REPORT

Transgenerational phenotypic plasticity under future atmospheric conditions

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Abstract

Organisms often exhibit transgenerational phenotypic changes in response to an increased risk of parasitism or predation. Shifts in global atmospheric composition could modify these phenotypic effects through changes in either nutrient quantity/quality or altered interactions with higher trophic levels. Here we show that future atmospheric conditions alter a natural enemy-induced wing polyphenism in aphids. Winged offspring production by *Uroleucon nigrotuberculatum* aphids on goldenrod (*Solidago canadensis* var. *scabra*) does not differ in enriched CO_2 and/or O_3 atmospheres. However, proportionally more winged offspring are produced in response to search cues from both coccinellid predators (*Coccinella septempunctata*) and hymenopteran parasitoids (*Aphidius polygonaphis*) relative to plants not searched by natural enemies. Moreover, the magnitude of this response differs under enriched CO_2 and O_3 environments. Aphids produce more winged offspring in response to predators under elevated CO_2, but produce more winged offspring in response to parasitoids under elevated O_3. Thus, global atmospheric changes influence natural enemy-mediated phenotypic expression, with potentially far-reaching consequences for trophic dynamics.

Keywords

Air pollution, atmospheric change, carbon dioxide, climate change, greenhouse gas, ozone, plasticity, polyphenism, predation risk, trait-mediated effects.

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INTRODUCTION

Both plants and animals alter the phenotypes of their offspring in response to increased risk of attack (Agrawal *et al.* 1999; Weisser 2001; Agrawal 2002; Elliot *et al.* 2003; Lass & Spaak 2003). Transgenerational phenotypic changes are believed to be adaptive as organisms with the induced phenotype experience a decreased predation rate, and resulting greater fitness, than individuals with the unaltered morphology (Luning 1992; Agrawal *et al.* 1999; Agrawal 2001). Natural enemy-induced phenotypic plasticity can also significantly alter prey population dynamics (Kusch 1998). As the induced morph increases in frequency, predation risk for the original phenotype may be further elevated (Kopp & Tollrian 2003; Kunert & Weisser 2003). Thus, natural enemy-induced polyphenisms may have wide-reaching effects on population and community-level processes (Werner & Peacor 2003).

Natural enemy-mediated phenotypic plasticity does not occur in ecological isolation, however, and may be influenced by the quantity and quality of resources at lower trophic levels (Walls *et al.* 1997; Shine & Downes 1999). As defensive behaviours and morphological structures are believed to be costly, organisms experiencing resource limitation may have a reduced ability to produce alternate phenotypes (Fyda & Wiackowski 1998; Tollrian & Harvell 1998; Dahl & Peckarsky 2002). If organisms have abundant resources, however, inducible responses to higher trophic levels may be readily attainable (Wiackowski & Szkarlat 1996; Hanazato *et al.* 2001; Weetman & Atkinson 2002).

Carbon dioxide (CO_2) and tropospheric ozone (O_3) levels, which have both increased dramatically since the mid-1800s (IPCC 2001), can markedly influence host plant productivity and quality. As many plants are currently carbon limited, vegetative growth is generally positively affected by elevated CO_2 and reduced by elevated O_3 (Ceulemans *et al.* 1999; Karnosky *et al.* 2003). Nutritive quality and concentrations of secondary metabolites in plant tissues can also change under elevated levels of CO_2 or O_3 (Bezemer & Jones 1998; Koricheva *et al.* 1998; Coviella & Trumble 1999). Furthermore, several studies have shown that both the abundance and efficacy of natural enemies

differ under elevated CO_2, as opposed to elevated O_3, levels (Gate *et al.* 1995; Stiling *et al.* 1999; Percy *et al.* 2002). Whether parasitoids and predators of aphids respond to elevated greenhouse gases in a differential or similar manner cannot yet be affirmed. Therefore, if phenotypic plasticity of herbivores is dependent on resource quantity or quality (Müller *et al.* 2001; Teder & Tammaru 2002) or stimuli from the parasitoid or predator, such as is true for aphids (Dixon & Agarwala 1999; Weisser *et al.* 1999; Sloggett & Weisser 2002), then global atmospheric change may alter the proportion of individuals exhibiting alternate phenotypes.

