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Effects of different atmospheric CO_2 concentrations and soil moistures on the populations of bird cherry-oat aphid (*Rhopalosiphum padi*) feeding on spring wheat

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Key words. CO_2, soil moisture, spring wheat, bird cherry-oat aphid *Rhopalosiphum padi*, population size, chemical composition

Abstract. Spring wheat plants were grown in pots at three CO_2 concentrations (350, 550 and 700 ppm) and three soil water levels (40, 60 and 80% of field water capacity) in field open top chambers and were infested with bird cherry-oat aphids (*Rhopalosiphum padi* Linnaeus). Aphid population dynamics were recorded throughout the growing season and analysis of the chemical composition of spring wheat leaves was conducted at the same time. Results showed that: (1) Aphid populations increased with raised atmospheric CO_2 concentrations. (2) The aphid populations showed different responses to different CO_2 concentrations. The population size, population growth rate and population density found under the 350 ppm CO_2 treatment was far less than those recorded under the 550 and 700 ppm CO_2 treatments. The population size, population growth rate and population density recorded under the 700 ppm CO_2 treatment was slightly higher than those recorded under the 550 ppm CO_2 treatment. (3) The effect of CO_2 concentration on the aphid population was correlated with soil water level. The highest aphid population size was achieved under the 60% soil water treatment. (4) Atmospheric CO_2 and soil moisture had significant effects on the chemical composition of the wheat leaves. (5) Aphid population size correlated positively with the concentration of leaf water content, soluble proteins, soluble carbohydrates and starch, while correlating negatively with the concentration of DIMBOA and tannin.

INTRODUCTION

Atmospheric CO_2 concentrations have increased by about 30% since the beginning of the industrial revolution and are predicted to double during the 21st century (Houghton et al., 1996; Watson et al., 1996). This increase along with projected rises in other "greenhouse" trace gases is likely to cause changes in precipitation patterns in the next 50–70 years (Washington & Meehl, 1984; Wilson & Mitchell, 1987). The frequency of extreme climate events such as heat and drought stresses is also predicted to increase (Mearns et al., 1984).

There is a substantial body of research focusing on the effects of elevated CO_2 on plant-herbivore interactions, including leaf-chewers (Lindroth et al., 1993; Wu, 1993; Watt et al., 1995; Kinney et al., 1997; Brooks & Whittaker, 1998; Cannon, 1998; Roth et al., 1998; Wang, 1999; Peters et al., 2000; David et al., 2001), sap-suckers (Tripp et al., 1992; Awmack et al., 1996, 1997; Smith, 1996; Docherty et al., 1997; Bezemer et al., 1998, 1999; Cannon, 1998; Diaz et al., 1998; Brooks & Whittaker, 1999; Newman et al., 1999; Joutei et al., 2000; Hughes & Bazzaz 2001), and leaf-miners (Salt et al., 1995; Smith & Jones, 1998). Larvae of leaf-chewers show poor performances under elevated CO_2 concentrations, but the performance of leaf-suckers does not always follow this trend (Bezemer & Jones, 1998). There are fewer studies on the responses of leaf-suckers to different CO_2 concentrations. Studies on the interaction of CO_2 with other climatic factors on insects focus mainly on temperature (Bezemer et al., 1998; Cannon, 1998; Dury et al., 1998; Williams et al., 2000). As far as we are aware there is only one study on how insect-plant relationships are influenced by the interaction of CO_2 and soil water. No change in insect populations was reported (Butler et al., 1986). Precipitation is limited in large parts of the world, and water is and will be a limiting factor for agricultural production in this area and many other regions (Zhao, 1996). As interactions of CO_2 and soil water alter many traits of plants (Jiang, 1995; Lin, 1998; Wang, 1999; Korner, 2000; Wu & Wang, 2000), we propose that the interactions of CO_2 and soil water would probably change the performance of insects feeding on these plants, but the tendency is not clear. In this experiment, spring wheat was grown in a factorial design with three CO_2 concentrations and three soil water levels, and plants grown in each of the nine treatments were infested with bird cherry-aphids (*Rhopalosiphum padi* Linnaeus). The aims of this experiment were: (1) to evaluate the responses of the bird cherry-oat aphid to different CO_2 concentrations; (2) to evaluate the interactions of CO_2 and soil water treatments on the population of bird cherry-aphid, and (3) to find the relationships between the alterations of aphid population and the changes of wheat chemical compositions.

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TABLE 1. The nine treatments and their symbols used in the paper.

Treatments		CO_2 concentration		
		350 ppm (c3)	550 ppm (c5)	700 ppm (c7)
Soil water level	FWC 40% (w4)	c3-w4	c5-w4	c7-w4
	FWC 60% (w6)	c3-w6	c5-w6	c7-w6
	FWC 80% (w8)	c3-w8	c5-w8	c7-w8

Notes. The nine treatments consisted of factorial combinations of three CO_2 concentrations (700, 550 and 350 ppm) and three soil water levels (80%, 60% and 40% of field water capacity, FWC). 350 ppm CO_2 represents the ambient CO_2 concentration, 700 ppm CO_2 represents double the ambient CO_2 concentration, and 550 ppm CO_2 represents the doubled pre-industrial CO_2 concentration. 80% FWC represents the favorable soil water level, 60% FWC represents moderate drought conditions, and 40% FWC represents severe drought conditions.

