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Response of spring crops and associated aphids to elevated atmospheric CO_2 concentrations

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Summary

Having evolved a parasitic relation to their host plants, aphids may serve as indicators of plant responses to environmental changes. The present rise in atmospheric CO_2 concentrations is expected to alter plant leaf chemistry and may thus alter host plant – aphid relations. We involved a climate chamber system and used bird cherry-oat aphid (*Rhopalosiphum padi* L.) and green peach aphid (*Myzus persicae* **S**.) and their respective host plants, spring wheat (*Triticum aestivum* L. cv. "Triso") and oilseed rape (*Brassica napus* cv. "Campino"), to elucidate the effects of atmospheric CO_2 enrichment on such bitrophic systems. Spring wheat grown at elevated CO_2 (600 ppm) generally had greater above ground biomass than plants grown at ambient CO_2 (400 ppm). Bird cherry-oat aphid infestation resulted in reduced spring wheat above ground biomass compared to the non-infested control. Relative crop growth rate (RGR) was increased by elevated CO_2. In our study, the relative developmental stage (rDS) and intrinsic rate of increase (r_m) of the aphids was only slightly and non-significantly increased under elevated atmospheric CO_2 conditions. The response of aphid weight and RGR to elevated CO_2 differed, increasing by 24% and 18.2% for bird cherry-oat aphid and decreasing by 12% and 12.5% for green peach aphid, respectively. Aphids reared on spring wheat at elevated CO_2 had a shorter lifespan, whereas the opposite effect was found for aphids reared on oilseed rape. The average number of nymphs of the two pest species showed both an increase under elevated CO_2. No consistent picture emerges from these findings, and further investigation on host – aphid relations under changing atmospheric conditions such as CO_2 enrichment appear necessary.

Introduction

Atmospheric carbon dioxide (CO_2) concentration has increased from 290 ppm (parts per million) in 1850 to 375 ppm in 2007 (IPCC, 2007) and will continue to rise in the coming decades due to anthropogenic activities. According to current climate scenarios CO_2 concentration will increase up to 450-550 ppm at the middle of this century. Besides indirect impacts due to climate change CO_2 enrichment will directly affect both plants and insects (MASTERS et al., 1998; HUGHES, 2000).

Several effects of CO_2 enrichment on plants have been observed such as an increase in photosynthesis rates, leaf area, dry weight and other growth characteristics (OWENSBY et al., 1999). Many studies have shown an increase in plant growth in elevated compared to ambient CO_2 (NORBY et al., 1999; LONG et al., 2004; AINSWORTH and LONG, 2005). In earlier work when a doubling of atmospheric CO_2 was considered, CURE and ACOCK (1986) reported an increase in yield by 41% on average after assembling yield data for 10 major crops (leaf, grain, tuber and fiber). Corresponding results were obtained by AMTHOR (2001) who estimated an increase in wheat grain mass by 31% on average based on wheat yield data from 50 publications. In more recent work involving FACE technology (Free Air Carbon dioxide Enrichment) at only ca. 200 ppm above ambient instead of doubling, elevated CO_2 increased aboveground biomass by 12% and

grain yield by 10-15% in wheat (KIMBALL et al., 2002a). For oilseed rape, only few data are available on yield and growth response to CO_2 enrichment. According to FRANZARING et al. (2008b), shoot biomass of summer oilseed rape tended to be 20% greater and seed output increased by approximately 17% under elevated CO_2. In this study, plant height and the dry weight of reproductive organs was also significantly increased under elevated CO_2, indicating a speeding up of plant development. The significant increase in the dry weights of senescent leaves in plant specimens from the elevated CO_2 treatment strongly suggests that plant phenology is also affected.

