

# Evidence for positive population-level responses but not individual performance of sycamore aphids under elevated CO<sub>2</sub>

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## Abstract

1. While being one of the most destructive agricultural pests globally, aphids are also important components of herbivory networks in forest and woodland habitats. They are predicted to be among the few insect herbivore ‘winners’ under future elevated CO<sub>2</sub> (eCO<sub>2</sub>) scenarios, but additional field experiments are needed to determine species-specific responses, including impacts on fecundity and mortality at the population level.
2. The impact of eCO<sub>2</sub> on populations of aphids on common sycamore, *Acer pseudoplatanus*, was investigated within a temperate woodland at the Birmingham Institute for Forest Research (BIFoR) Free-Air CO<sub>2</sub> Enrichment (FACE) facility.
3. A survey of the aphid species, *Drepanosiphum platanoidis*, *Periphyllus testudinaceus* and *P. acericola*, showed an increase in the abundance and population density of all three species under eCO<sub>2</sub> (150 ppm above ambient), although differences were only significant for *D. platanoidis*.
4. The number of nymphs produced by individual *D. platanoidis* alates isolated in clip cages was not significantly affected by the eCO<sub>2</sub>.
5. These results suggest that *D. platanoidis* could be a species of aphid that may increase in abundance under eCO<sub>2</sub>, but that population-level responses are not driven by improved individual performance. Further experiments are needed to determine the relative contribution of competition and attack by natural enemies as drivers of population-level effects on aphid populations under climate change.

## KEYWORDS

climate change, *Drepanosiphum platanoidis*, forest, herbivory, insect, *Periphyllus acericola*, *Periphyllus testudinaceus*

## INTRODUCTION

The responses to increasing global concentrations of atmospheric CO<sub>2</sub> differ between insect species (Bezemer & Jones, 1998; Sanders et al., 2004), with both ‘winners’ and ‘losers’ emerging within

different plant-insect systems. Elevated CO<sub>2</sub> (eCO<sub>2</sub>) indirectly impacts insect herbivores via changes to host plant quality, most notably C:N ratios (Hillstrom et al., 2014). Feeding guild is a key trait influencing an insect herbivore’s response to eCO<sub>2</sub>, with performance varying depending on plant tissue consumed and feeding mechanism. Based

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on current data, phloem feeders appear to be the only guild expected to experience improved performance under eCO<sub>2</sub> (Sun et al., 2016).

Aphids (Hemiptera: Aphididae) are abundant insect herbivores that feed on plant phloem and are an important model group for studying the effects of climate change on insects. Phloem nutritional quality is defined principally by amino acid quantity and quality (McNeil & Southwood, 1978), which drives aphid life history. Declining food quality (i.e., decreasing total amino acid concentration) triggers a switch from parthenogenesis to sexual reproduction in many species (Douglas, 2003). Previous evidence suggests aphids respond positively under eCO<sub>2</sub>, with increased growth rate, fecundity, survival and abundance (Robinson et al., 2012; Sun & Ge, 2011), although reduced fecundity has also been reported (Carreras Navarro et al., 2020). One proposed mechanism is compensatory feeding – increased phloem ingestion to offset lower amino acid concentrations (Sun & Ge, 2011) – though this individual-level response may vary across generations (Li et al., 2021) and individual performance does not necessarily predict population level responses (Awmack et al., 2004). Changes in phloem composition under eCO<sub>2</sub> may also increase sieve element osmotic pressure (Pritchard et al., 2007). For any given species, responses can vary between host plants (Bezemer et al., 1999), potentially linked to differing plant defence mechanisms under eCO<sub>2</sub> (Ryan et al., 2010), and shifts in reproductive allocation may reduce carrying capacity and aphid abundance (Awmack & Harrington, 2000).

Sycamore, *Acer pseudoplatanus* L., is a common deciduous tree naturalised in the UK (Peterken, 2001). Twelve aphid species are known to feed on sycamore (Blackman & Eastop, 2008), of which eight occur in the UK (Baker, 2020). The three most common are *Drepanosiphum platanoidis* (Schrank, 1801), *Periphyllus testudinaceus* (Ferne, 1852) and *Periphyllus acericola* (Walker, 1848), which are often abundant in late spring before entering aestivation for up to 8 weeks in summer (Wellings et al., 1985). While *D. platanoidis* and *P. acericola* are specialised on sycamore, *P. testudinaceus* is oligophagous on Aceraceae (Wilkaniec & Sztukowska, 2008).