MATERIALS AND METHODS

Experimental design. This experiment was conducted in 1999 and 2000 respectively in field Open-Top Chambers (OTCf) (ϕ1.5m × 2m) at Lanzhou (103.9°E, 36.0°N), Gansu, in the semi-arid region of Loess Plateau of China as described previously (Wu & Wang, 2000). The experiment consisted of nine treatments with factorial combinations of three CO_2 concentrations (700, 550 and 350 ppm) and three soil water levels (80, 60 and 40% of field water capacity, FWC). All the treatments of factorial combinations and the corresponding symbols used in the paper are listed in Table 1. Nine OTCf were used in the experiments: three with ambient CO_2 concentrations (a seasonal average of 350 ppm), three with 550 ppm CO_2 and three with 700 ppm CO_2. Three soil water levels, 80%, 60% and 40% FWC, were applied to each chamber. Host plant seeds were sown in plastic pots, and there were six pots for each treatment: three were assigned for the record of aphid population dynamics and three for the analysis of plant chemical composition. In terms of each OTCf, six pots were placed in it, with three groups of two for each water treatment. Of the two pots in each group, one was assigned for the record of aphid population dynamics and one for the analysis of plant chemical composition.

Plant materials and growth conditions. Seeds of the local commonly-used spring wheat, "Longchun 292", were purchased from the Crop Institute of Gansu Agriculture Academy and sown on March 22 in brown plastic pots (33 cm in diameter, 30 cm in height) filled with loessial soil, with 50 seeds per pot. When seedlings emerged from the soil, they were thinned to 30 stems per pot. Fertilizer (compound fertilizer, carbamide and ammonium phosphate) was applied prior to planting to reach the local favorable nutrient level. The soil was then sampled and analyzed for its chemical composition. The soil properties were: pH 7.8, organic matter 3.4%, available N 171.9 mg kg^{-1} (i.e. hydrolic N, 1 N NaOH hydrolysis), available P 209.8 mg kg^{-1} (0.5 M $NaHCO_3$ extraction), available K 224.6 mg kg^{-1} (1N CH_3COONH_4 extraction), field water capacity 30%. The soil was irrigated to 80% of field water capacity (FWC) before sowing. On April 12 (20 days after sowing) all the planted pots were put into OTCf for CO_2 treatment and control of water. As wheat seedlings cannot survive under the severe drought until the tri-blade stage, and CO_2 and soil water treatment should both begin at the same time in the experiment, we conducted the treatment at the tri-blade stage (20 days after sowing).

CO_2 was supplied from three 2.5 t storage tanks with vaporization facilities. Elevated atmospheric CO_2 was maintained for the whole experimental season. CO_2 concentrations were continuously monitored using a CO_2 infrared gas analyzer (CID, USA) and controlled by a computer. Individual blowers made the air inside each chamber change twice per minute. A WHM3 thermo-hygrograph (Tianjin, China) was fixed to each chamber to continuously record temperature and relative humidity.

The soil water contents were controlled by the "weight method" as reported in Wu & Wang (2000). The soil water content and soil field water capacity were measured before sowing. The total control weight for each experiment pot was the sum of the pot weight, soil dry weight in it and the expected soil water content level. The pots were weighed every other day and supplemented with a determinate quantity of water calculated from the controlled weight minus the actual weight. In the later growth stage of wheat the pot control weight was corrected by adding total plant wet weight in each pot to its initial control weight. To minimize the position effects, the places of pots were changed when the pots were weighed. The soil in the pots were sampled and analyzed. Fertilizers were added every 10 days.

Aphid infestation and population dynamics record. The wheat aphid used in the experiment was the bird cherry-oat aphid *Rhopalosiphum padi* Linnaeus. This aphid species is widespread in China. In the area north of the Huai River, they oviposit on *Malus* plants in winter and immigrate on to cereals in early spring after reproduction (Huang et al, 1978; Anonymous, 1981). The experimental aphids were collected from other wheat in the fields as soon as they arrived and were then reared on wheat "Longchun 292", which was the same cultivar as the treatment wheat in the OTCf and was planted in the field under normal conditions. On May 15, apterous adult aphids were selected to infest the treated wheat, with 15 aphids per pot. Every pot was covered with a nylon net to prevent the aphids escape. Five days after infestation, the aphid number on wheat in each of the three pots of each treatment was counted at intervals of three or seven days. We counted the aphid numbers on all 10 wheat stems per pot each time. The mean value of the 10 records for each pot was regarded as one replicate, so the total number of replicates for the population parameters of each treatment was three.

Plant chemical composition assays and above ground biomass measurement. Wheat leaves were sampled on May 29 and stored in liquid nitrogen for 3 hours and then transferred to a –50°C freezer for later analysis of plant chemical composition. Foliar water content was measured gravimetrically. Soluble carbohydrates, starch, cellulose were analyzed according to Lao (1988) as follows: Plant leaf samples were freeze-dried and ground to a fine powder, then extracted with 80% ethanol at 80°C for 20 min. The mixtures were filtered and the filtrates were used for the analysis of soluble carbohydrates using anthrone reagent. The residuals were hydrolyzed with 2% HCl (36% HCl was regarded as 100%) at 100°C for 3.5 hours, neutralized with 2% NaOH, filtered, and the filtrates were used for the analysis of starch using the anthrone method. The residuals were hydrolyzed with 40% HCl at 100°C for 3.5 hours, neutralized with 40% NaOH, filtered, and the filtrates were used for the analysis of cellulose using the anthrone method. Glucose was used as a standard. Nonstructural carbohydrate (NSC) = soluble carbohydrates + starch. Soluble proteins were analyzed according to Kinney et al. (1997). Tannin was analyzed using the F-D method (Lao, 1988). The F-D reagent was prepared as follows: $Na_2WO_4.2H_2O$ (100 g), $H_2[P(Mo_2O_7)_6].xH_2O$ (20 g) and H_3PO_4 (50ml) were added to 750 ml water, circulized for 2 hours, and added with water to a volume of 1000 ml after the

