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Individual growth rates do not predict aphid population densities under altered atmospheric conditions

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Abstract

1 Altered atmospheric composition, associated with climate change, can modify herbivore population dynamics through CO_2 and/or O_3-mediated changes in plant quality.

2 Although pea aphid *Acyrthosiphon pisum* genotypes exhibit intraspecific variation in population growth in response to atmospheric composition, the proximate mechanisms underlying this variation are largely unknown.

3 By rearing single (green, pink) and mixed (green + pink) pea aphid genotypes on red clover *Trifolium pratense* at the Aspen Free Air CO_2 and O_3 Enrichment (Aspen FACE) site, we assessed whether: (i) elevated CO_2 and/or O_3 concentrations alter aphid growth and development and (ii) individual aphid growth rates predict aphid population densities.

4 We showed that growth and development of individual green and pink aphids were not influenced by CO_2 and/or O_3 concentrations when reared as individual or mixed genotypes. Individual growth rates, however, did not predict population densities.

5 Reared as a single genotype, green pea aphid populations decreased in response to elevated CO_2 concentrations, but not in response to elevated $CO_2 + O_3$ concentrations. Pink pea aphid populations reared as a single genotype were unaffected by augmented CO_2 or O_3. Populations of mixed genotypes, however, were reduced under elevated CO_2 concentrations, irrespective of O_3 concentrations.

6 Herbivore population sizes may not readily be predicted from growth rates of individual organisms under atmospheric conditions associated with global climate change.

Keywords *Acyrthosiphon pisum*, aphid, carbon dioxide, climate change, genetic variation.

Introduction

As CO_2 and O_3 concentrations are increasing at an unprecedented rate (IPCC, 2007; Raupach *et al*., 2007), they have the potential to influence the performance of a multitude of plant species in both natural and managed ecosystems (DeLucia *et al*., 1999; Karnosky *et al*., 2003; Poorter & Navas, 2003). Elevated CO_2 and O_3 atmospheres typically have opposing effects on plant productivity (Makino & Mae, 1999; Krupa *et al*., 2001), with elevated CO_2 tending to ameliorate the negative effects of elevated O_3 on plants (Heagle *et al*., 1998; Dickson *et al*., 1998; Donnelly *et al*., 2000; Percy *et al*., 2002).

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Global change may alter not only the relative abundance and fitness of plant genotypes (Van der Kooij *et al*., 2000; Lindroth *et al*., 2001; Castells *et al*., 2002; Goverde *et al*., 2002; McDonald *et al*., 2002), but also the performance of higher trophic levels through CO_2- and O_3-mediated shifts in plant quality (Kangasjärvi *et al*., 1994; Brown, 1995; Bezemer *et al*., 1999; Valkama *et al*., 2007). Evidence would suggest that insect genotypes differ in their ability to tolerate the effects of climate change (Rank & Dahlhoff, 2002; Balanyá *et al*., 2006), although it is important to discount any maternal effects (*sensu* Rossiter, 1991). A previous field experiment indicated that substantial genetic variation exists in the growth of aphid populations under elevated CO_2 and/or O_3 atmospheres (Mondor *et al*., 2005). Some pea aphid *Acyrthosiphon pisum* Harris genotypes are highly susceptible

to changes in atmospheric conditions, whereas others exhibit consistent life-history patterns regardless of environmental conditions (Mondor *et al*., 2005).

To increase our predictive ability of population-level dynamics, the life-history changes underlying such responses should be investigated further (Newman *et al*., 2003). For example, are individual-level changes in growth and development responsible for the observed intraspecific differences in pea aphid population sizes under altered atmospheric conditions (Mondor *et al*., 2005)? Individual growth patterns may not directly translate into population-level responses (Leather & Dixon 1984; Bezemer *et al*., 1999), as a result of altered somatic/reproductive tissue trade-offs (e.g. *Cepegillettea betulaefoliae* Granovsky aphids) (Awmack *et al*., 2005).

Under natural conditions, aphid genotypes (clones) rarely exist in isolation from other genotypes (Losey *et al*., 1997; Simon *et al*., 1999; Caillaud & Via, 2000). Factors such as nutrient assimilation, development, fecundity and/or survivorship would be anticipated to take on increasing importance when genotypes co-occur (Pearson, 1986). To date, however, the degree to which atmospheric conditions alter intraspecific interactions in herbivore populations has not been assessed (Mondor *et al*., 2005). Co-occurrence of genotypes under increased CO_2 and/or O_3 concentrations may result in very different overall population sizes of different genotypic composition than would be produced under ambient atmospheric conditions.

