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Effects of Elevated Ozone on Yield and Carbon Allocation in Strawberry Cultivars Differing in Developmental Stage

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S u m m a r y

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The effects of elevated ozone (O_3) on yield, growth, photosynthetic rate, whole-plant ^{14}C-allocation and biomass of two strawberry (*Fragaria x ananassa* Duch.) cultivars were investigated. The two cultivars (Bogota and Elsanta) were at the beginning and end of fruiting, respectively, when exposed to 74 ppb ozone (O_3) (8-h day^{-1}) for 7 and 11 weeks, respectively, in open-top chambers. O_3 reduced yield without affecting growth and biomass in cv. Bogota. The photosynthetic rate was lower in O_3 in cv. Bogota and there was a trend that increased ^{14}C-allocated after 24-h to developing leaves in O_3. In post-fruiting Elsanta, O_3 did not significantly affect the photosynthetic rate, growth and above-ground biomass. However, root biomass was significantly lower in O_3; O_3 also caused an increase in ^{14}C-allocated after 27 days to the old leaves.

Introduction

Tropospheric ozone (O_3) is a phytotoxic gaseous pollutant which is not confined to large metropolitan areas, but transported long distances to rural areas such that many of the world's most productive agricultural regions are affected (CHAMEIDES & al. 1994). O_3 at current ambient levels has been shown to reduce

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growth and yield in many agronomic crop and fruit trees (e.g. COOLEY & MANNING 1987, RETZLAFF & al. 1997). The magnitude of ozone effects on growth and yield has frequently been related to the timing of ozone exposure. In wheat, ozone sensitivity is higher between flowering and seed maturity than before anthesis (AMUNDSON & al. 1987, LEE & al. 1988, SOJA 1996, PLEIJEL & al. 1998, MEYER & al. 1997, GELANG & al. 2001). Similar growth stage dependent effects on yield and growth were also shown in bean (BLUM & HECK 1980, KOHUT & LAURENCE 1983, YOUNGLOVE & al. 1994, VANDERMEIREN & al. 1995), tomato and alfalfa (YOUNGLOVE & al. 1994).

Although it is clear that the partitioning priorities during the lifespan of a crop play a significant role in O_3 effects on yield, little is known about whether this is mediated by negative effects on photosynthesis and/or carbon allocation. The findings of MCKEE & LONG 2001 highlight the importance of carbon allocation processes rather than the accompanying decline in photosynthesis and biomass accumulation, in the effects of elevated O_3 on wheat yield. However, few efforts have yet been made to elucidate the importance of allocation processes and the timing of O_3 stress in perennial fruit species. The fast growth habit and great demand for carbon to accommodate fruit yield, initiate flower buds and also sustain the next year's growth may alter the effects of elevated O_3 in perennial fruit species, compared with annual crop and vegetable species. The objective of the present study was to investigate the effects of O_3 on yield, photosynthesis and carbon allocation in two strawberry cultivars Elsanta and Bogota, differing in developmental stage because they were early and later fruiting cultivars. These cultivars were previously classed as resistant and sensitive, respectively, to elevated O_3 (8-h mean 85 ppb, for 41 days) in a closed chamber fumigation study on the basis of effects on photosynthetic rate and plant biomass (DROGOUDI & ASHMORE 2002).

Material and Methods

The experiment was carried out in eight open-top chambers (OTCs) arranged in pairs, four receiving O_3 and four receiving filtered air. Each chamber was 1.5 m high and 1.5 m in diameter. Ambient air was pumped through charcoal filters into each pair of chambers. O_3 was distributed to four chambers, entering the air supply after the filters. Air samples were taken from the centre of all O_3 fumigation chambers and one of the filtered air chambers and O_3 concentration was recorded for 10-min each hour. Details of the fumigation conditions are described in DROGOUDI & ASHMORE 2000. Cold stored, 1-yr-old crowns of the strawberry (*Fragaria x ananassa* Duch.) cultivars Bogota and Elsanta (RW Walpole Ltd. Norfolk, UK) were planted in 7.5-l pots containing a multipurpose Levington compost, and grown in a glasshouse for 40 days at a temperature of approx. 18 ^{0}C. Plants were transferred outdoors to acclimatize for four days and then they were randomly allocated to each of eight OTCs (28 plants, 3-4 per chamber in Bogota and 40 plants, 5 per chamber in Elsanta), four receiving filtered air and four O_3. Throughout the experimental period stolons were removed as soon as they appeared. The O_3 fumigation was carried out between 10:00 h and 18:00 h, from 18 June (day 1) until 2 September (day 78), apart from days on which it rained or it was too windy, when all plants received filtered air. The target O_3 concentration was 80 ppb. Pots were moved to a different position within each chamber every week and moved between replicate chambers within the two treatments every two weeks. All plants received tap water as required though a sprinkle irrigation system positioned 1 m above the vegetation.

