



Elevated carbon dioxide impairs the performance of a specialized parasitoid of an aphid host feeding on *Brassica* plants

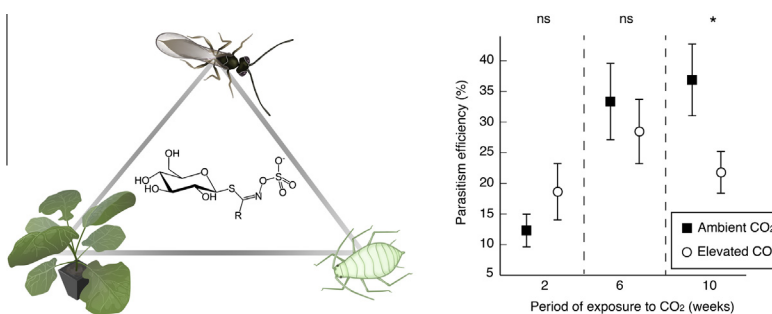
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HIGHLIGHTS

- Effects of elevated CO₂ on a *Brassica* – aphid – parasitoid system were investigated.
- Secondary metabolites induced by plant acclimation to elevated CO₂ were quantified.
- Glucosinolates increased in *Brassica* and decreased in aphids under elevated CO₂.
- Aphid body mass remained approximately 20% lower under elevated CO₂.
- Parasitism efficiency by *Diaeretiella rapae* was impaired under elevated CO₂.

GRAPHICAL ABSTRACT



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ABSTRACT

Elevated concentrations of atmospheric carbon dioxide (CO₂), a consequence of anthropogenic global change, may profoundly interfere with tritrophic interactions. Such effects with a focus on parasitoids as natural antagonists of herbivores have rarely been investigated. In particular, studies on effects of secondary metabolites induced by crop plant acclimation to elevated CO₂ on higher trophic levels were yet missing. We used the system composed of *Brassica* plants, the aphid *Brevicoryne brassicae* and the endoparasitoid *Diaeretiella rapae*, which is specialized on aphids feeding on brassicacean plants, to compare effects of elevated CO₂ (800 ppm) versus ambient CO₂ (400 ppm). Plants were exposed to the CO₂ concentrations for up to 10 weeks, aphids for 2–3 generations, and parasitoids for 1 generation, to allow for acclimation. Concomitant bioassays with herbivore-infested plants and parasitoids showed a significantly lower proportion of hosts parasitized under elevated compared to ambient CO₂ after a 10-week plant exposure. Parasitoid progeny emerged earlier but offspring adults were shorter lived. Plant glucosinolate concentrations were higher under elevated compared to ambient CO₂, whereas, contrary to expectation, aphid glucosinolate concentrations were significantly lower. Likewise aphid body mass remained approximately 20% lower under elevated compared to ambient CO₂. Thus, elevated CO₂ seems to have enhanced plant direct defense by an increase of natural plant defense compounds, however, it led to a decrease in indirect defense, likely due to the reduced host size. Our results point, for the first time, to a conflict between bottom-up and top-down control under elevated CO₂.

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1. Introduction

Parasitoid performance may be altered in a tritrophic context by environmental factors predicted to change under the future climate scenario (Roth and Lindroth, 1995; Sun et al., 2011b). The

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atmospheric concentration of carbon dioxide (CO₂), which has constantly increased since the pre-industrial era, is predicted to double by the end of this century (Houghton et al., 2001). Plants grown under elevated CO₂ could potentially alter the production of plant secondary metabolites (Coley et al., 2002; Klaiber et al., 2013a,b), which are important defense compounds against herbivores (Bennett and Wallsgrave, 1994). Parasitoids could also be affected by such changes via their herbivore host (Harvey et al., 2011; Kos et al., 2012; Ode, 2006), but such tritrophic studies are scarce.

Plant acclimation over several weeks to elevated CO₂ may result in altered secondary plant chemistry (Karowe et al., 1997; La et al., 2009), with responses being dependent upon plant species and the duration of exposure, as well as the defense compounds considered. Under elevated CO₂, secondary metabolites including glucosinolates, tannins, phenolics, flavonoids, cardenolides, terpenes and gossypol have been found to increase (Coviella et al., 2002; Karowe and Grubb, 2011; Stiling and Cornelissen, 2007), decrease (Karowe et al., 1997; Klaiber et al., 2013b; Vannette and Hunter, 2011) or remain unchanged (Bidart-Bouzat et al., 2005; Karowe et al., 1997; Stiling and Cornelissen, 2007). In contrast to pronounced effects gained after long durations of plant exposure, short durations have often led to marginal or negligible effects (e.g. Karowe et al., 1997; Vannette and Hunter, 2011). Significant changes in secondary plant chemistry could cascade via the herbivore to its natural antagonists (e.g. Lampert et al., 2008), which are considered key components of integrated pest management (Boivin et al., 2012). So far, herbivore-mediated effects of CO₂-induced changes in secondary plant chemistry on parasitoids and predators have only been examined using tree-based systems, i.e. aspen, oak, birch and maple (Holton et al., 2003; Roth and Lindroth, 1995). However, little or no effects were found. Elevated CO₂ was shown to have negligible effects on the performance of the dipteran parasitoid *Compsilura concinnata* (Meigen) when its lepidopteran host, the forest tent caterpillar *Malacosoma disstria* (Hübner), was feeding on aspen trees grown under elevated CO₂, possibly due to negligible effects of CO₂ on aspen secondary metabolites (Holton et al., 2003). In a similar study, parasitoid survival was the only performance parameter found to be negatively affected by elevated CO₂ on aspen trees (Roth and Lindroth, 1995). A possible accumulation of phenolic glycosides due to compensatory feeding by the parasitoid's host, the gypsy moth *Lymantria dispar* (Linnaeus), feeding on aspen trees, was presumed to be an important factor mediating parasitoid response (Roth and Lindroth, 1995). How CO₂-induced changes in secondary plant chemistry, mediated via the herbivore host, might affect parasitoid performance in crop systems is yet unknown.