Here we examine whether elevated levels of CO_2 and O_3 influence natural enemy-mediated transgenerational phenotypic changes in the aphid *Uroleucon nigrotuberculatum* when feeding on goldenrod, *Solidago canadensis* var. *scabra*. We assess whether cues from previously searching predators or parasitoids induce aphids to produce higher proportions of winged offspring, as has been previously documented in pea aphids (Dixon & Agarwala 1999; Weisser *et al.* 1999) and cotton aphids (E.B. Mondor, J.A. Rosenheim & J.F. Addicott, unpubl. results). We concurrently address whether this transgenerational polyphenism is influenced by CO_2 and O_3 via effects on host plant quality or via effects on natural enemies.

MATERIALS AND METHODS

Free-air CO_2 enrichment experiment

The Aspen Free-Air CO_2 Enrichment (FACE) site, located near Rhinelander, WI, USA (45.7° latitude, 89.7° longitude), consists of 12, 30 m rings arranged in a randomized complete block design (Dickson *et al.* 2000). Four treatments comprise each block: (1) control (*c.* 367 μL L^{-1} CO_2 and 38 nL L^{-1} O_3), (2) elevated CO_2 (+CO_2, *c.* 537 μL L^{-1}), (3) elevated O_3 (+O_3, *c.* 51 nL L^{-1}), and (4) elevated CO_2 and O_3 (+CO_2 +O_3, *c.* 537 μL L^{-1} + 51 nL L^{-1}, respectively). Elevated CO_2 levels represent concentrations predicted for the year 2060 (Dickson *et al.* 2000). Meanwhile, O_3 levels are elevated *c.* 1.5 times that of background levels, based on a diurnal profile of a moderately polluted city (Leelenaw, MI, USA) in the Great Lakes Region of North America (Dickson *et al.* 2000). As each ring is fully open to the prevailing weather conditions, a computer-controlled trace-gas monitoring system continually adjusts the concentrations of both gases, which are disseminated through vertical vent pipes surrounding each ring (Dickson *et al.* 2000).

Each FACE ring is divided into three habitat types: (1) mixed trembling aspen (*Populus tremuloides* Michx.) genotypes, (2) mixed trembling aspen and sugar maple (*Acer saccharum* Marsh.), and (3) mixed trembling aspen and paper birch (*Betula papyrifera* Marsh.). Sites were tilled and 1000 trees planted inside each ring in 1997, and fumigation treatments commenced in 1998 (Dickson *et al.* 2000). The understory of each FACE ring, where our experiments were conducted, is a diverse community of *c.* 60 plant species (C.S. Awmack & A.J. Weldon, University of Wisconsin, Madison, WI, USA, unpubl. results). These understory plants are derived from the soil seed bank or from natural dispersion of seeds into the rings.

Insect bioassay

In each of the 12 rings, nine aphid-free goldenrod plants, *S. canadensis* var. *scabra* (= *Solidago altissima*), were selected at random. To minimize microclimate variation, all plants were chosen from within the aspen–maple sector. A 15 × 30 cm mesh bag was placed over the terminal end of each plant and attached with metal twist ties. Inside each bag one of the following treatments, which were assigned at random using paper chits, was placed: (1) no natural enemy (control), (2) a field collected adult predatory coccinellid, *Coccinella septempunctata*, or (3) a field collected female hymenopteran parasitoid, *Aphidius polygonaphis* (*n* = 3 of each treatment per ring). Natural enemies were permitted to search the aphid-free goldenrod plants for 72 h. We felt this to be a reasonable time for natural enemy searching, as predators and parasitoids were consistently observed on neighbouring plants over the same time period.

Natural enemies were subsequently removed from the plants and an individual adult, apterous *U. nigrotuberculatum* aphid which had been field collected from tall goldenrod outside the gas treatments (i.e. under ambient conditions) was placed on each plant. Aphids were obtained from a 5 × 5 m low-density area, to minimize any prior effects of crowding or natural enemy disturbance on aphid offspring production. Aphids were allowed to produce offspring over 3 days, after which time they were removed and the progeny allowed to mature for 11 days. Prior observations indicated that this was an adequate time for aphid development under our field conditions. At the conclusion of the experiment, plants were thoroughly examined for numbers and phenotypes of offspring. A small number of second-generation progeny, from a few first-generation adults reaching maturity, were easily distinguished on the basis of their small size (< 2 mm) compared to adults (> 4 mm), and were not included in the aphid counts.