The length of each individual leaflet was measured approximately every 15 days. The relative growth rate (RGR) of total leaflet length was calculated from log-transformed data. Mature fruits were harvested when most of their colour was red. The number of fruits, the individual fruit fresh weight, and the total fruit fresh weight harvested from each plant are presented in 8-day interval periods. Gas-exchange measurements were made between 10:30-13:00 hours, after removing the plants from the chambers, using an LCL-1 portable infrared gas analyser (ADC, Hoddesdon, UK) with supplementary light (1100 $\mu mol\ m^{-2}s^{-1}$). Measurements were made on the first or second most recent fully expanded leaf on days 0, 26, 42, 61 and 73. Bogota plants were harvested on day 50 and Elsanta plants were harvested 28 days later. The dry weights of root, crown, petiole and leaf blade were measured, and the above-ground biomass and root:shoot ratio were calculated.

Whole-plant assimilate labeling was made with $^{14}CO_2$ on days 49, 51 and 52 and translocation parameters (sink strength and relative specific uptake) were determined 24-h later in Bogota, which was at a fruiting growth stage and 27-d later in Elsanta, which was at a post fruiting growth stage at the time of ^{14}C exposure. Immediately before ^{14}C labelling all leaves were tagged in Elsanta, so that the ones expanding later could be distinguished. There were six and 10 replicate plants from each treatment for Bogota and Elsanta, respectively. Exposures took place in an enclosed system consisting of a Perspex box (70 x 70 x 80 cm) inside a controlled environment chamber (Sanyo Gallenkamp, Leicestershire, UK) (250 $\mu mol\ m^{-2}\ s^{-1}$ PAR, 20 ^0C, 50% relative humidity). Plants were acclimatized in the fumigation chamber for 4 h. $^{14}CO_2$ was injected into the main air inlet from a cylinder containing $^{14}CO_2$, providing a total of 2294 KBq during a 30-min fumigation. After the $^{14}CO_2$ injection was halted, air was circulated for an additional 30-min and the chamber was vented. The plants were replaced in their previous positions in the OTCs during their post labeling period. At harvest, plants were separated into root, crown, petiole, leaf blade and fruit. In addition, in Bogota leaf blades were separated into fully expanding and not fully expanding. In Elsanta, leaf blades were separated into existing leaf blades at the time of ^{14}C exposure, later expanding leaves, and those showing signs of senescence. ^{14}C specific activity was measured in each plant part as described in DROGOUDI & ASHMORE 2001. Approx. 300 mg dry matter from each plant part was oxidized for 1 min in an automatic sample oxidizer and $^{14}CO_2$ was absorbed in a 20-ml scintillation cocktail and trapped in polyethylene vials. ^{14}C activity was measured by scintillation counting. The amount of ^{14}C recovered from each plant part was calculated as the product of tissue d. wt and specific activity. Total ^{14}C recovered was the sum of ^{14}C recovered in all plant parts. The sink strength of a plant part was calculated as the percentage ^{14}C in this plant part of the total recovered. The relative specific uptake (RSU) was calculated as the percentage ^{14}C recovered in a plant part divided by the percentage of the total dry weight that this plant part represented.

