33
DL-Limonene	8.93	100	β -Cubebene	20.11	4
1,3,6-Octatriene	9.37	100	Bergamotene	20.14	83
Chrysanthenone	11.58	33	γ -Cadinene	20.47	8
Borneol	13.06	25	β -Farnesene	20.60	33
			β -Selinene	20.76	8
			α -Caryophyllene	20.79	92
			α -Selinene	21.19	25
			γ -Curcumene	21.27	17
			Germacrene-D	21.43	100
			Aromadendrene	21.61	17
			Bicyclogermacrene	21.76	88
			δ -Cadinene	22.28	29
			β -Sesquiphellandrene	22.40	4
			α -Gurjunene	22.63	4
			Elemol	23.00	4
			Germacrene B	23.31	46
			endo-1-Bourbonanol	23.71	42

R.T. retention time (min), D.F. detection frequency (presented as percentage occurrence in all extract samples)

and 1,3,6-octatriene) and two sesquiterpenes (β -caryophyllene and germacrene-D; Table 2).

The results demonstrated that elevation in CO₂ mixing ratio concentration significantly influenced the relative concentrations of the major mono- and sesquiterpenes (Fig. 1). The relative concentrations of the major mono- and sesquiterpenes increased in conjunction with CO₂ elevation as follows: β -myrcene (203%), DL-limonene (105%), 1,3,6-octatriene (258%), β -caryophyllene (421%) and germacrene-D (138%).

Discussion

The main foliar mono- and sesquiterpenes identified in the present study included three monoterpenes (β -myrcene, DL-limonene and 1,3,6-octatriene) and two sesquiterpenes (β -caryophyllene and germacrene-D), consistent with previous investigations. Chalchat et al. (2004) reported that the main components of essential oils obtained from common

ragweed shoots by steam distillation were germacrene-D (24.1%), DL-limonene (16.8%), α -pinene (8.0%), β -myrcene (7.4%) and borneol (2.9%) (Chalchat et al. 2004). Similarly, Kim and Kim (1999) found octene (15.67%), 1,3,6-octatriene (15.00%), β -myrcene (12.98%), borneol (10.30%) and α -pinene (3.21%) to be the most abundant monoterpenes in essential oils from common ragweed leaves (Peñuelas and Llusà 1997). However, the proportion of major essential oil components in the present study was considerably less than in previous studies. This apparent discrepancy may result from the fact that Chalchat et al. (2004) analysed essential oil from steam distillation of 100 g of dried flowering shoots rather than 4 g of fresh young leaves in the current study. Moreover, Chalchat et al. (2004) analysed flowering shoots of common ragweed in September, and Kim and Kim (1999) averaged the amount of foliar monoterpenes from late March to September, whereas 60-day-old leaves were used in the present study, resulting in smaller amounts of allelochemicals. Peñuelas and Llusà (1997) suggested that the concentration of volatile terpenes in plants is influenced by environmental factors such as seasonality (larger content in autumn) and age (larger content in older plants). Indeed, Kim and Kim (1999) observed a seasonal variation: the total monoterpene concentration in ragweed leaves increased continuously from a plastochron index of 2.0 (early spring) to 11.89 (immediately prior to flowering).

The ecological effectiveness of allelopathy is concentration-dependent (Lotina-Hennsen and King-Diaz 2005); therefore, changes in the concentration of allelochemicals in response to environmental or habitat conditions determine the degree to which these compounds are exposed to neighbouring plants, and hence their allelopathic potential. Environmental stresses such as elevated atmospheric CO₂ mixing ratio may enhance the allelopathic potential of plants (Anaya 1999). The current study showed that increased C supply (i.e., elevated CO₂ mixing ratio) increased the relative concentrations of major mono- and sesquiterpenes. The degree to which changes in CO₂ mixing ratio influenced each major mono- or sesquiterpene was variable and dependent on the type of compound. These compounds may have differing biosynthetic origins and thus respond differently to environmental variables. It would be worthwhile examining the magnitude of the responses to elevated CO₂ mixing ratio in terms of differences in their structures and synthetic mechanisms (i.e., expression of genes encoding synthase enzymes for each compound) in future studies.