Statistics

Data were analyzed using a three-factor split plot ANOVA (JMP version 4.0.4, SAS Institute Inc. 2001). Whole plot effects consisted of the atmospheric treatments CO_2 (ambient vs. elevated) and O_3 (ambient vs. elevated), fully crossed, and with ring block incorporated as a random blocking variable (Dickson *et al.* 2000). Natural enemy

treatment (clean plant vs. predator search cue on plant vs. parasitoid search cue on plant) was incorporated as a sub-plot factor, within gas treatments. All interactions between gas treatments and the natural enemy treatment were included as sub-plot interactions. In the split plot analysis, a whole plot error term (block × atmospheric gases error) was used to test whole plot effects, while a split plot error term (residual error) was used to test sub-plot effects. We initially incorporated aphid density (i.e. total number of aphids per plant) into our model as a covariate, as this may affect the proportion of winged offspring produced (Sutherland 1969). Because this variable was nonsignificant, however, it was removed prior to running the final analysis.

As experimental replication of the fumigation treatments involves entire FACE rings, individual assays of each natural enemy treatment within each ring are not true replicates. Thus, our dependent variable was the overall mean proportion of winged offspring produced per natural enemy treatment per FACE ring. Assays in which no offspring were produced were not included in these proportions. Overall proportions were transformed $[x' = \text{arcsin}(\text{sqrt}(x))]$ to achieve normality (Zar 1984) prior to being analyzed. *Post hoc* analyses were conducted using Fisher's LSD with a sequential Bonferroni correction (Rice 1989). A significance value of $P < 0.10$ was selected to determine significance, which is appropriate in FACE experiments due to the reduced sample sizes and power resulting from the experimental design (Filion *et al.* 2000).

RESULTS

Aphids did not produce different proportions of winged offspring in response to elevated CO_2 ($F_{1,7} = 0.06$, $P = 0.810$), O_3 ($F_{1,7} = 0.92$, $P = 0.369$), or the combined effects of CO_2 and O_3 ($F_{1,7} = 0.47$, $P = 0.515$) when pooled across natural enemy treatments. Pooled across gas treatments, however, aphids did respond to previously searching natural enemies by producing greater proportions of winged offspring when encountering either predator or parasitoid search cues, compared to aphids on clean (no enemy cue) plants (mean ± 1 SE: no search cue, 0.24 ± 0.06; predator search cue, 0.78 ± 0.06; parasitoid search cue, 0.74 ± 0.06: $F_{2,2} = 357.62$, $P = 0.003$).

Greenhouse gas treatments and natural enemy treatments interacted to affect phenotypic plasticity, as evidenced by divergent patterns of wing-induction in response to natural enemy search cues under elevated concentrations of CO_2 (CO_2 × natural enemy; $F_{2,2} = 53.27$, $P = 0.018$; Fig. 1a) and O_3 (O_3 × natural enemy; $F_{2,2} = 59.29$, $P = 0.017$; Fig. 1b). Following a sequential Bonferroni correction, *post hoc* tests indicated that aphids did not bear different proportions of winged offspring on clean plants under ambient vs. elevated CO_2 (Fig. 1a) or O_3 (Fig. 1b).
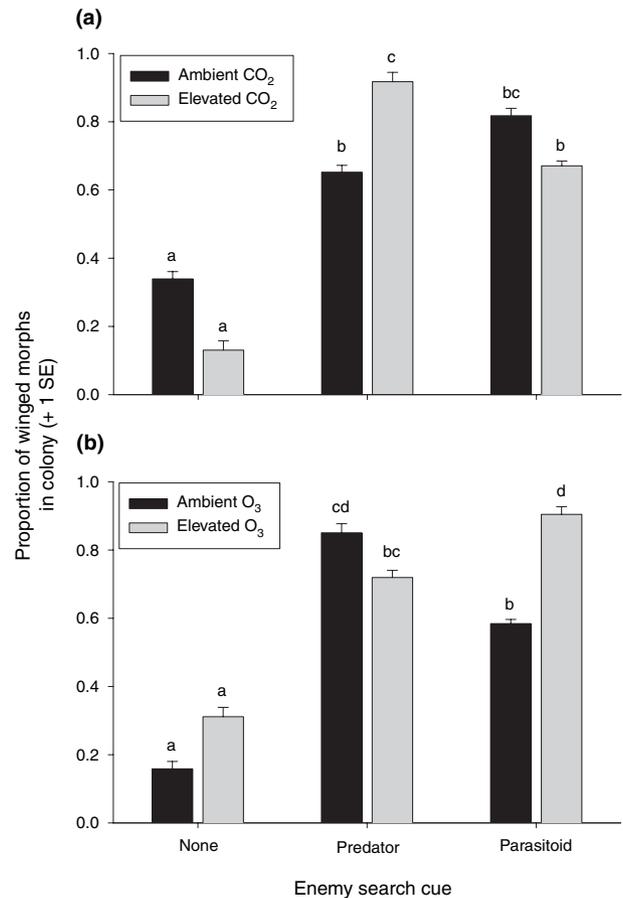