Analysis of variance was performed to test the effect of air quality, using the Statsoft statistical package, Statistica (Statsoft, Tulsa, OK, USA). Results from one filtered air chamber were discarded because plants were eaten by rabbits during the fumigation period. In Bogota, analyses were based upon the replicate plants, because the number of replicates per chamber was variable between chambers. In Elsanta, analyses were based upon the replicate chamber means, calculated from the values of five plants per chamber. ^{14}C allocation analyses were based upon the replicate ^{14}C exposures. For the RGR of total leaf length, analyses were made with repeated measures analysis. Percentage data were arcsine transformed, while the relative specific uptake parameter was log-transformed, prior to analysis.

Results

The fumigation period lasted 47 days (June 18 - August 3, 1997) and 78 days (June 18 - September 2, 1997) in Bogota and Elsanta, respectively. O_3 was applied mainly in July and August, and only during 6 days of June due to rainy weather. In Bogota, O_3 fumigation was carried out on 36 days, resulting in a mean cumulative AOT40 of 9780 ppb.h and in Elsanta, the O_3 fumigation was carried out

on 63 days and the mean cumulative AOT40 was 16369 ppb.h. During the days of O_3 fumigation the 8 h mean daily O_3 concentration in chambers receiving O_3 was 74 ppb. The mean (8 h) O_3 concentration in the one chamber receiving filtered air which was monitored fluctuated according to the ambient air O_3 concentration, providing a mean reduction of 46.9 % in the ambient air O_3 concentration (36.4 ± 2.0 ppb).

There was no significant effect of O_3 on the relative growth rate (RGR) of total leaf length in Bogota and Elsanta and there was no significant interaction between air quality and time (data not shown).

In Bogota, the mean total fruit fresh weight and individual fruit fresh weight were 41% and 30%, respectively, lower in O_3 at the last measurement interval (Table 1). The total numbers of harvested fruits per plant were also lower in O_3, without showing any significant difference between the two air quality treatments. Elsanta fruited mostly during the first two weeks of the fumigation period and there was no significant effect of O_3 on yield parameters (data not shown).

Table 1. Effects of 74 ppb O_3 fumigation for 50 days on the mean total harvested fruit weight, individual fruit fresh weight and number of harvested fruits per plant during the fumigation period, in cv. Bogota.

Harvest interval	Treatment	Total fruit (g fresh weight)[1]	Individual fruit (g fresh weight)[2]	Harvested fruits (number)[1]
Day 18-26	Filtered air	21.96 ± 6.0	10.98 ± 1.0	2.00 ± 0.6
	O_3	20.59 ± 5.5	11.65 ± 1.1	1.77 ± 0.5
	P	0.872	0.673	0.754
Day 27-35	Filtered air	43.51 ± 5.3	13.30 ± 1.2	3.56 ± 0.5
	O_3	32.92 ± 6.5	13.34 ± 1.5	2.77 ± 0.7
	P	0.263	0.982	0.388
Day 36-49	Filtered air	33.16 ± 6.7	9.38 ± 0.6	3.22 ± 0.9
	O_3	19.66 ± 2.5	6.99 ± 0.6	2.15 ± 0.4
	P	0.053	0.010 **	0.224

[1] df = 1, 20; [2] df = 1, 15-17. Values represent means ± SE; significant differences: $^{**}P<0.01$

In Bogota, the rate of photosynthesis decreased 15% in O_3 only on the last measurement day; this was significant at 10% level (P=0.075) (Fig. 1). In Elsanta, the rate of photosynthesis did not significantly differ between treatments on all measurement days.

In Bogota, the biomass of different plant parts and root:shoot ratio were not significantly affected by O_3 fumigation (Table 2). In Elsanta, O_3 significantly reduced the root dry weight by 15%, but there was no significant effect of O_3 on the biomass of the other plant parts and root:shoot ratio.

In Bogota, the sink strength of developing leaves was 32% higher in ozone, while that of the petioles was 30% higher; both these effects were only significant

at 10% level (P=0.086 and 0.099) (Table 3). There was no significant effect of ozone on the sink strength of the other plant parts (Table 3) and the relative specific uptake of all separated plant parts (data not shown). However, the data suggest that the increased sink strength of developing leaves and petioles was partly at the expense of reduced sink strength of fruit.