It was also revealed that elevated CO_2 influences the primary and secondary metabolism of plants (PENUELAS and ESTIARTE, 1998). Many studies have shown changes in foliar sugars, starch and increases in concentrations of carbon based secondary structural compounds due to elevated CO_2 (PENUELAS and ESTIARTE, 1998; STILING et al., 1999). The foliar nitrogen content in plants grown under increased CO_2 was often reported to be reduced by up to 15% (COTRUFO, 1998; HEAGLE et al., 2002).

The rise in CO_2 can thus indirectly affect herbivores by biochemically altering the nutritive value of the host plants. The increase in the carbon:nitrogen ratio in host plants generally decreases the nutritive quality for some feeding guilds of pests (e.g. phloem-feeders, leaf miners, xylem-feeders, seed-eaters, whole-cell-feeders and leaf-chewers), leading to an increase in their food consumption rates in order to compensate for the reduced quality (SALT et al., 1995; MARKS and LINCOLN, 1996; BEZEMER and JONES, 1998). The increased siphoning from phloem-feeders in turn causes a massive reduction in host plant assimilates (WATT et al., 1995). The change in the allocation patterns of compounds and the chemical composition of plant tissues indirectly affects the food ecology of phytophagous insects (HUNTER, 2001).

RHODES et al. (1996) have shown that phloem-feeding aphids use amino acids for their protein metabolism, and carbohydrates for energy. The phloem of plants contains high amounts of carbohydrates (0.8-1.8 M), small amounts of amino acids (60-200 mM) and very few lipids (KLINGAUF, 1987; DILLWITH et al., 1993; SANDSTÖM and MORAN, 2001; WILKINSON and DOUGLAS, 2003; DOUGLAS, 2006). In order to obtain the necessary amounts of amino acids required for growth, aphids thus consume considerable amounts of carbohydrates from the phloem. Improved food quality of a host plant with respect to aphids expresses itself in a higher amino acid to carbohydrate ratio within the phloem (MITTLER and MEIKLE, 1991). Elevated CO_2 may change the concentrations of some individual amino acids in the phloem sap, thereby affecting the performance of aphids. A study of DOCHERTY et al. (1997) proved that reduction of total amino acid concentration in phloem sap was 31% at elevated CO_2.

The reduction in food quality due to elevated CO_2 also impacts the behaviour and physiology of leaf miner insects (STILING and CORNELISSEN, 2007). Many species of herbivorous insects tend to show altered behaviour and characteristics under CO_2 enrichment. The consequences differ between species and include retarded growth rates, increased nymphal development times and higher mortality rates (LINDROTH et al., 1993; SMITH and JONES 1998; COVIELLA and TRUBLE, 1999; GOVERDE and ERHARDT, 2003). In

contrast, some studies concluded that the development time of phloem-feeding insects may be reduced by 17%, and that adult weight, relative growth rate (RGR) and population size may actually increase due to elevated CO_2 (BEZEMER and JONES, 1998; NEWMAN et al., 2003).

In this paper, we investigated the responses of host plants to elevated CO_2 in order to observe the indirect effects on phloem feeding insects. The experiment was carried out with bird cherry-oat aphids (*Rhopalosiphum padi* L.) on spring wheat (*Triticum aestivum* L. cv. "Triso") and with green peach aphid (*Myzus persicae* S.) on oilseed rape (*Brassica napus* cv. "Campino"). Determining the effects on these sap-feeding insects is very important for agriculture. *Myzus persicae* causes both direct (leaf curling) and indirect damage of plants (transmission of plant viruses such as lettuce mosaic virus (LMV) and cucumber virus I) (NAMBA and SYLVESTER, 1981). *Myzus persicae* can achieve very high population densities on plant tissue, retarding plant growth rate and thereby causing a perceptible reduction in yield of root and foliage crops (PETITT and SMILOWITZ, 1982). *Rhopalosiphum padi* in turn causes a significant decrease in yield on cereal crops via feeding damage, resulting in a reduction of kernel amount and mass. Kernel amount was reduced by 36-50% in winter wheat, 24-48% in rye, 41-60% in barley and 41-63% in winter oats. The reduction of thousand kernel weight was 33-65% in winter wheat, 13-26% in rye, 25-47% in winter barley and 43-75% in winter oats (KUROLI, 2009).