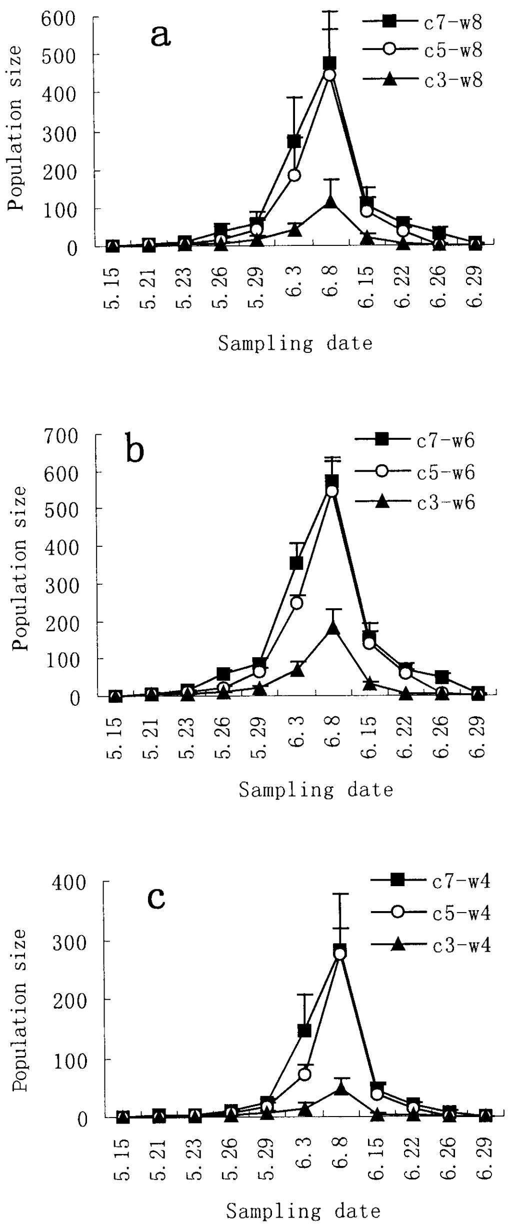

Fig. 1. Effects of CO_2 and soil water on the population dynamics of bird cherry-oat aphid (*Rhopalosiphum padi*) raised on spring wheat "Longchun 292" in open top chambers with different CO_2 concentrations in 1999. a – 80% FWC treatment; b – 60% FWC treatment; c – 40% FWC treatment.

Notes. 1. c7-w8 represents the 700 ppm CO_2 and 80% FWC treatment, the other are analogous to c7-w8 (see Table 1). 2. Data are presented as means ± sd.

solution was cooled. For the analysis of tannin contents, 0.5 g of plant leaf sample was clipped to pieces, added to 50 ml water, maintained at 60°C for 12 hours and then the mixture was filtered. The filtrate was collected, and the residual sample was extracted with 30 ml water at 80°C for 20 minutes and filtered. This process was repeated several times until the filtrate did not display a blue or green colour with 1% $FeCl_3$. All the filtrate was collected and added to water to a total volume of 250 ml. 2 ml of this filtrate was added to 5 ml F-D reagent, 10 ml Na_2CO_3 saturated solution and 83 ml water to a total volume of 100 ml. The OD value was calorimetrically recorded at 760 nm after 30 minutes. Tannic acid was used as standard. DIMBOA (cyclic hydroxamate) was analyzed according to the method reported by Long & Routley (1974).

TABLE 2. ANOVA analysis for population dynamics parameters of aphid *R. padi* under interactions of different CO_2 concentration and soil moistures in 1999.

Variates	Replicates	Factors	df	F	p
Population dynamics	3	CO_2	2	23.78	**
		water	2	13.46	**
		CO_2*water	4	20.49	**
Population size	3	CO_2	2	33.71	**
		water	2	7.26	**
		CO_2*water	4	5.09	**
Population density	3	CO_2	2	40.77	**
		water	2	10.97	**
		CO_2*water	4	5.62	**
Population growth rate	3	CO_2	2	16.44	**
		water	2	6.54	**
		CO_2*water	4	0.61	NS
Net increases in population size	3	CO_2	1	21.29	**
		water	2	11.13	**
		CO_2*water	2	2.93	*
Net increases in population density	3	CO_2	1	43.57	**
		water	2	9.21	**
		CO_2*water	2	10.87	**

Notes. * – significant at 0.05 level; ** – significant at 0.01 level; NS – not significant.

At harvest on July 6, the above ground biomass of wheat was measured gravimetrically. We weighted 5 stems in every pot. The mean value of the five stems biomass in each pot was regarded as one replicate, so the total number of replicates was three.