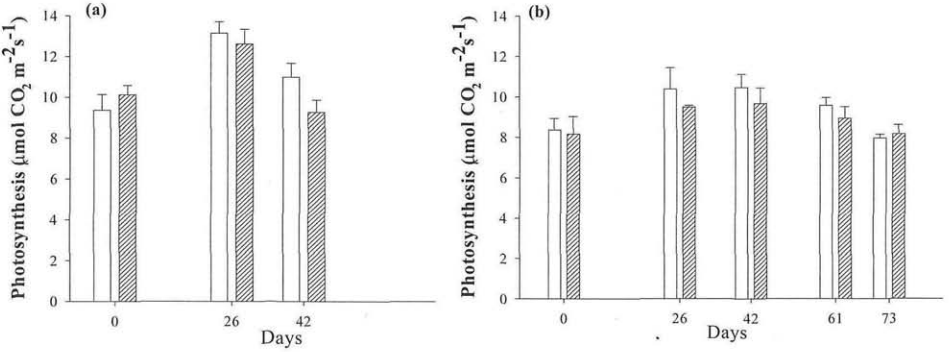

Fig. 1. Effects of O_3 on the rate of photosynthesis (µmol $m^{-2}s^{-1}$) in cvs. (a) Bogota and (b) Elsanta. Measurements were made on the 1st or 2nd most recent fully expanded leaf. Values are means (±SE) of 9 or 13 replicate plants for Bogota and 4 replicate chambers for Elsanta. Open bars represent plants exposed to filtered air, hatched bars represent plants exposed to ozone.

Table 2. Effects of 74 ppb O_3 fumigation for 50 and 78 days, in cvs. Bogota and Elsanta on the mean root, crown, petiole, leaf blade and root/shoot ratio.

	Treatment	Root (g)	Crown (g)	Petiole (g)	Leaf blade (g)	Root/shoot
Bogota	Filtered air	5.4 ± 0.5	1.8 ± 0.1	8.3 ± 0.8	20.6 ± 1.6	0.176 ± 0.00
	O_3	5.2 ± 0.6	1.8 ± 0.2	7.9 ± 0.8	18.3 ± 1.4	0.185 ± 0.01
	P (df= 1, 9)	0.802	0.850	0.768	0.308	0.440
Elsanta	Filtered air	10.1 ± 0.2	3.9 ± 0.1	10.1 ± 0.2	31.0 ± 0.5	0.230 ± 0.01
	O_3	8.6 ± 0.2	3.8 ± 0.1	9.7 ± 0.7	29.2 ± 1.6	0.204 ± 0.01
	P (df= 1, 5)	0.005 *	0.804	0.687	0.406	0.166

Values represent means ± SE; significant differences: *, P<0.05

In Elsanta, the sink strength (Table 3) and relative specific uptake (data not shown) of leaf blades with signs of senescence increased significantly (P<0.05) by 79% and 23%, respectively, in O_3. There was no indication of any O_3 effect on the translocation of assimilates to other plant parts.

Table 3. Effects of O_3 on the sink strength (% dpm) (means ±SE) of different plant parts in cvs. Bogota and Elsanta, after a 24-h and 27-d post-labeling period, respectively.

Treatment	Root	Crown	Petiole	Young leaf blade[1]	Mature leaf blade[1]	Fruit
Bogota						
CF	6.2 ± 1.3	3.2 ± 0.4	12.4 ± 0.7	15.4 ± 1.5	43.6 ± 4.3	19.2 ± 6.9
O_3	6.4 ± 0.9	3.3 ± 0.4	16.0 ± 1.5	20.4 ± 2.2	40.6 ± 3.4	13.4 ± 1.7
P (df=1, 9)	0.842	0.859	0.099	0.086	0.614	0.542
Elsanta						
				Existing leaf blade[1]	Later expand leaf blade[1]	Old leaf blade[1]
CF	13.9 ± 1.5	7.7 ± 0.8	21.5 ± 1.7	3.9 ± 0.5	48.8 ± 1.1	4.2 ± 0.5
O_3	12.8 ± 0.7	7.2 ± 0.7	22.5 ± 1.9	3.0 ± 0.6	47.0 ± 2.2	7.5 ± 1.2
P (df=1,16)	0.545	0.605	0.728	0.252	0.502	0.044

[1]For Bogota, young and mature leaf blades are not fully and fully expanded, respectively, at the time of ^{14}C labeling, for Elsanta, existing and later expanding leaf blades refer to the time of ^{14}C labeling, old leaf blades are those showing signs of senescence.