Population dynamics of these species are governed by seasonal cycles linked to biotic and abiotic factors, including amino acid availability, intraspecific competition (Dixon et al., 1993) and temperature (Wellings, 1981). A previous study by Docherty et al. (1997) found that relative growth rates of *D. platanoidis* and *P. testudinaceus* were unaltered under 600 ppm CO<sub>2</sub> in growth chambers. It remains unclear, however, how eCO<sub>2</sub> affects these species at an ecological scale within complex systems where natural enemies and other interacting species may limit or reverse responses. *D. platanoidis* is known to aggregate on leaves in a uniformly spaced distribution dependent on intraspecific competition (Dixon & Logan, 1972), and while larger leaves support more aphids at greater densities (Dixon & McKay, 1970), the effect of eCO<sub>2</sub> on this relationship is undetermined.

This study examined the effect of eCO<sub>2</sub> and associated changes in leaf elemental composition on the abundance and distribution of three sycamore feeding aphids, with individual growth rates and fecundity also assessed for *D. platanoidis*. Work was conducted at the Birmingham Institute for Forest Research Free-Air CO<sub>2</sub> Enrichment

(‘BIFoR FACE’) facility, where eCO<sub>2</sub> has been shown to increase photosynthetic rates, tree biomass, soil nitrogen mineralisation and invertebrate herbivory (Foyer et al., 2025). Whilst biochemical changes suggest future herbivore diets will be carbon-rich but nutrient-poor, the impact on aphids has yet to be tested at an open ecosystem scale.

## METHODS

### Experimental site

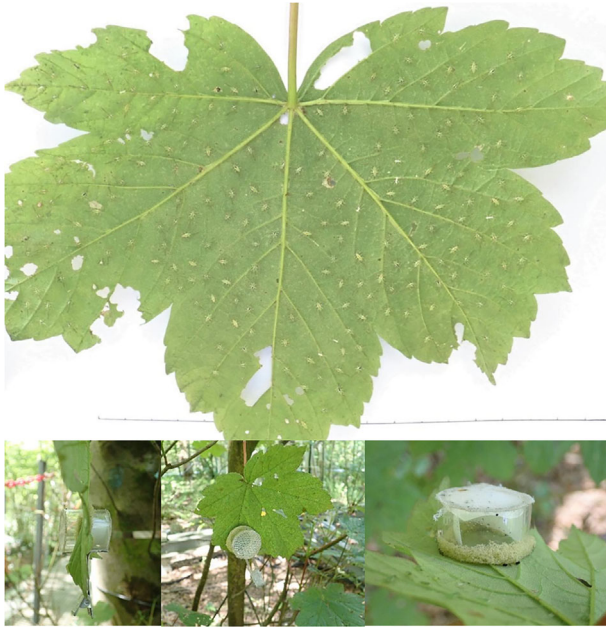
The BIFoR FACE facility is located in Staffordshire, UK (52°47′58″ N, 2°18′15″ W; Hart et al., 2019), within 21 hectares of mature semi-natural broadleaved woodland (>200 years continuous tree cover) dominated by >150-year-old *Quercus robur* L. standards with a previously coppiced *Corylus avellana* L. understorey, plus dispersed *Acer pseudoplatanus* L., *Crataegus monogyna* Jacq. and *Fraxinus excelsior* L. Three treatment arrays fumigate a 30 m diameter area with +150 ppm CO<sub>2</sub> above ambient (~570 ppm total), monitored in real time (Norby et al., 2016); three control arrays fumigate with ambient air (~420 ppm). Fumigation commenced April 2017 and will continue until at least 2031. The two largest, most mature sycamore trees per array (12 total), aged 20–40 years, were selected as experimental trees.