Statistical analysis. The statistical analysis was performed using the SPSS package. One-way ANOVA was used to detect the effects of CO_2 on the population dynamics. Two-way ANOVA was used to detect the effects of CO_2 and soil moisture, and their interaction for all variates. The population size (N) was defined as the aphid number per wheat stem. Population growth rate (r) was calculated according to the formula: $r = (\ln (Nf/Ni))\ \Delta t^{-1}$ (Casaretto & Corcuera, 1998), where Nf and Ni are the final and initial number of individuals, respectively, and Δt, time in days. Population density (D) was defined as the aphid number per gram of plant dry weight and was calculated by dividing the aphid number by the aboveground dry weight of wheat. The values of population size, population growth rate and population density used in the analysis were the mean for the corresponding observations recorded during the days from May 21 to June 8. The correlations between the population size and the plant chemical composition were also analyzed.

RESULTS

Effects of atmospheric CO_2 concentration and soil moisture on the populations of *R. padi* in 1999

Population dynamics. As shown in Table 2 and Fig.1, the population size increased after infestation and reached maximum size on June 8 (grain-filling stage), then declined as the wheat was going into the maturing stage.

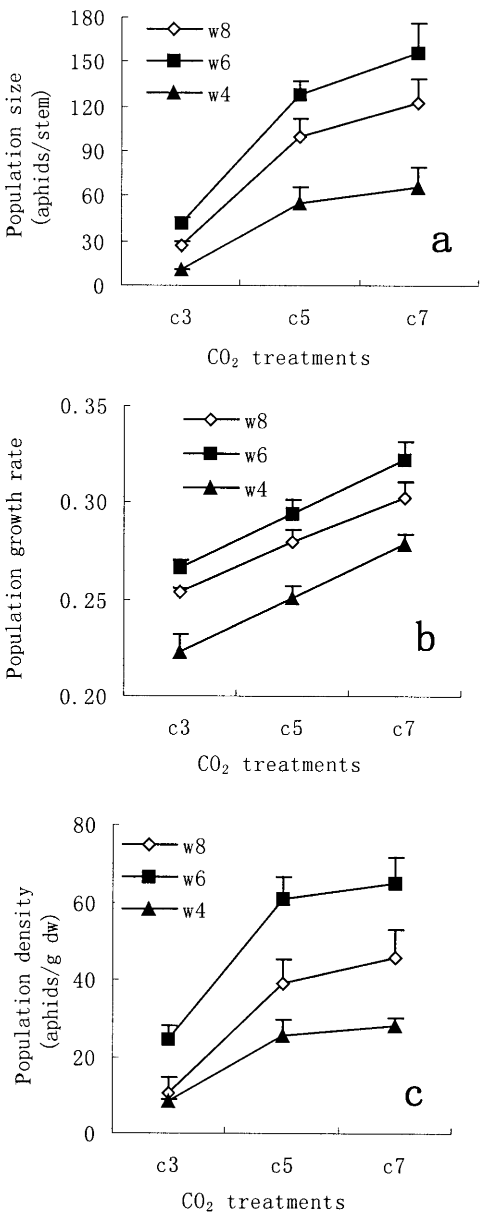

Fig. 2. Interaction of CO_2 and soil water on a – mean population size; b – mean population growth rate and c – mean population density of bird cherry-oat aphid (*Rhopalosiphum padi*) in field open top chambers in 1999.

Notes. 1. c3, c5 and c7 represent 350, 550 and 700 ppm CO_2 treatment; w80, w60 and w40 represent 80%, 60% and 40% FWC treatments. 2. Data are presented as means ± sd.

The curves of the population dynamics of the c3 treatment were far below those of the c5 and c7 treatments ($p < 0.01$), and the curves of the population dynamics of the c5 treatment were slightly below that of the c7 treatments under every soil water treatment ($p < 0.05$). The results listed in Table 2 indicate that the effects of CO_2 and soil water on the population dynamics were significant.

Population size. Aphid population size increased with increasing CO_2 concentration and showed a positive response to CO_2 enrichment under every soil water treatment (Fig.2 a) (Table 2). Aphid population size for treatment Nc3 was far less than that for Nc5 and Nc7 ($p < 0.01$) (Nc3, Nc5, Nc7 represent the population size under 350, 550 and 700 ppm CO_2 treatment, respectively), and that for Nc7 was slightly more than that for Nc5 ($p < 0.05$) (Table 2). These trends were observed under the conditions of all three FWC treatments. The effect of soil moisture on aphid population size was significant ($p < 0.01$). The aphid population size for Nw4 was far less than that for Nw6 and Nw8 ($p < 0.01$) (Nw4, Nw6 and Nw8 represent the aphid population sizes under 40%, 60% and 80% FWC treatment, respectively), and that for Nw6 was higher than that for Nw8 ($p < 0.01$), under all three CO_2 treatments. The results also indicated significant interactions between CO_2 and soil moisture on aphid population size ($p < 0.01$) (Table 2).