In the present study, we report the results of an experiment conducted at the Aspen Free Air CO_2 and O_3 Enrichment (Aspen FACE) site in northern Wisconsin, U.S.A. This experiment examined the developmental responses of two genotypes (a green and a pink clone) of the pea aphid, reared as single genotypes and in combination under augmented concentrations of CO_2 and/or O_3 on red clover *Trifolium pratense* L., to better understand whether: (i) elevated CO_2 and/or O_3 concentrations alter aphid growth and development and (ii) individual aphid growth rates predict aphid population densities.

Materials and methods

The Aspen FACE site

The Aspen FACE site is a fully replicated factorial experiment with ambient and elevated concentrations of CO_2 and O_3. The experimental design consists of three true replicates of each of four CO_2 and/or O_3 treatments: (i) control (ambient CO_2, ambient O_3; approximately 367 μL/L CO_2 and 38 nL/L O_3); (ii) + CO_2 (elevated CO_2, ambient O_3; +CO_2, approximately 537 μL/L); (iii) +O_3 (ambient CO_2, elevated O_3; +O_3, approximately 51 nL/L); and (iv) +CO_2 +O_3 (elevated CO_2, elevated O_3; +CO_2 +O_3, approximately 537 μL/L + 51 nL/L, respectively). Trembling aspen *Populus tremuloides* Michx., paper birch *Betula papyrifera* Marsh. and sugar maple *Acer saccharum* Marsh., trees were planted in each ring in 1997 and full-scale CO_2 and O_3 augmentation commenced in 1998. A diverse ground flora has developed in each ring subsequent to the Aspen FACE project being initiated (Awmack *et al*., 2007). The experiments reported here were conducted in the summers of 2000 and 2002 in the aspen-sugar maple sector, when the dominant tree species were young and the overstory canopy had not yet fully developed.

The Aspen FACE site was designed to assess the effects of realistic concentrations of atmospheric CO_2 on common deciduous tree species for the year 2060 (Dickson *et al*., 2000). Because natural O_3 production is dependent on factors such as ambient temperature, sunlight and precipitation, the O_3 gas treatment follows a dynamic diurnal profile determined by prevailing weather conditions. Augmented O_3 rings receive approximately 1.5-times the current ambient O_3 concentrations (Dickson *et al*., 2000). Further details on the design, construction and operation of the Aspen FACE site are provided in Dickson *et al*. (2000) (see also http://aspenface.mtu.edu/).

Experiment 1: Do elevated CO_2 and/or O_3 concentrations alter aphid growth and development?

Green and pink pea aphid genotypes were collected from red clover plants *T. pratense*, grown under ambient CO_2 and O_3 concentrations, on the margins of the Aspen FACE site. In pea aphids, body colour is a genetic polymorphism (Tomiuk & Wöhrmann, 1982). Because the frequency of this polymorphism is stable across generations, body colour can be used as a simple genetic marker to distinguish aphid genotypes (Tomiuk & Wöhrmann, 1982; Conner & Hartl, 2004). Two asexual lineages (derived from single parthenogenetic green and pink female pea aphids) were maintained on broad bean *Vicia faba* L. cv. Long Pod (Ed Hume Seeds Ltd, Puyallup, Washington) at ambient CO_2 and O_3. Aphids were reared on broad bean for three generations prior to the start of the experiment to equalize any maternal effects.

To determine birth weights, groups of newborn nymphs (produced over 24 h) were weighed on a microbalance to the nearest microgram (Mettler Toledo MT5 Microbalance; Mettler, Columbus, Ohio). Nymphs were then confined to the stems of three naturally-occurring red clover plants in each FACE ring in mesh bags (width 10 cm, length 15 cm). One bag was placed on each of three stems on each plant: one containing four green aphids, one containing four pink aphids, and one containing two green + two pink aphids. Any herbivores or predators on the stems were removed prior to the addition of aphids. This experimental design allowed the effects of CO_2 and O_3 to be investigated on four sets of pea aphid genotypes: green alone, pink alone, green (with pink) and pink (with green). Although standard procedure in species competition/co-occurrence studies is to simultaneously assess two mixed treatments (i.e. green + pink; pink + green), we did not duplicate this treatment to reduce counting and weighing efforts. Aphids were reweighed 7 days after being put onto the plants. Aphid performance was assessed using mean relative growth rate (MRGR), which is the natural log of the increase in weight of each aphid over a set time period (Radford, 1967; Leather & Dixon, 1984):

$$\text{MRGR} = [\ln(\text{final weight}) - \ln(\text{initial weight})]/7 \text{ days}$$

Because aphid performance was slightly different for aphids in different atmospheric treatments, we used a set time period

(7 days) to determine MRGR rather than using the time period from birth to adulthood. Using a 7-day time period also simplified data collection procedures. Aphids were returned to the same shoot on the same clover plant and observed daily until the adult moult. Development time was the number of days from birth to adult.