Plants from the family Brassicaceae, in particular from the genus *Brassica* and their associated insects represent particularly well-studied tritrophic systems (Gols and Harvey, 2009; Hopkins et al., 2009). *Brassica* plants are grown worldwide as annual crops due to their nutritional, medicinal and bio-industrial properties (Singh et al., 2006; <http://faostat.fao.org>). They are also important model plants used to study the chemical basis of plant-insect interactions (Gu and Dorn, 2000; Gutbrodt et al., 2011). We recently found that Brussels sprout plants *Brassica oleracea* Linnaeus var. *gemmifera* exposed to elevated CO₂ for 2, 6 or 10 weeks responded with decreased stomatal conductance and volatile emission, particularly of monoterpenes, with the longer the duration of exposure, the stronger the plant response (Klaiber et al., 2013b). Plant responses correlated after a 6- and 10-week exposure with a markedly reduced plant colonization rate (Klaiber et al., 2013b), and with an impaired performance of the cabbage aphid *Brevicoryne brassicae* (Linnaeus) (Hemiptera: Aphididae) in terms of intrinsic rate of increase (Klaiber et al., 2013a).

Brassica plants and their characteristic secondary metabolites, the glucosinolates, are also well-established models to investigate how changes in secondary plant chemistry signal to third trophic level organisms (Hopkins et al., 2009; Mattiacci et al., 2001; Scacighini et al., 2005). As glucosinolates act as defense compounds against herbivores, specialized insects feeding on *Brassica* species must be able to tolerate or detoxify glucosinolates and their breakdown products (Gutbrodt et al., 2012; Hopkins et al., 2009; Kos et al., 2012). However, altered environmental conditions might change plant glucosinolate content, and effects might cascade not only to the herbivores but also to their parasitoids, via their herbivore hosts.

In this study, we moved from the bitrophic system comprised of Brussels sprout plants and the cabbage aphid (Klaiber et al., 2013b) to a tritrophic system complemented by the aphid's solitary endoparasitoid *Diaeretiella rapae* (McIntosh) (Hymenoptera: Braconidae). *D. rapae* is one of the most important parasitoids in *Brassica* crops (Desneux et al., 2006), with the ability to parasitize many aphid species feeding on *Brassica* plants (Pike et al., 1999), thus it is specialized at the plant level (Dorn et al., 2001). As a koinobiont parasitoid, *D. rapae* allows its host to further feed and develop (Zhang and Hassan, 2003). However, during parasitoid larval development, it may be exposed to glucosinolates sequestered by the aphids from the phloem sap (Opitz and Müller, 2009). Thus, in this system there is scope for the effects of CO₂ on plant secondary chemistry to cascade up to higher trophic levels (Gols et al., 2008a,b).

We hypothesized that potential effects of plant acclimation to elevated CO₂ on plant glucosinolate content might affect the performance of the parasitoid *D. rapae*. We quantified the glucosinolate contents of *Brassica* plants exposed either to elevated or to ambient CO₂ concentrations for up to 10 weeks. As indicators of aphid host quality, we quantified aphid glucosinolate contents and body mass. Focusing on post-landing events, parasitoid performance was characterized by measuring parasitism efficiency (i.e. the proportion of hosts successfully parasitized by a single female wasp), and important life-history traits including progeny development time, longevity and sex ratio of *D. rapae*.

2. Materials and methods

2.1. Study organisms and CO₂ concentrations

Four-week-old Brussels sprout (*Brassica oleracea* L. var. *gemmifera*) plants were placed in groups of 80 into one of two walk-in climate chambers (Convion PGV36 – Controlled Environments Limited, Winnipeg, MB, Canada) that maintained two different CO₂ concentrations: (1) ambient CO₂ (corresponding to the background concentration of air entering the climate chamber facility; 400 ± 10 ppm) or (2) elevated CO₂ (double the ambient concentration; 800 ± 10 ppm) (Ballhorn et al., 2011; Frenck et al., 2011; Karowe and Migliaccio, 2011). Two sets of plants were grown under either of the two CO₂ concentrations for 2, 6 or 10 weeks. Chamber conditions were set at 24 °C at day and 20 °C at night, 50% r.h. and a 16:8 h L:D regime with 250 μmol m⁻² s⁻¹ light intensity (based on Himanen et al., 2009). Both elevated CO₂ concentration and temperature level were chosen based on the moderate climate change scenario values predicted for the end of this century (Houghton et al., 2001). Growth chamber conditions were monitored with a 'Telair 7001 CO₂ and temperature monitor' (Ge Measurement & Control, Fremont, CA, USA) connected to a HOBO data logger (Onset Computer Corporation, Bourne, MA, USA) throughout the experiments. Plants were grown on the commercial soil 'Klasman Substrat 2' (Klasmann-Deilmann GmbH, Geeste, Germany; a peat substitute with pH-value 5.5, NPK: 280, 320,

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