Although a single population approach and experiments in controlled environments such as growth chambers can have some limitations when attempting to draw general conclusions, the findings of the present study improve our understanding of how the invasiveness of common ragweed is induced by

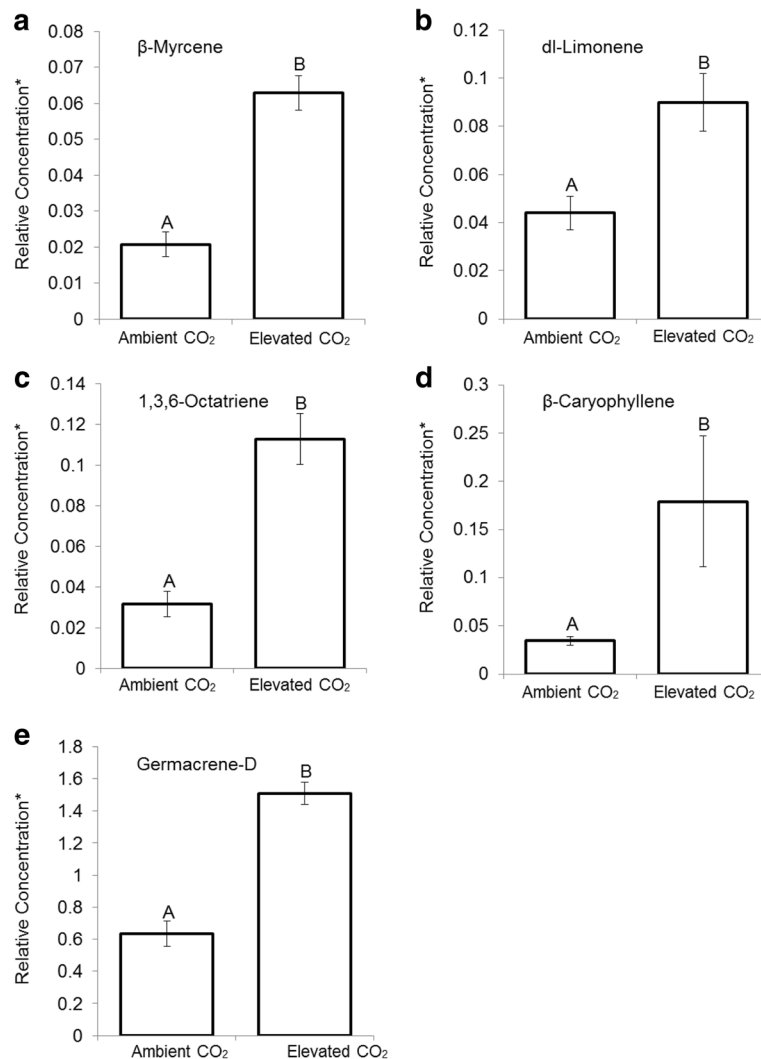


Fig. 1 Relative concentrations of major mono- and sesquiterpenes of *A. artemisiifolia* var. *elatior* in response to ambient (389 ± 2.55 ppm) and elevated (802 ± 2.69 ppm) CO₂ treatment. The effects of CO₂ on the relative concentration of **a** β-myrcene, **b** dl-limonene, **c** 1,3,6-octatriene, **d** β-caryophyllene and **e** germacrene-D were determined. Asterisk denotes that relative concentration was obtained from the ratio of the peak area of the analyte to that of the internal standard. Values are means \pm standard error. Bars not connected by the same letter are significantly different ($p < 0.05$)

allelochemicals and how elevated CO₂ mixing ratio can affect this process. We want to emphasise that elevated CO₂ increases allelochemicals of common ragweed and it may be one of many possible reasons that common ragweed is highly invasive these days.

Conclusion

We have experimentally proven that elevated CO₂ can increase the growth and the concentrations of alleochemicals in common ragweed which is one of most well-known invasive plants. The relative concentrations of the major monoterpenes (β-myrcene 203%, dl-limonene 105%, and 1,3,6-Octatriene 258%) and sesquiterpenes (β-caryophyllene 421% and germacrene-D 138%)

increased in conjunction with CO₂ elevation. Our finding indicated that one of the key mechanisms connecting elevated CO₂ and plant invasiveness is alleochemicals. We suggest the following studies on the effect of increased CO₂ on alleochemicals using other invasive plants in different environment to generalise our finding.

Nomenclature

Common ragweed, *Ambrosia artemisiifolia* var. *elatior*

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Availability of data and materials

All relevant data are available from the Figshare database (https://figshare.com/articles/Common_ragweed_allelopathy_allelochemical_data/6337004/1).

Authors' contributions

JB carried out the experiment and data analysis and wrote the draft of the manuscript. CB wrote the draft of the manuscript and revised the manuscript. YA assisted in the data analysis. JC assisted in the data analysis. DL conceived the concept of this paper and revised the manuscript. HK revised the manuscript. All authors read and approved the final manuscript.

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

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