Experiment 2: Do individual growth rates predict aphid population densities?

Aphids were allowed to remain on the plant for a further 12 days, after moulting into adults. This time period is approximately equivalent to one aphid generation under field conditions, allowing ample time for population growth. After this time, plant stems were harvested and searched intensively for aphids. All individuals were removed, sorted into pink and green individuals if necessary, and counted.

Statistical analysis

To determine whether the effects of CO_2 and/or O_3 influenced aphid MRGR and development times, data were analysed using split-plot analysis of variance (ANOVA) in Proc Mixed (SAS Institute, Cary, North Carolina) (Littell *et al*., 1996). Split-plot analyses were the most suitable analyses for our hierarchical experimental design because aphid clones (subplots) were nested within the atmospheric treatments (whole plots). Fixed effects were CO_2, O_3 and $CO_2 \times O_3$, whereas block and plant (block) were entered as random factors. A separate analysis was conducted for the four combinations of pea aphid genotypes: green, pink, green (with pink) and pink (with green). As noted previously, two mixed genotype treatments are often assessed to determine the effects of genotype competition/co-occurrence.

To determine whether individual growth rates predict overall population sizes under the CO_2 and/or O_3 treatments, data were analysed using a split-plot ANOVA, using the same fixed and random factors as the previous analyses. Separate ANOVAs were conducted for the green genotype, pink genotype and mixed (green + pink) genotypes. Abundance data were $\log_{10}$-transformed prior to analysis, to better meet the assumptions of normality (Zar, 1984). For all analyses, $P < 0.05$ was considered statistically significant, whereas $P < 0.10$ is considered marginally significant, reflecting the reduced replication of FACE studies (Filion *et al*., 2000).

Results

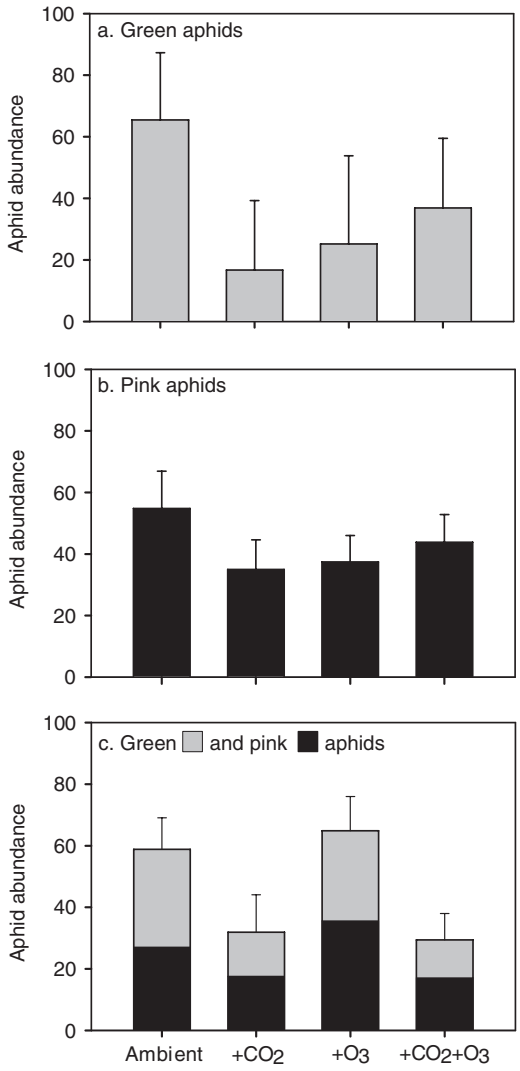
Elevated CO_2 and/or O_3 concentrations did not alter the growth and development of the aphid genotypes used in the present study. The MRGR and development times of individual green and pink pea aphids were unaffected by elevated CO_2 and O_3 atmospheres, regardless of whether reared as single or mixed genotypes (Table 1).