Other researchers have conducted experiments on the indirect effects of elevated CO_2 on *Myzus persicae* feeding on *Brassica napus* (HIMANEN et al., 2008) and on *Solanum dulcamara* (HUGHES and BAZZAZ, 2001), but the growth parameters of aphids were not taken into account. Review of literature showed that the relative growth rate of aphids may be increased under elevated CO_2. However, these observations were carried out with other species of aphid as *Aulacorthum solani* (AWMACK et al., 1997) and *Sitobion avenae* (CHEN and WU, 2006) on host plants such as *Vicia faba*, where the relative growth rate of *Sitobion avenae* was increased by 33% at 550 ppm CO_2 and by 74% at 750 ppm CO_2.

Unfortunately insect response to elevated CO_2 differs between host plants and aphid species (BEZEMER et al., 1998). It is thus necessary to observe specific species of aphids on specific host plants. For the first time, in this study the development of *R. padi* on spring wheat and development of *M. persicae* on oilseed rape from the nymph to the adult stage under elevated CO_2 was observed, making record of the relative developmental stage, population growth rate and relative growth rate of the aphids.

Materials and methods

Cultivation of plants and experimental conditions

The experiment was carried out on spring wheat (*T. aestivum* L. cv. "Triso") from 16 June to 13 August 2008 and on oilseed rape (*Brassica napus* cv. "Campino") from 27 May to 17 August 2009 at the Institute for Landscape and Plant Ecology of Hohenheim University, Germany. A pot experiment was conducted in six controlled-environment chambers (Vötsch Bioline®) with two levels of CO_2 (ambient, 400 ppm and elevated, 600 ppm). Seeds of spring wheat and oilseed rape were sown in pots (Ø 18 cm) with a mixture of substrate (Fruhstorfer Erde Typ LD 80, Industrie-Erdenwerk Archut, Lauterbach, Germany) and sand (9:1). Germination took place at 22 ± 2ºC, 80% relative humidity and 18:6 hour L: D photoperiod. Out of the sixteen host plants in each chamber, ten were chosen for aphid infestation and six for plant analysis. Plants were grown having a photoperiod of 18 h, photosynthetic photon flux density (PPFD) of approximately 520 µmol $m^{-1}s^{-1}$, a day/night temperature of 22/12ºC, irrigated daily with 50 ml water and fertilized weekly using 50 ml of 0.3% nutrient solution (Wuxal®, Aglukon

GmbH). Host plants and climate profiles were rotated weekly between chambers in order to ensure results were not chamber specific. Further chamber characteristics are given in details in FRANZARING et al. (2008a).

Biomass production and plant phenology

In order to determine the aboveground biomass of plants at ambient and elevated CO_2, spring wheat and oilseed rape were harvested at growth stages 12 and 30 (BBCH code) according to ZADOKS et al. (1974) and WEBER and BLEIHOLDER (1990), respectively, dried at 105 ºC to constant weight and then weighed on a balance (Sartorius analytics A 120 S). Subsequently, relative growth rate (RGR, HUNT, 1982) of the plants was calculated using equation (1). Since in any experiment start weight was similar, we did not refer to start weight as required by HUNT (1982).

(1) $RGR = (ln\ W_2 - ln\ W_1)\ /\ t_2\text{-}t_1$

where W_1 is the dry weight (DW) at start of the experiment (t_1), W_2 is the final DW at the end of the experiment (t_2), and $t_2\text{-}t_1$ is the time (days) elapsed between the weighing.