Figure 1 Proportions (mean + 1 SE) of winged offspring produced by *Uroleucon nigrotuberculatum* in response to predator and parasitoid search cues under: (a) ambient (mean of control and +O_3 treatments) and elevated (mean of +CO_2 and +CO_2 + O_3 treatments) CO_2 atmospheres, and (b) ambient (mean of control and +CO_2 treatments) and elevated (mean of +O_3 and +CO_2 + O_3 treatments) O_3 atmospheres. Bars with different letters are significantly different ($P < 0.10$); Fisher's LSD with sequential Bonferroni correction.

Production of winged offspring under enriched CO_2 atmospheres increased, however, in response to predator cues but not in response to parasitoid cues (Fig. 1a). In contrast, wing induction under elevated O_3 increased in response to parasitoid cues but was not influenced by predator cues (Fig. 1b). CO_2 and O_3 had independent (non-interactive) effects on aphid responses to natural enemy cues (CO_2 × O_3 × natural enemy; $F_{2,2} = 7.81$, $P = 0.114$; Fig. 2).

DISCUSSION

We are just beginning to understand the extent to which organisms adjust the phenotypes of their offspring in
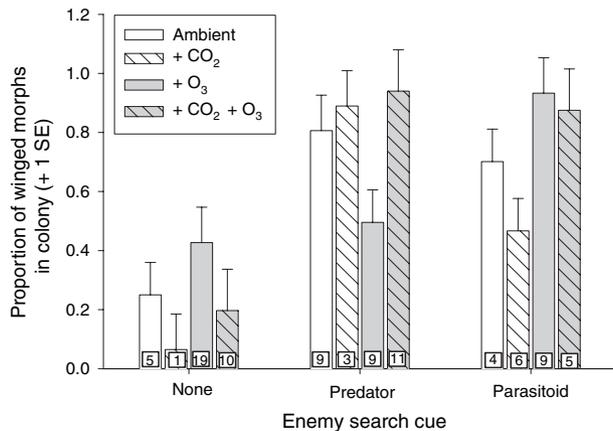
Figure 2 Proportions (mean + 1 SE) of winged offspring produced by *Uroleucon nigrotuberculatum* in response to predator and parasitoid search cues under all atmospheric treatments (ambient, $+CO_2$, $+O_3$, and $+CO_2 + O_3$). Values inside columns are the mean numbers of offspring per colony.

response to increased risk of attack from natural enemies (Agrawal *et al.* 1999; Weisser 2001; Agrawal 2002; Elliot *et al.* 2003; Lass & Spaak 2003). Here, our results show that *U. nigrotuberculatum*, on goldenrod which had been previously searched by either a predatory coccinellid or a hymenopteran parasitoid, produced *c.* threefold more winged offspring than those that had not encountered natural enemy search cues. Aphids did not produce increased proportions of winged offspring in response to elevated CO_2 and O_3 *per se*, but produced more winged offspring in response to predator and parasitoid cues, under elevated concentrations of CO_2 and O_3, respectively.

Uroleucon nigrotuberculatum exhibit very high levels of wing-induction as, averaged across gas treatments, 76% of offspring are winged in response to natural enemy stimuli. Parasitism and predation can be extremely high on this species under field conditions (E.B. Mondor, unpubl. results), thus a large inducible response to increased risk of attack is likely adaptive. By producing winged offspring, aphids have the ability to disperse to other plants, with a lower conspecific density and, as many natural enemies attack prey in a density dependent fashion, with a lower parasitism and predation risk (Minoretti & Weisser 2000; Colfer & Rosenheim 2001). Thus, even if winged individuals have a lower intrinsic rate of increase than unwinged individuals (Dixon 1998), winged offspring production may be adaptive to ensure individual, and hence clone, survival (Weisser 2001).