The effects of CO_2 and O_3 on aphid population sizes were, however, genotype-dependent. Numbers of the green pea aphid genotype decreased when CO_2 concentrations increased, but not when CO_2 and O_3 concentrations both increased (Fig. 1a; marginally significant $CO_2 \times O_3$ interaction). By contrast, numbers of the pink pea aphid genotype were unaffected by CO_2 and O_3 concentrations, when reared in single-genotype groups (Fig. 1b). Co-occurrence of genotypes exacerbated these population-level effects. In mixed-genotype populations, elevated CO_2 atmospheres greatly reduced the total number of

Table 1 Effects of elevated CO_2 and/or O_3 atmospheres on the growth and development of individual green and pink pea aphids

	Mean relative growth rate (μg/μg/day)							
Treatment	Green		Pink		Green (with pink)		Pink (with green)	
Control	0.307 ± 0.016		0.305 ± 0.010		0.319 ± 0.016		0.304 ± 0.023	
+CO_2	0.326 ± 0.016		0.309 ± 0.010		0.310 ± 0.017		0.317 ± 0.024	
+O_3	0.296 ± 0.015		0.315 ± 0.010		0.306 ± 0.015		0.252 ± 0.025	
+CO_2 +O_3	0.301 ± 0.015		0.291 ± 0.010		0.316 ± 0.016		0.325 ± 0.024	
ANOVA	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
$CO_{2(1,6)}$	0.62	0.459	1.01	0.354	0.00	0.970	3.34	0.118
$O_{3(1,6)}$	1.38	0.285	0.14	0.726	0.03	0.861	0.86	0.390
$CO_2 \times O_{3(1,6)}$	0.23	0.646	1.91	0.217	0.31	0.600	1.60	0.253
	Development time (days)							
Control	10.9 ± 0.4		10.8 ± 0.3		10.9 ± 0.6		11.1 ± 0.5	
+CO_2	11.5 ± 0.4		11.0 ± 0.3		11.2 ± 0.6		11.5 ± 0.5	
+O_3	11.1 ± 0.4		10.4 ± 0.3		10.7 ± 0.7		10.8 ± 0.6	
+CO_2 +O_3	11.3 ± 0.4		10.4 ± 0.3		11.4 ± 0.6		10.9 ± 0.5	
ANOVA	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
$CO_{2(1,6)}$	0.00	0.948	0.15	0.712	1.39	0.303	0.37	0.567
$O_{3(1,6)}$	1.48	0.270	2.92	0.139	0.00	0.951	1.32	0.302
$CO_2 \times O_{3(1,6)}$	0.40	0.548	0.31	0.599	0.29	0.621	0.10	0.763

Data are treatment mean ± SE. ANOVA, analysis of variance.



	$F_{1,5}$	P
CO_2	0.31	0.601
O_3	0.17	0.698
$CO_2 \times O_3$	5.58	0.065

	$F_{1,5}$	P
CO_2	0.11	0.750
O_3	0.30	0.606
$CO_2 \times O_3$	0.52	0.502

	$F_{1,5}$	P
CO_2	10.47	0.032
O_3	0.28	0.624
$CO_2 \times O_3$	0.56	0.497

Figure 1 Effects of CO_2 and/or O_3 on pea aphid population sizes, when feeding on red clover. Data shown are the number of aphids arising from a population initiated with: (a) four green adults, (b) four pink adults and (c) two green and two pink adults. Columns represent the mean ± SE of three replicate FACE rings. Statistics indicate the significance of the main effects (CO_2 and O_3) and their interaction ($CO_2 \times O_3$).

aphids, irrespective of O_3 concentrations (Fig. 1c; significant CO_2 effect).

Discussion

The effects of climate change on animal populations have been of foremost concern (Fleming & Volney, 1995; Körner & Bazzaz, 1996; Thomas *et al*., 2004). Although we are just beginning to investigate how insect genotypes respond to global change (Mondor *et al*., 2005; Balanyá *et al*., 2006), our ability to predict population-level effects is hampered by our lack of understanding of the altered life-history patterns underlying such effects (Stacey & Fellowes, 2002; Mondor *et al*., 2004a, 2005; Awmack *et al*., 2005). This Aspen FACE experiment addressed whether: (i) aphids have altered growth or development in response to elevated CO_2 and/or O_3 concentrations and (ii) individual growth rates predict aphid population densities. We found that the growth of pea aphid populations in response to increasing CO_2 and O_3 concentrations are not readily predictable on the basis of individual differences in growth or development. In addition, co-occurrence of genotypes further alters population-level responses under altered atmospheric conditions.