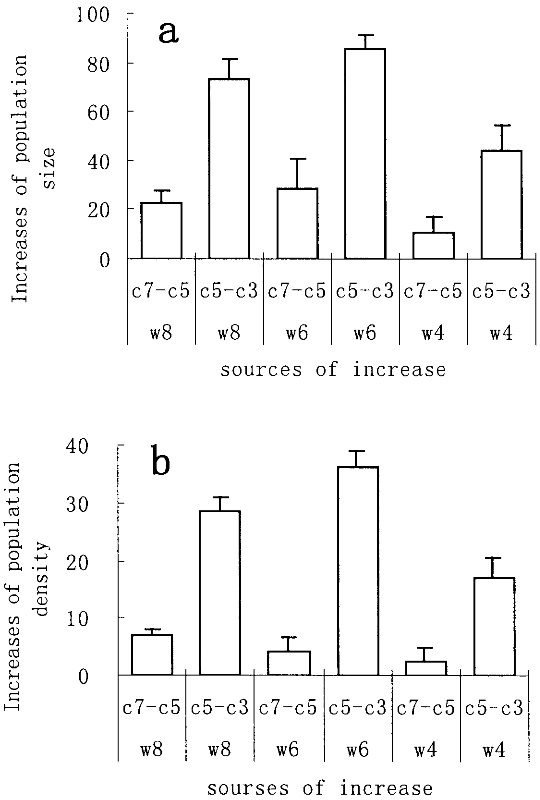

Fig. 3. Effects of CO_2 and soil moisture on net increases in a – population size and b – population density of bird cherry-oat aphids (*Rhopalosiphum padi*) in field open top chambers in 1999.

Notes. 1. c7-c5 w8 represent the increases when CO_2 concentration increased from 550 to 700 ppm under 80% FWC treatment, the other are analogous to c7-c5 w8. 2. Data are presented as means ± sd.

Population growth rate and population density. The effect of CO_2 and soil water on aphid population growth rate (Fig. 2b) (Table 2) and population density (Fig. 2c) (Table 2) was similar to the effect on mean population size. However, the interaction of CO_2 and soil moisture on the population growth rate was not significant ($p > 0.05$) (Table 2).

Effects of CO_2 and soil water on the net increase of population size and population density. Evident effects of CO_2 on the net increase of *R. padi* population size and

TABLE 3. Mean population size, density and growth rate of the aphid *R. padi* in 1999 and 2000 under the effects of CO_2 and soil water.

Parameters		Population size		Population density		Population growth rate	
	year	1999	2000	1999	2000	1999	2000
Treatments	c7-w8	121.9 ± 16.9	109.5 ± 16.3	45.9 ± 5.1	41.4 ± 5.0	0.30 ± 0.008	0.32 ± 0.020
	c7-w6	155.7 ± 20.7	121.1 ± 7.9	64.9 ± 6.9	50.5 ± 3.3	0.32 ± 0.010	0.33 ± 0.015
	c7-w4	65.3 ± 13.4	58.8 ± 7.1	27.8 ± 2.1	25.0 ± 3.7	0.28 ± 0.015	0.30 ± 0.038
	c5-w8	99.2 ± 12.1	76.9 ± 6.9	39.1 ± 4.2	35.5 ± 9.9	0.29 ± 0.006	0.31 ± 0.018
	c5-w6	127.5 ± 9.2	100.4 ± 12.6	60.6 ± 6.1	47.7 ± 6.0	0.29 ± 0.007	0.33 ± 0.039
	c5-w4	54.5 ± 11.2	49.1 ± 13.7	25.3 ± 4.2	19.6 ± 1.8	0.26 ± 0.011	0.30 ± 0.019
	c3-w8	26.4 ± 3.8	24.2 ± 5.4	10.4 ± 2.2	9.4 ± 2.0	0.25 ± 0.002	0.28 ± 0.011
	c3-w6	41.8 ± 4.1	34.6 ± 6.2	24.4 ± 3.9	20.2 ± 3.6	0.26 ± 0.014	0.28 ± 0.026
	c3-w4	10.6 ± 0.8	9.8 ± 2.0	8.1 ± 0.9	7.4 ± 1.6	0.22 ± 0.009	0.22 ± 0.029
ANOVA		p = 0.139		p = 0.088		p = 0.067	

Notes. 1. Data are presented as means ± sd; 2. c7-w8 presents 700 ppm CO_2 and 80% FWC treatment, the other are analogous to c7-w8, see Table 1.

TABLE 4. ANOVA analysis for leaf chemical composition and above ground biomass of spring wheat "Longchun 292" under interactions of different CO_2 concentration and soil moistures in 1999.

Variates	Replicates	Factors	df	F	p
Soluble proteins	3	CO_2	2	20.74	**
		water	2	15.42	**
		CO_2*water	4	0.91	NS
Soluble carbohydrates	3	CO_2	2	15.19	**
		water	2	19.39	**
		CO_2*water	4	0.95	NS
Starch	3	CO_2	2	31.35	**
		water	2	21.99	**
		CO_2*water	4	3.23	*
Cellulose	3	CO_2	2	40.82	**
		water	2	63.90	**
		CO_2*water	4	4.01	*
NSC	3	CO_2	2	45.94	**
		water	2	38.48	**
		CO_2*water	4	2.95	*
Tannins	3	CO_2	2	7.67	**
		water	2	35.74	**
		CO_2*water	4	0.91	NS
DIMBOA	3	CO_2	2	49.71	**
		water	2	39.97	**
		CO_2*water	4	13.13	**
Water content	3	CO_2	2	11.96	**
		water	2	39.29	**
		CO_2*water	4	0.34	NS
Above ground biomass	3	CO_2	2	28.81	**
		water	2	44.71	**
		CO_2*water	4	2.91	NS

Notes. * – significant at 0.05 level; ** – significant at 0.01 level; NS – not significant.

density were observed. The net increase in population size (Fig. 3a) and density (Fig. 3b) for CO_2 concentrations increasing from 350 to 550 ppm were much larger than those for CO_2 concentrations increasing from 550 to 700 ppm ($p < 0.01$) (Table 2). Moreover, the net increases in population size and density reached under the 60% soil water treatment was the greatest found in the three soil water treatments when CO_2 concentrations increased from 350 ppm to 550 ppm (Fig. 3a, 3b).