Cultivation of aphids

In order to infest the experimental plants with similar aged aphids, synchronized colonies of *R. padi* and *M. persicae* were established. A synchronised long-term cultivation was carried out in greenhouse at 20 ± 1°C, relative humidity 60-70%, a lighting duration of 16 h and PPFD of approximately 22.5 µmol $m^{-2}\ s^{-1}$. Then the synchronised adult, female apterous aphids were placed on plants, grown in climate chambers under two levels of CO_2 to produce progeny. Petri dishes that had been converted into small plexiglass cages (Ø 3.5 cm) and attached with clip on the second leaf of each plant (BBCH code 12) were used for aphid rearing. After five hours, female aphids were removed and five newly born nymphs (L_1) were allowed to develop until they reach late-nymphal instars in order to determine the relative developmental stages (rDS), developmental time and preimaginal mortality. The cages nymphs were observed daily. To assess longevity of adults and reproduction, one of the five aphids per cage after adult moult was put separately in a cage on a young leaf and observed until death. Nymphs deposited per female were counted and removed with a paintbrush daily. Excess freshly born nymphs and adult pre-reproductive aphids were weighed to determine body size and relative growth rate (RGR).

Determination of aphids' growth parameters

The development of *R. padi* and *M. persicae* was observed and counted daily from start of the experiments until entering the adult stage. To depict any indirect effect of elevated CO_2 into aphid development, the relative developmental stage (rDS), implemented to show the effects if insect growth regulators (ZEBITZ, 1984), was calculated after daily counting and subsequential removal of exuviates of nymphs using equation (2):

(2) $rDS = \sum (n_t\ S_p \bullet F_p)\ /\ N_t S$

where $n_t\ S_p$ is the number of individuals per development stage at time t, F_p the multiplication factor of relevant development stage (nymphal stages 1-4, adult stage 5) and $N_t S$ the total number of individuals per cage.

The intrinsic rate of increase (r_m, WYATT and WHITE, 1977) of *R. padi* and *M. persicae* were calculated from the number of offspring per female after one generation time using the following equation:

(3) $r_m = (0.754\ (ln\ M_d))\ /\ d$

where M_d is the number of offspring per generation time and d is the generation time (days).

In order to determine the relative growth rate (RGR, Howard and Dixon, 1995) of *R. padi* and *M. persicae*, weights of single adults were measured using a precision balance (Sartorius analytic 4504 MP8) and calculated following equation (1).

Statistical analyses

The effects of elevated CO$_2$ concentration on growth parameters of *R. padi* and *M. persicae* (e.g. nymphs and adult weight as well as the relative growth rate of aphids) were tested using analysis of variance (ANOVA, Visual-XSel® 9.0/ DoE & Weibull). The combined effect of CO$_2$ elevation and aphids on plant above ground biomass and relative growth rate were analysed by ANOVA with CO$_2$ treatment and aphid infestation as independent variables. Treatment means were compared by means of LSD-test. Comparison of relative development stages of aphids was done applicating the Kruskal-Wallis-Test. As the fecundity was not normally distributed, treatments were analysed using the non-parametric Mann-Whitney U-test. The suitable statistical test methods were chosen according to Köhler et al. (2002).

Results

Plant biomass and phenology

In 2008, the phenology of spring wheat was determined from leaf development (9 DAS, days after sowing) until stem elongation (57 DAS). The results suggest that plant development was not significantly altered due to elevated CO$_2$ during these developmental stages (data not shown).

Spring wheat grown under elevated CO$_2$ significantly increased above ground biomass by 41% as biomass was 7.25 ± 0.24 g DW at 400 ppm and 10.19 ± 0.058 g DW at 600 ppm when the plants were not infested with aphids (Tab. 1). This CO$_2$-induced increase was even higher (+ 48%) in spring wheat infested with *R. padi*, above ground biomass being 6.25 ± 0.071 g DW at 400 ppm and 9.27 ± 0.259 g DW at 600 ppm. As expected, the infestation by *R. padi* impacted plant above ground biomass negatively, reducing it by 14% at 400 ppm CO$_2$ and by 9.1% at 600 ppm CO$_2$. However, no statistically significant interactions between CO$_2$ enrichment and aphid infestation on wheat above ground biomass were detected. The relative growth rate (RGR) of *T. aestivum* was significantly increased due to elevated CO$_2$ (on average by 19%) and significantly reduced when the plants were infested with aphids (on average by 6.1%). There was a slightly higher depression of wheat RGR due to aphid infestation at ambient compared to elevated CO$_2$ (7.9 vs. 4.6%), however, these CO$_2$ by aphid interactions were below statistical significance.