Pea aphid genotypes (i.e. pink and green clones) showed similar MRGR and development times under all atmospheric gas treatments, regardless of whether reared as single or mixed-genotype populations. Individual performance, therefore, did not predict the population responses of pea aphids to elevated CO_2 and O_3 atmospheres, corroborating the results reported for other aphid species (Bezemer *et al*., 1999; Awmack *et al*., 2005). Even though insects may develop at similar rates, differences in allocation to reproductive and somatic tissues may lead to longer-term population changes (Leather, 1988; Awmack *et al*., 2005). Furthermore, other traits, such as nutrient assimilation or survivorship, may become positively or negatively affected only when densities increase. Adding additional complexity, aphids may have altered life-history patterns depending on host plant ontogeny (Holopainen, 2002). Athough it is difficult, if not impossible, to examine all the life-history traits of an organism, these results indicate

that a multifaceted approach (i.e. simultaneously examining multiple traits, in the insects and the host plants) is required to understand the effect of altered atmospheric conditions on aphid populations. Predictions of the future impacts of elevated CO_2 and O_3 on herbivore populations that are based solely on measures of the performance of single traits of individual insects may be of limited value.

When green pea aphids were reared as a single genotype, there was a strong trendency towards population sizes decreasing under enriched CO_2 but not under enriched $CO_2 + O_3$. By contrast, pink pea aphids reared as a single genotype were unresponsive to CO_2 and O_3 concentrations. Green pea aphid genotypes had previously been found to be more susceptible to atmospheric changes than pink pea aphid genotypes (Mondor *et al*., 2005). When green and pink genotypes were reared in combination, however, increased CO_2 concentrations decreased aphid abundance irrespective of O_3 concentrations. Previous studies have not investigated interactions among co-occurring genotypes in elevated CO_2 and O_3 atmospheres. There are several non-mutually exclusive hypotheses for these observations. First, some genotypes may be able to incorporate nitrogen into their diets more efficiently than other genotypes (Newman *et al*., 2003). Differential nutrient assimilation between genotypes may also explain why the pink clone produces greater numbers of winged offspring compared with the green clone (Mondor *et al*., 2005), especially as wings and flight are considered to be energetically costly (Dixon, 1998). Second, although growth and development may be similar, allocation to somatic and reproductive tissue may differ among individuals, clones or species (Leather, 1988; Awmack *et al*., 2005). Third, interactions between co-occurring genotypes may only become evident when populations are of sufficient magnitude that competition ensues (Klomp, 1964). Only further experimentation will provide insight into this phenomenon.

In the present study, aphid colour was used as a simple genetic marker to distinguish between the two aphid genotypes (Tomiuk & Wöhrmann, 1982; Conner & Hartl, 2004). Because only one green and one pink genotype were used, it is premature to conclude that future elevated CO_2 atmospheres will have adverse effects on all green pea aphids. If the data presented here, along with data on other pea aphid colour morphs (Mondor *et al*., 2005), represent a general trend, global change may alter pea aphid population dynamics through altered interactions with higher-order trophic levels (Stacey & Fellowes, 2002; Mondor *et al*., 2004a, b). For example, parasitoid larvae are less able to assimilate nutrients from pink than from green pea aphids (Li *et al*., 2002). Adverse effects of future global change on green pea aphids may alter the availability of suitable hosts for a key top-down population regulatory factor; but see also Hoover & Newman (2004). Other aphid species also exhibit colour polymorphisms that affect their vulnerability to natural enemies (Ankersmit *et al*., 1986; Kuosell & Eggers, 1987; Michaud & Mackauer, 1995), fungal pathogens (Yu *et al*., 1995) and synthetic insecticides (Kerns & Gaylor, 1992). Thus, if our accumulating knowledge accurately reflects the asymmetric effects of elevated CO_2 on pea aphid genotypes, global change may affect our ability to control aphids using biological and chemical methods.

In conclusion, CO_2 and tropospheric O_3 have complex interacting effects on pea aphids, and the magnitude of these effects differ among populations consisting of single versus mixed genotypes. The mechanisms underlying these altered life-history patterns are yet to be understood, although research continues aiming to better understand the phenomena. Altered genotype by environment interactions complicates our predictive abilities of herbivore population dynamics (Leather, 1988; Bezemer *et al*., 1999; Awmack *et al*., 2005). If other species respond similarly, we can conclude that interactions among genotypes are likely to intensify the effects of future atmospheres on insect population dynamics.

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