Comparing population parameters between 1999 and 2000

The effects of CO_2 and soil water on aphid population size, density and growth rate were similar, although the population parameters for 2000 were slightly lower than those for 1999; the difference was very small ($p > 0.05$) (Table 3).

Effects of CO_2 and soil water on chemical compositions of wheat leaves and on the above ground biomasss in 1999

Foliar water content (Fig. 4a), soluble proteins (Fig. 4b), soluble carbohydrates (Fig. 4c), starch (Fig. 4d), cellulose (Fig. 4e) and nonstructural carbohydrates (NSC) (Fig. 4f) increased with CO_2 concentration ($p < 0.01$) (Table 4). The highest content for tannin was obtained under the c5 treatment and the lowest was obtained under the c3 treatment (Fig. 5a). DIMBOA content was highest under the c5 treatment and the lowest under the c7 treatment (Fig. 5b). Foliar water content (Fig. 4a), soluble proteins (Fig. 4b), soluble carbohydrates (Fig. 4c), starch (Fig. 4d) and nonstructural carbohydrates (NSC) (Fig. 4f) content increased and cellulose content (Fig. 4e) decreased with soil moisture. Tannin content increased with the rising of soil moisture (Fig. 5a). DIMBOA content was the lowest under w6 treatment and the highest under w4 treatment (Fig. 5b).

Biomass increased with the CO_2 concentration and soil water (Fig. 5c) ($p < 0.01$). The interaction between CO_2

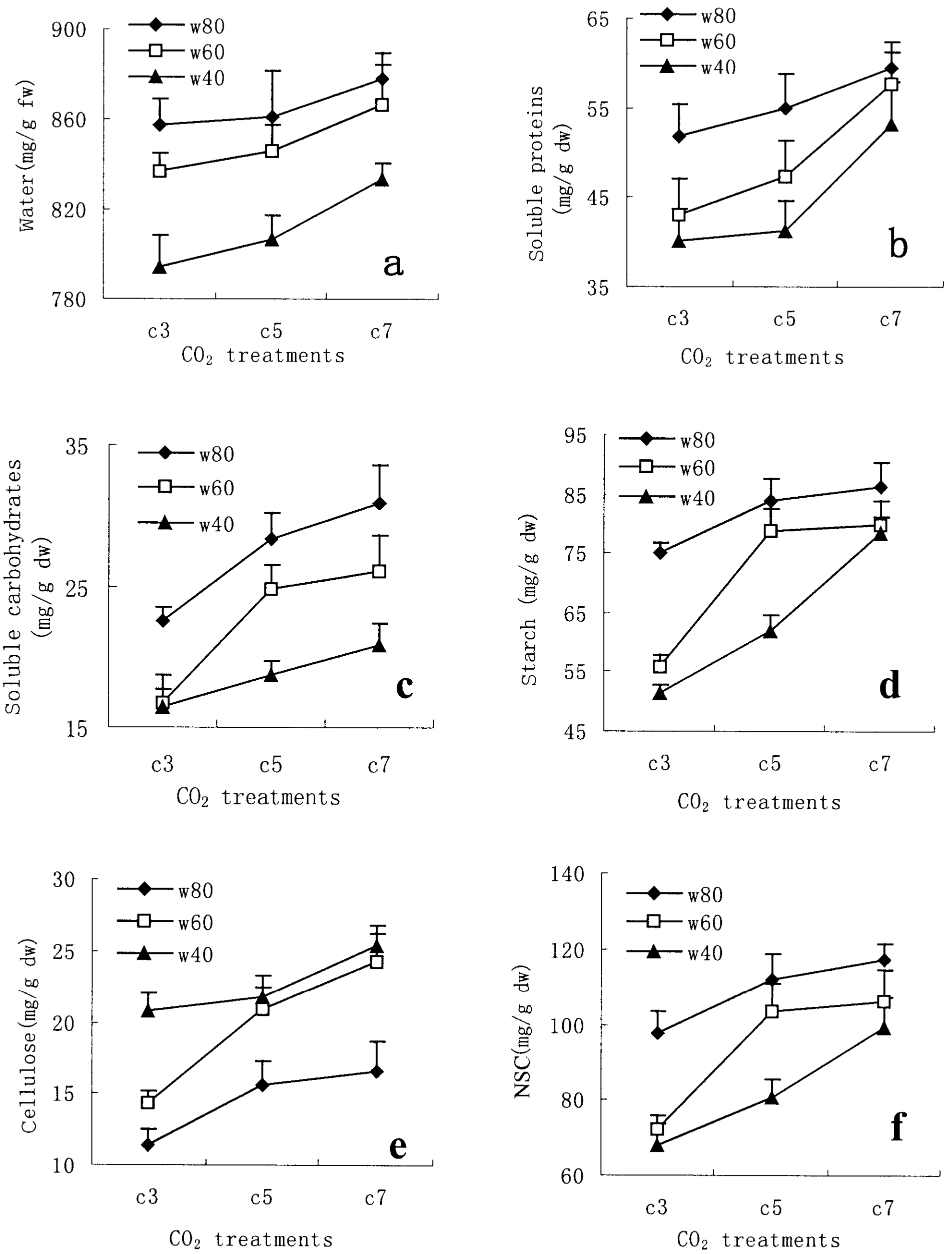

Fig. 4. Effects of CO_2 concentrations and soil moisture on leaf water content (a), soluble proteins (b), soluble carbohydrates (c), starch (d), cellulose (e) and nonstructural carbohydrates (NSC) (f) in spring wheat leaves.