### Aphid survey

On 06/06/2019, five leaves from each experimental tree were surveyed haphazardly from within reach (<3 m height; 10 leaves per array, 30 per treatment). Digital photographs of leaf undersides were taken against a white background with a scale measure, minimising disturbance (Figure 1), then analysed for aphid number, identity and developmental stage. Leaf area was calculated in ImageJ (Schneider et al., 2012) and aphid density expressed as individuals per unit leaf area.

### Clip-cage experiment

On 14/05/2019, individual 4th instar *D. platanoidis* nymphs were enclosed in clip cages (c.f. MacGillivray & Anderson, 1957) on two leaves per experimental tree, giving 4 cages per array (12 per treatment). Fourth instars were selected to synchronise sample age and maximise the likelihood that individuals had developed on their experimental tree for at least one generation. Each cage comprised two 25 mm diameter plastic tube sections, with one end covered with fine gauze and the other with a ring of foam, held together with a sprung metal clip (Figure 1), enclosing each aphid on a 4.91 cm<sup>2</sup> area of leaf underside. Weekly offspring production, time to moult to the alate stage, and mortality were recorded until 11/06/2019, when reproduction plateaued prior to summer aestivation. The number of surviving



**FIGURE 1** Images of *Drepanosiphum platanoidis* alates feeding on a sycamore, *Acer pseudoplatanus*, leaf with characteristic even distribution; the clip cages used to isolate sycamore aphids on sycamore leaves in situ. Clip cages comprise two 25 mm diameter plastic cages held together by a sprung clip attached to a leaf to form a contained 490 mm<sup>2</sup> area of leaf surface where aphids could be isolated and development tracked.

nymphs that moulted each week was used to indicate developmental rate (% moulted per week).

### Climate data

Hourly mean air temperature was recorded by a Campbell Scientific 107 Thermistor on a Campbell Scientific CR300 datalogger mounted at upper canopy height (~21 m) on each array tower. Weekly mean air temperature was calculated for the 7 days preceding each measurement throughout the experimental period.

### Leaf elemental composition

Two Sycamore leaves were collected from each array in July 2019 to capture peak foliar nutrient content, flash frozen at  $-196^{\circ}\text{C}$ , freeze-dried and ground. A  $2000 \mu\text{g} \pm 200 \mu\text{g}$  sample was analysed for total C and N by flash combustion using an Elemental Analyser (Exeter Analytical CE-440) with thermal conductivity detection.

### Statistical analyses

All analyses were performed in R v3.5.2 (R Core Team, 2015). The effects of eCO<sub>2</sub> on *D. platanoidis* and *P. testudinaceus* abundance were

assessed using generalised linear mixed effects models (GLMMs) with tree nested within array and a Conway-Maxwell-Poisson distribution; *P. acericola* data were insufficient for analysis due to the distribution of dimorphs. Population density for each species was tested using GLMMs with tree nested within array and a Tweedie distribution. All GLMMs were validated using the DHARMA package. Nymph production in clip cages was compared between treatments using a Wilcoxon rank-sum test, and developmental rate (proportion moulted per time point) with a paired *t*-test. Treatment effects on leaf C, N and C:N were assessed using *t*-tests.