In 2009, the phenology of oilseed rape under CO$_2$ enrichments was determined during leaf development (from 12 until 78 DAS). Plant development was not significantly altered due to elevated CO$_2$ (data not shown).

Effects of CO$_2$ enrichment and presence of aphids on oilseed rape above ground biomass and RGR were consistently below statistical significance because of large variation between replicates. Correspondingly, no significant interactions between CO$_2$ enrichment and aphid treatment could be detected. Nevertheless, elevated CO$_2$ tended to increase rape RGR (on average by 34% across both aphid treatments) (Tab. 1).

Effect of elevated CO$_2$ on aphid performance

Elevated CO$_2$ concentrations resulted in several changes of growth parameters of bird cherry-oat and green peach aphids. However, the relative developmental stage (rDS) of the aphids remained almost unaffected in enhanced CO$_2$ environments (Tab. 2).

The comparison of average imaginal weight of *R. padi* and *M.*

Tab. 1: Above ground biomass [g pot^{-1}] and relative growth rate (RGR) of spring wheat and oilseed rape under ambient or elevated CO$_2$ concentration and with or without aphid colonization shortly before stem elongation stage. Values represent treatment average ± standard error from three replicate climate chambers, respectively.

Plant species / plant trait	ambient CO$_2$, without aphids	elevated CO$_2$, without aphids	ambient CO$_2$, with aphids	elevated CO$_2$, with aphids	Significance of treatment effects (F-test)		
					CO$_2$	aphids	CO$_2$*aphids
Wheat biomass	7.25 ± 0.24 [A]	10.19 ± 0.058 [B]	6.25 ± 0.071 [C]	9.27 ± 0.259 [D]	< 0.001	0.001	ns
Wheat RGR	1.99 ± 0.033 [A]	2.34 ± 0.008 [B]	1.84 ± 0.011 [C]	2.23 ± 0.024 [D]	< 0.001	< 0.001	ns
Rape biomass	4.66 ± 2.10 [A]	6.72 ± 1.35 [A]	5.19 ± 0.642 [A]	6.07 ± 0.660 [A]	ns	ns	ns
Rape RGR	1.32 ± 0.435 [A]	1.94 ± 0.136 [A]	1.51 ± 0.003 [A]	1.85 ± 0.001 [A]	ns	ns	ns

Different letters in superscript within one row indicate significantly different treatment means at P < 0.05 (LSD-test), ns is not significant

Tab. 2: Relative development stages of *R. padi* and *M. persicae* from first nymphal instar to apterous virgo. Columns 1-9 (*R. padi*) or 1-10 (*M. persicae*) refer to days after leaving five instar nymphs in the cages.

rDS of *Rhopalosiphum padi* (from L$_1$ to apterous virgo) [days]									
CO$_2$ treatment	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
400 ppm	1.0	1.7	2.2	2.7	3.1	3.7	4.3	4.7	5.0
600 ppm	1.0	1.8	2.1	2.6	3.1	3.7	4.4	4.8	5.0

rDS of *Myzus persicae* (from L$_1$ to apterous virgo) [days]										
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
400 ppm	1.0	1.1	1.7	2.1	2.5	2.9	3.2	3.9	4.3	5.0
600 ppm	1.0	1.2	1.8	2.1	2.5	3.0	3.4	4.0	4.4	5.0

Tab. 3: Mean imaginal weight (IW), relative growth rate (RGR), increase rate (r_m-values) and mean adult longevity of *R. padi* and *M. persicae* under ambient and enhanced CO_2 conditions.