The most puzzling question arising from this experiment is: why do aphids respond so differently to predator and parasitoid search cues under different atmospheric conditions? To answer this question, the proximate mechanisms

underlying natural enemy-mediated aphid wing-induction must be understood. Unfortunately, little is known about the mechanisms underlying this phenomenon (Weisser 2001). A general mechanism such as a 'pseudo-crowding' effect is believed to underlie wing-induction (Sloggett & Weisser 2002), as aphids alter offspring phenotypes in response to ladybird beetle adults and larvae (Dixon & Agarwala 1999; Weisser *et al.* 1999), hoverfly and lacewing larvae (Kunert & Weisser 2003), and parasitoids (Sloggett & Weisser 2002). After being knocked off a plant by natural enemies, aphids crawling back onto plants encounter a large number of conspecifics and experience a stimulus similar to that of crowding (Sloggett & Weisser 2002). This mechanism, however, is unable to explain individual aphids' propensities to produce winged offspring when exposed to parasitoid and predator search cues, as conspecifics are not present (Dixon & Agarwala 1999; E.B. Mondor, J.A. Rosenheim & J.F. Addicott, unpubl. results).

As winged progeny are produced by either individual or group-living aphids in response to natural enemies (Weisser *et al.* 1999; Sloggett & Weisser 2002; Kunert & Weisser 2003) or their search cues alone (Dixon & Agarwala 1999; E.B. Mondor, J.A. Rosenheim & J.F. Addicott, unpubl. results), we hypothesize that a more general mechanism may be responsible for wing-induction. Increased aphid movement (Dixon & Agarwala 1999) and accompanying reduced feeding times or rates in response to compounds left by searching enemies (Kosaki & Yamaoka 1996; Yasuda *et al.* 2000) may alter an insect's physiological state to trigger the production of winged offspring. Reduced resource acquisition resulting from natural enemy disturbance may, as a result, be functionally equivalent to declining host plant quality (Mittler & Sutherland 1969; Dixon & Glen 1971).

Therefore, as parasitoid and predator efficacies are altered under elevated CO_2 and O_3 (Gate *et al.* 1995; Stiling *et al.* 1999; Percy *et al.* 2002), we hypothesize that natural enemies may have differential search behaviour and leave different amounts of search cue on plants under altered atmospheric conditions. Natural enemy behaviour will likely be altered under enriched CO_2 and/or O_3 atmospheres, as herbivore behaviour is known to change (Awmack *et al.* 1997; Mondor *et al.* 2004). Under this scenario, aphids may then adjust their feeding times/rates and produce dissimilar numbers of winged offspring under different greenhouse gases.

An alternative hypothesis is that different atmospheric conditions may result in the differential production or breakdown of plant- or insect-derived compounds that elicit phenotypic changes. *Solidago* spp. produce a wide array of volatile compounds (Kalemba 1998; Schmidt *et al.* 1999) and plants radically alter volatile emissions under enriched atmospheres (Snow *et al.* 2003; Vuorinen *et al.* 2004). Thus, detection of parasitoid and predator chemical compounds

may be altered by changing background levels of plant volatiles. Furthermore, changing atmospheric conditions also influence the rate at which pheromone structures are destabilized (Arndt 1995). Thus, additional experimental work is required to determine the actual mechanism underlying atmospheric mediation of transgenerational effects in aphids.

Irrespective of the mechanism underlying such transgenerational effects, rapidly progressing atmospheric changes clearly have the potential to alter an organism's phenotypic responses to higher trophic levels. While it is difficult to infer population and community-level processes from studies conducted on individuals, our results suggest that atmospheric changes will likely alter prey–natural enemy interactions. *A priori*, it is difficult to determine whether altered wing-induction responses under changing atmospheres result in better-protected morphs or individuals with unnecessary defences. The extent to which induced traits are adaptive is complex, being determined by factors such as the presence of con- and hetero-specifics as well as resource abundance and quality (Peacor 2002). Therefore, while much is yet to be learned about natural enemy-induced polyphenisms, altered phenotypic expression resulting from global atmospheric changes may have far reaching effects on trophic dynamics.

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