Notes. 1. c3, c5 and c7 represent the 350, 550 and 700 ppm CO_2 treatments; w80, w60 and w40 represent the 80%, 60% and 40% FWC treatments. 2. Data are presented as means ± sd.

and soil water on biomass was not significant ($p > 0.05$) (Table 4).

Relationships between aphid population size and the chemical composition of wheat leaves

Aphid population size showed a positive correlation with wheat water content, soluble proteins, soluble carbohydrates, starch and nonstructural carbohydrates, and a negative correlation with DIMBOA, and no correlation with cellulose or tannin concentrations (Table 5).

DISCUSSION

CO_2 enrichment enhanced the rate of population increase of bird cherry-oat aphid under three soil water levels in our experiment. The observation that, under normal soil water conditions, the population size of bird cherry-oat aphid increased with raised CO_2 concentration was consistent with several previous reports (Smith, 1996; Awmack et al., 1996, 1997; Bezemer et al., 1998), but did differ from some other reports (Thompson et al., 1993; Docherty et al., 1997; Diaz et al., 1998; Bezemer et al., 1999; Newman et al., 1999; Hughes & Bazzaz, 2001). Bezemer et al. (1999) found that the response of aphids to CO_2 concentration was influenced by host plant and aphid species. Newman's experiment and the present results also support this conclusion. Both experiments studied the response of bird cherry-oat aphid to elevated CO_2

TABLE 5. Pearson Correlation coefficients between population size of *R. padi* and the chemical composition of the wheat leaves under interactions between different CO_2 and soil moisture treatments in 1999.

Leaf constituents	Correlation coefficient (r)	Significance (p)
Water content	0.599	**
Soluble proteins	0.626	**
Soluble carbohydrates	0.674	**
Starch	0.706	**
Cellulose	0.318	NS
Nonstructural carbohydrates	0.722	**
Tannins	0.303	NS
DIMBOA	–0.637	**

Notes. ** – correlation is significant at the 0.01 level (2-tailed); NS – not significant.

concentrations, but in Newman's experiment the host plant was endophyte-free *Festuca arundinacea* var. Kentucky-31 and the population size of bird cherry-oat aphid decreased in elevated CO_2 concentrations.

In addition, in this study the population size of bird cherry-oat aphid showed varying responses to different CO_2 concentrations. The population size, population growth rate and population density under the 350 ppm CO_2 treatment were far less than those found under the 550 and 700 ppm CO_2 regimes, but the population size, population growth rate and population density under the 700 ppm CO_2 treatment were slightly higher than those under the 550 ppm CO_2 treatment. This meant that the population of bird cherry-oat aphid would grow more quickly when CO_2 concentrations increased from 350 to 550 ppm than that found when CO_2 concentrations further increased from 550 to 700 ppm. Why did this happen? The reason might be attributed to the effects of CO_2 concentrations on plants. Since elevated CO_2 concentration alters many traits of plants, such as photosynthesis and water use efficiency (Jiang, 1995; Korner, 2000; Wu & Wang, 2000), as well as plant chemical composition (Lincoln et al., 1993; Goudriaan & Zadoks, 1995; Lin, 1998; Wang, 1999). As aphids are phloem feeders, they should show altered responses to the changes in the plant chemical composition.

The effects of CO_2 concentration on the aphid population were correlated with soil water. We found that in ambient CO_2 concentrations the population size, population density and population growth rate of aphids reared under moderate drought conditions were higher than those reared under favorable soil water and severe drought conditions. This observation is consistent with those observed in previous works (Wearing & van Emden, 1967; Braun & Fluckiger, 1984; Mattson & Haack, 1987; Riedell, 1989). Raising CO_2 concentrations did not alter this tendency but made it more obvious. Aphid population size, population density and population growth rate had their highest values at 700 and 550 ppm CO_2 in 60% FWC in all the nine treatments. The net increase in population density under the 60% FWC treatment was higher than the values found under the 80% FWC and 40% FWC treatments when CO_2 concentrations increased from 350 to 550 ppm. The net increase of population size under the 60% FWC treatment was higher than those under the 80% and 40% FWC treatments when CO_2 concentrations increased from 550 to 700 ppm. These results suggest that bird cherry-oat aphid populations grow quickly with increased CO_2 concentrations in arid and semiarid conditions.