Parameters	Ambient CO_2	Elevated CO_2	*P* values (ANOVA)
		Rhopalosiphum padi	
Imaginal weight (IW) [μg] [1]	570.6 ± 15.8	707.2 ± 34.0	0.01
Relative growth rate (RGR) [μg/μg/day] [1]	0.11 ± 0.003	0.13 ± 0.01	0.01
Increase rate r_m [d^{-1}] [2]	0.354 ± 0.01	0.358 ± 0.015	ns
Duration of life [days] [2]	39.3 ± 3.2	39.0 ± 3.5	ns
		Myzus persicae	
Imaginal weight (IW) [μg] [1]	416.5 ± 17.2	366.5 ± 1.1	0.001
Relative growth rate (RGR) [μg/μg/day] [1]	0.08 ± 0.00	0.07 ± 0.00	0.001
Increase rate r_m [d^{-1}] [2]	0.30 ± 0.01	0.31 ± 0.01	ns
Duration of life [days] [2]	39.0 ± 6.5	41.1 ± 9.2	ns

[1] n = 50, [2] n = 30, ns, not significant

persicae before the nymph reproduction and RGR of aphids clearly revealed a CO_2 effect (Tab. 3). Average weight of *R. padi* imago was 570.6 ± 15.8 μg FW at ambient CO_2 and 707.2 ± 34.0 μg FW at elevated CO_2 treatment which means a significant increase by 24%. On the other hand, average weight of *M. persicae* imago decreased significantly from 416.5 ± 17.2 μg at ambient CO_2 to 366.5 ± 1.1 μg at elevated CO_2 which corresponds to a decrease by 12% due to elevated CO_2. The RGR of *R. padi* feeding on wheat achieved 0.11 ± 0.003 at ambient CO_2 and 0.13 ± 0.01 at 600 ppm CO_2. RGR of *R. padi* was higher than RGR of *M. persicae* on oilseed rape, the latter which achieved 0.08 ± 0.00 at 400 ppm CO_2 and 0.07 ± 0.00 at 600 ppm CO_2. Thus, CO_2 enrichment increased the RGR of *R. padi* by 18.2%, while it decreased the RGR of *M. persicae* by 12.5%.

R. padi lifespan was slightly shorted under elevated CO_2 concentration, although this effect was not significant. The lifespan was 39.0 days (ambient) and 39.3 days (elevated CO_2). In contrast, lifespan of *M. persicae* was slightly prolonged by 2.1 days.

Elevated CO_2 not also affected growth but also reproductive characteristics of aphids. The intrinsic rate of increase (r_m) of both aphids was slightly but not significantly higher under elevated CO_2. The average number of *R. padi* nymphs per female in plants grown under elevated CO_2 was increased by 6.0%, although this was not significant. The respective values were 69.2 ± 8.7 nymphs in ambient and 73.3 ± 12.4 nymphs under elevated CO_2. The average number of *M. persicae* nymphs per female in plants grown under elevated CO_2 was increased by 3.5%. The respective values were 59.3 ± 7.8 nymphs in ambient and 61.4 ± 9.5 nymphs under elevated CO_2. In order to establish the frequency with which the female aphids reproduced under normal and CO_2 enriched conditions, the daily appearance of nymphs was recorded. During reproduction, the number of *R. padi* nymphs increased, peaking on day nine. Afterwards, it tapered off, the last nymph produced on day 20 (Fig. 1). Significant CO_2 effects were found on days 5 to 7 and on days 13 and 14. Regarding *M. persicae,* the number of nymphs increased during the first sixteen days, after which it declined, the last nymph produced on day 32 (Fig. 2). A significant CO_2 effect was found on day 21.