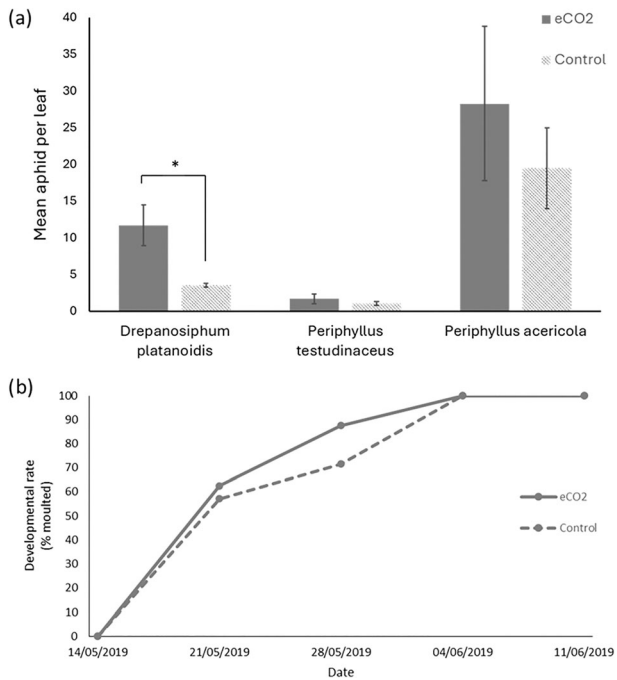
## RESULTS AND DISCUSSION

### Aphid survey

A total of 1979 aphids across all three species were recorded from the 60 leaves surveyed: 460 *D. platanoidis*, 85 *P. testudinaceus* and 1434 *P. acericola*. The majority (71.8%) were *P. acericola* dimorphs aestivating in dense clusters of up to 346 individuals. *D. platanoidis* were significantly more abundant and at greater densities under eCO<sub>2</sub> ( $p = 5.85 \times 10^{-5}$  and  $p = 0.000978$  respectively; Figure 2a). *P. testudinaceus* were also more abundant and denser under eCO<sub>2</sub>, though not significantly so (abundance  $p = 0.445$ ; density  $p = 0.59$ ). *P. acericola* were more abundant under eCO<sub>2</sub> but data were insufficient for statistical analysis.

The positive response of all three species to eCO<sub>2</sub> supports previous findings that aphids benefit under eCO<sub>2</sub> (Sun et al., 2016), though this is not universal – Facey et al. (2017) found no significant change in sap-sucking herbivore abundance at the EucFACE woodland experiment. The differing population-level responses between *D. platanoidis* and the two *Periphyllus* species are consistent with species-specific outcomes reported elsewhere (Newman et al., 2003), and likely reflect differences in life history and phenology. *P. acericola* aestivates as nymphal dimorphs from around May in dense clusters (Shearer, 1976) and had already completed its pre-summer growth phase, whereas *D. platanoidis* enters aestivation later (Dixon, 1969) and populations were probably still growing. Understanding these temporal dynamics is important: Smith (1996) noted that *Brevicoryne brassicae* began reproducing earlier under eCO<sub>2</sub>, and for most UK aphid species, an earlier seasonal start to migration is strongly associated with greater abundance (Bell et al., 2015). Small phenological shifts can also desynchronise predator–prey interactions and enhance aphid numbers (Fuchs et al., 2017).

An alternative explanation for increased aphid abundance is reduced top-down regulation. eCO<sub>2</sub> has been shown to reduce alarm pheromone signalling in aphids (Boullis et al., 2017), decrease VOC diversity and quantity in honeydew (Boullis et al., 2018), and reduce honeydew volume and sugar content (Blanchard et al., 2022), all of which could impair natural enemy host-location. Parasitoids have also shown lower survival and parasitism rates under eCO<sub>2</sub>, linked to reduced nutritional quality of host aphids (Najar-Rodriguez et al., 2024). Shifting phenologies under climate change may further



**FIGURE 2** (a) The mean number of each aphid species per leaf from the survey of 30 leaves under eCO<sub>2</sub> and 30 leaves under control conditions ( $\pm$  1 SE). \* denotes significance at >95% confidence. (b) Weekly developmental rate of *Drepanosiphum platanoidis* (represented as the percentage of ultimately surviving nymphs which have moulted) in all 12 clip cages under eCO<sub>2</sub> and all 12 clip cages in the ambient air control.

create trophic mismatches between aphids and natural enemies (Crowley et al., 2021; Senior et al., 2020). One or more of these mechanisms could account for the increased abundance observed, independently of host plant quality.

Although limited dispersal by these species cannot be entirely excluded (Dixon, 1969), the aphids surveyed were likely second-generation individuals deposited onto maturing leaves by fundatrices earlier in spring, and movement into eCO<sub>2</sub> arrays is unlikely to be the primary driver of treatment differences. Importantly, our survey of abundance represents just one time window within the seasonal cycle and multiple years of data would be useful to further explore the responses measured.