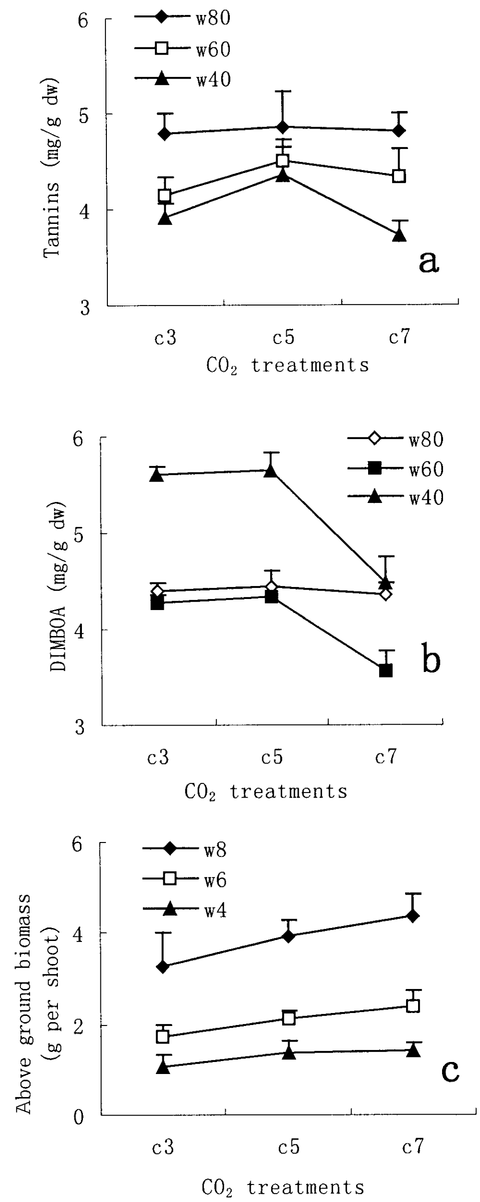

Fig. 5. Effects of CO_2 and soil moisture on a – tannin contents; b – DIMBOA content of leaves and c – above ground biomass of spring wheat "Longchun 292".

Notes. 1. c3, c5 and c7 represent the 350, 550 and 700 ppm CO_2 treatments; w80, w60 and w40 represent the 80%, 60% and 40% FWC treatments. 2. Data are presented as means ± sd.

As plants are foods and habitats for aphids, CO_2 enrichment and soil water might indirectly affect aphid performance (i.e. fecundity, development time and survival) through direct effects on plant traits (i.e. physical structure, chemical composition). In this experiment, we found the general tendency that the population size of the bird cherry-oat aphid showed a positive correlation with the plant water contents, soluble proteins, soluble carbohydrates and starch, and showed a negative correlation with DIMBOA and no correlation with cellulose and tannin. There are a lot of studies proving the importance of soluble proteins and soluble carbohydrates as the basic nutrients for aphids (Auclair, 1963; Qin, 1987). Mattson (1980) reported that the growth, oviposition ability or population size of many insects increased with the nitrogen abundance of their hosts. He et al. (1991) also found that the availability of total soluble nitrogen and soluble carbohydrates was beneficial to aphids, and that the contents of total soluble nitrogen and soluble carbohydrates were negatively correlated with aphid-resistance ability in sorghum. Our results suggest that aphid population size increased with the concentration of soluble proteins, soluble carbohydrates and starch and also indicated the close relationship between aphid population size and nutrient availability. CO_2 and soil water affected aphid population size partly through their effects on plant nutrients. DIMBOA (cyclic hydroxamate) is one of the plant flavonoids and its aphid resistance role has attracted some attention (Argandona et al., 1980, 1981; Copaja et al., 1999). We found that aphid population size was negatively correlated with the foliar DIMBOA content under the 60%, 40% FWC and 700 ppm CO_2 treatments. On the other hand, aphid population size was not negatively correlated with the foliar DIMBOA content under the 550 and 350 ppm CO_2 treatments, and it seemed that aphid population size had less correlation with the concentration of tannin. We hypothesize that this phenomenon may be explained by the different effects of primary and secondary metabolites on aphids. Suppose that the question of whether plant tissues would be the ideal food for insects is determined firstly by its nutrients content and secondly by the quality and quantity of the plant's secondary metabolites. The content of primary substances (soluble proteins, soluble carbohydrates and starch) in the wheat leaves under the 40% FWC or 350 ppm CO_2 treatments was lower than those found in the leaves under the 60% and 80% FWC or 550 and 700 ppm CO_2 treatments. Whether the content of secondary metabolites was high or not, the leaves under the 40% FWC or 350 ppm CO_2 treatments would not be ideal for aphids in respect of nutrients, and the aphid population sizes were low under these treatments. Then we consider the leaves with high nutrients under the 60% and 80% FWC or 550 and 700 ppm CO_2 treatments, and we find that aphid population size was negatively correlated with the concentrations of DIMBOA ($r = -0.91$, $p < 0.001$) and tannin ($r = -0.92$, $p < 0.001$).

In conclusion, we studied the effects of different CO_2 concentrations and soil water content on the population dynamics of the bird cherry-oat aphid *R. padi*, in Open Top Chambers. Under the experimental conditions, aphid population size increased with CO_2 concentrations increasing from 350 ppm to 700 ppm. In addition, the aphid populations showed different responses to the range of the CO_2 concentration. The population size, population growth rate and population density under the 350 ppm CO_2 treatment was far less than those under the 550 and 700 ppm CO_2 treatments, but the population size, population growth rate and population density under the 700 ppm CO_2 treatment were slightly higher than those under the 550 ppm CO_2 treatment. We deduced that the population of bird cherry-oat aphid would grow quickly when CO_2 concentration increased from 350 to 550 ppm and then grow more slowly when CO_2 concentrations further increased from 550 to 700 ppm. The effects of CO_2 concentration on the aphid population were correlated with the soil water level. The highest aphid population size was achieved under the 60% soil water treatment. Meanwhile, the chemical composition of wheat leaves was altered profoundly by the interaction between CO_2 and soil water. We deduce that this interaction is important in explaining the different responses of aphid populations to different CO_2 concentrations and soil water.

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