Discussion

According to the current predictions, plants and insects will be influenced due to increasing atmospheric CO_2. The responses of plants and aphids to these changes in our research corresponded par-
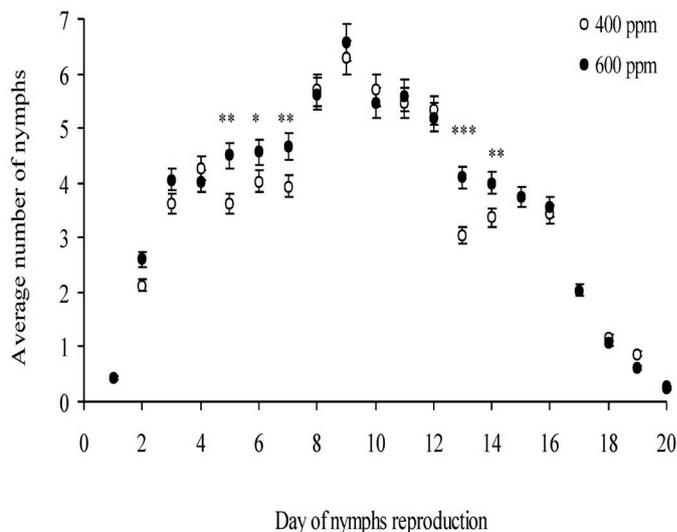

Fig. 1: Daily average number of *Rhopalosiphum padi* nymphs per treatment (n = 30). Asterisks indicate significant CO_2 effects according to the Mann-Whitney U-test (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

tially with predictions. The experiment in controlled-environment chambers was established in order to understand the positive or negative impacts of CO_2 enrichment on agricultural crops and phloem feeding aphids such as *R. padi* and *M. persicae*.

Our observations showed that the phenology of spring wheat and oilseed rape was not significantly altered due to elevated CO_2. SLAFER and RAWSON (1997) have argued that elevated CO_2 has no effect on growth and leaf development in wheat. However, FRANZARING et al. (2008b) suggested that phenological development of oilseed rape was significantly enhanced under elevated CO_2. Slight phenology acceleration under rising CO_2 was also found by KIMBALL et al., (2002b) on spring wheat. In our experiment, above ground biomass of spring wheat was increased by 41% due to elevated CO_2. This supports earlier findings on the fertilizing effects of CO_2 enrichment on C_3 plants (e.g. KÖRNER, 1991; TAYLOR et al., 1994) and is well in agreement with POORTER (1993) who surveyed literature (156 plant species) and found that with a doubling in atmospheric CO_2 plant biomass during vegetative growth was increased on
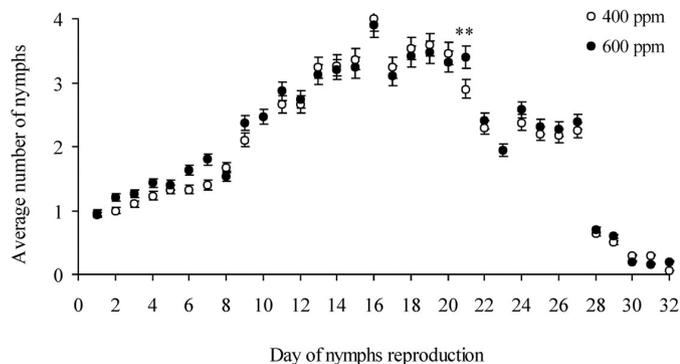
Fig. 2: Daily average number of *Myzus persicae* nymphs per treatment (n = 30). Asterisks indicate significant CO_2 effects according to the Mann-Whitney U-test (** $p < 0.01$).

average by 37% for C_3 crops. Correspondingly, the RGR of spring wheat was increased by 17% under elevated CO_2 in our study. Similarly, FLYNN et al. (2006) investigated potted plants (*Solanum dulcamara*) in glass-topped chambers under two conditions of atmospheric CO_2 concentration (350/ 750 ppm) and confirmed enhancement of RGR due to elevated CO_2.