### Leaf elemental composition

Mean leaf C was significantly greater under eCO<sub>2</sub> (46.32%) than ambient (45.40%;  $p = 0.05$ ). There was no significant difference in foliar N (eCO<sub>2</sub>: 2.52; ambient: 2.54;  $p = 0.825$ ), and the resulting C:N ratio was marginally but non-significantly greater under eCO<sub>2</sub> (18.16:1 vs. 18.01:1;  $p = 0.922$ ). This is consistent with findings for other tree species under eCO<sub>2</sub> (Foyer et al., 2025; Gardner et al., 2022). The modest increase in C:N after 2 years of fumigation suggests that herbivores typically more susceptible to elevated C:N ratios, such as leaf miners (Bezemer & Jones, 1998), are unlikely to have been negatively

impacted, making reduced interspecific competition an unlikely explanation for increased aphid abundance. Nevertheless, nutritional changes within phloem can differ substantially from bulk leaf tissue, for example Wang and Nobel (1995) reported 5% more sucrose and 50% more mannose contents but 17% less amino acids in phloem exudates under eCO<sub>2</sub>, further research is needed to understand how the balance of sugars and amino acids influences population growth within and across feeding guilds.

### Clip-cage experiment

Over the 4-week observation period, 82 progeny were produced by 24 aphids (mean 3.42 nymphs per aphid; SD = 1.6). By 21/05/2020, 60% of 4th instar nymphs had moulted into alates, with 100% having done so by 04/06/2020. Neither nymph production ( $W = 62$ ,  $p = 0.572$ ) nor developmental rate ( $df = 4$ ,  $p = 0.242$ ; Figure 2b) differed significantly between treatments. The absence of a significant temperature difference between arrays suggests similar day-degree accumulation under both treatments, making spatial temperature variation an unlikely primary driver of abundance differences. However, leaf-level microclimate may be important. Offsets of several degrees between leaf and air temperature are not uncommon because absorbed short and long-wave radiation cannot be fully dissipated through cooling processes (Hagan Brown et al., 2025), and eCO<sub>2</sub> can exacerbate this by reducing stomatal opening, decreasing transpiration and thus evaporative cooling (Hui et al., 2001). Hagan Brown et al. (2025) identified increased canopy warming in oak under eCO<sub>2</sub> at BIFoR FACE, and a similar effect in sycamore seems plausible. Even a small increase in leaf temperature could substantially affect day-degree accumulation and population growth across multiple generations, even if the effect within a single generation was non-significant.

### CONCLUSIONS

This study found increased abundance of the three most common UK sycamore aphid species under eCO<sub>2</sub> (150 ppm above ambient) in a mature temperate woodland ecosystem, but with no significant impact on developmental rate in *D. platanoidis*. This represents positive population level response to eCO<sub>2</sub> but there is no evidence that this is driven by increased individual performance. Overall, the results are consistent with the broader BIFoR FACE findings: eCO<sub>2</sub> effects on sycamore leaf elemental composition mirror those in other tree species (Foyer et al., 2025; Gardner et al., 2022), and the positive population-level response of aphids aligns with expected trends for phloem feeders relative to other herbivore guilds such as leaf chewers (Foyer et al., 2025). Future research should investigate the drivers of these responses by exploring the roles of competition and top-down pressure from natural enemies under eCO<sub>2</sub> over several growing seasons.

## AUTHOR CONTRIBUTIONS

**Liam M. Crowley:** Conceptualisation; Data Curation; Investigation; Formal Analysis; Methodology; Writing – Original Draft Preparation. **Carolina Mayoral:** Data Curation; Investigation. **Abigail Enston:** Data Curation; Investigation. **Jessica Money:** Data Curation; Investigation. **Jon P. Sadler:** Conceptualisation; Formal Analysis; Methodology; Supervision; Writing – Review & Editing. **Jeremy Pritchard:** Supervision; Writing – Review & Editing. **Rob A. MacKenzie:** Funding Acquisition; Writing – Review & Editing. **Scott A. L. Hayward:** Conceptualisation; Methodology; Supervision; Writing – Review & Editing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data used in this manuscript are available from the Dryad Digital Repository DOI: <https://doi.org/10.5061/dryad.9w0vt4bvn> (Crowley et al., 2025).

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