Increase of CO_2 led to significant gain in plant above ground biomass, while the presence of aphids reduced the above ground biomass of spring wheat in both ambient and enriched CO_2 environments. Our results showed that infestation with *R. padi* caused significant reductions in wheat biomass of 14% and 9.1% at 400 ppm and 600 ppm, respectively. However, no significant effects were found when oilseed rape was infested with *M. persicae*. HUGHES and BAZZAZ (2001) proved that out of five aphid species (*Acyrthosiphon pisum*, *Aphis nerii*, *Aphis oenotherae*, *Aulacorthum solani* and *Myzus persicae*) grown on five host plants (*Vicia faba*, *Asclepias syriaca*, *Oenothera biennis*, *Nicotiana sylvestris* and *Solanum dulcamara*) only *Aphis nerii* had significantly negative effects on the biomass of *Asclepias syriaca* at both ambient and elevated CO_2. The interaction between CO_2 and aphid presence on above ground biomass and RGR was insignificant for spring wheat and oilseed rape in our study. However, HUGHES and BAZZAZ (2001) suggested that there was highly significant interaction between CO_2 and presence of two species of aphid (*Myzus persicae* and *Aphis nerii*) on above ground biomass of *Asclepias syriaca* and *Solanum dulcamara*.

Regarding our findings on CO_2 effects on aphids, *R. padi* showed an increase in weight of 24% and RGR of 18.2% in the high-CO_2 treatment. Similar results were obtained by BEZEMER and JONES (1998), supporting the theory that insects perform better when feeding on plants grown under CO_2 enrichment. According to AWMACK et al. (1997), the aphid *Aulacorthum solani* (Homoptera: Aphididae) reared on bean (*Vicia faba*) and tansy (*Tanacetum vulgare*) also responded to elevated CO_2 conditions with increased growth. However, FLYNN et al. (2006) adduced evidence that CO_2 did not significantly affect the weight of aphids (*Macrosiphum euphorbiae* Thomas). Other studies concluded that CO_2 enrichment can negatively affect insect weight (JOHNS and HUGHES, 2002; ROTH and LINDROTH, 1995) and RGR of leaf-miner pests, reducing RGR by 8.3% (STILING and CORNELISSEN, 2007). In agreement, *M. persicae* showed decreased aphid weights by 12% and RGR by 12.5% under CO_2 enrichment in our study. In accordance with BALE et al. (2002) the decrease in weights reflect accelerated plant development due to global climate changes (increase of CO_2 or temperature), which decrease the amount of feeding time available to the aphids.

We observed that the rDS and r_m of aphids was only slightly and non-significantly increased under rising atmospheric CO_2 conditions. Our study showed that the fecundities of *R. padi* and *M. persicae* feed-

ing on plants grown at elevated CO_2 increased by 6.0% and 3.5%, respectively. In contrast, TRAW et al. (1996) reported reduced fecundity of insects. Additionally, WILLIAMS et al. (2003) concluded that elevated CO_2 has no impact on fecundity of phloem feeding insects. According to LINCOLN et al. (1993), CO_2-induced alterations in phytochemical constituents important to insects can potentially alter their behaviours.

In our study, the duration of aphids' life was prolonged by an average of 2.2 days for *R. padi* and shortened by an average of 0.3 days for *M. persicae* under elevated CO_2 concentration. COVIELLA and TRUBLE (1999) concluded that aphid's lifespan is likely to be extended under elevated CO_2.

Overall, climate change will impact plants and insects. CO_2 enrichment can have dramatic consequences for plants due to acceleration of phenological development, changes in phytochemical, biochemical and biosynthetic processes, which in turn may alter future phytophagous insect populations, behaviour, performance and feeding habits. However, from the work published so far, no clear systematic rules on the mode of action and the direction of responses can be derived; rather, experimental results appear to depend on the particular organisms investigated and the experimental conditions applied in the respective studies. Thus, further studies in this area are highly recommended.

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