Discussion

The impacts of O_3 on yield and carbon allocation were determined in strawberry cultivars differing in their initial developmental stage (beginning of fruiting in Bogota and end of fruiting in Elsanta). Yield was decreased in cv. Bogota and the timing of negative effects on yield coincided with a decrease in the photosynthetic rate. However there were no negative effects of elevated O_3 on growth and biomass, suggesting that growth had a partitioning priority over yield. This is supported by the ^{14}C data, which shows a trend of increased ^{14}C-allocation to developing leaves in O_3. Enhanced ^{14}C-assimilate distribution from a source leaf fed with $^{14}CO_2$ to young expanding leaves was previously shown in O_3 treated strawberry cv. Cambridge Favorite (DROGOUDI & ASHMORE 2001). In the present study, the source of ^{14}C-assimilates found in the developing leaves cannot be specified, and it is possible that O_3 had a less negative impact on the photosynthetic rate (and amount of ^{14}C activity) of young leaves compared with mature leaves. A similar mechanism linking growth and yield has also been shown in the response of strawberry to water stress, in which yield was reduced while changes in whole-plant morphology and leaf orientation acclimatized to the water deficit conditions (SAVE & al. 1993).

The O_3-induced decrease in yield was attributed to both a decrease in the individual fruit weight and in fruit numbers, although only the effects on individual fruit weight were statistically significant. The negative effects on yield coincided with the time of O_3 effects on the photosynthetic rate. Previously we also showed that O_3 decreased the individual fruit weight in cv. Cambridge Favorite, although negative effects on the photosynthetic rate were shown 3 weeks before effects on

the individual fruit weight were evident (DROGOUDI & ASHMORE 2000). In both cultivars, the fruits affected were those in the later harvests, which were about 40 days after the day when a mean of 1.5 flowers per plant was first recorded. The strawberry inflorescence shows a strong apical dominance and fruit size is dependent on the amount of available assimilates (JANICK & EGGERT 1968, NISHIZAWA & HORI 1988). Hence, O_3-induced reduction in the available assimilates did not affect the weight of the primary fruits, which had a stronger sink activity, but reduced the individual fruit weight only when the tertiary fruits were harvested. However, the possibility cannot be excluded that the effects on later harvests were due to a cumulative effect of ozone exposure.

Elsanta flowers earlier than Bogota (ANON 1986), and as fruiting occurred before, and at the very beginning of the fumigation period, the lack of any effect of O_3 on yield does not indicate resistance to O_3 in Elsanta. O_3 significantly reduced root biomass without affecting the above-ground biomass, a response that is frequently documented in relevant studies (see COOLEY & MANNING 1987, SANE & al. 1996 for reviews). However, in previous studies on strawberry, O_3 was not reported to reduce root biomass although it reduced yield, vegetative growth and/or above-ground biomass in cvs. Bogota and Cambridge Favorite (DROGOUDI & ASHMORE 2000, 2002). Differences in the developmental stage of the plant material used in the above studies (fruiting) and the present study (post fruiting) may be responsible for this difference.

The ^{14}C assimilate study in Elsanta showed that O_3 significantly increased the sink strength and relative specific uptake in the older leaves showing signs of senescence. This could be attributed to increased retention of carbon and/or a decrease in the remobilization that normally occurs during leaf senescence. Since the lower leaves mainly provide the majority of assimilates to the roots in non-fruiting strawberry (NISHIZAKA & HORI 1986, DROGOUDI & ASHMORE 2001), the observed carbon retention in older leaves would account for the observed decrease in root biomass. Remobilization of stored carbohydrates from the roots to the leaves might also have occurred and contributed to the decrease in the root biomass in response to ozone. This has been shown in potato, where the amount of reducing sugars increased in potato tubers in O_3 treated plants (PELL & PEARSON 1984). It would have been interesting to investigate whether the increased carbon allocation to leaves with signs of senescence coincided with altered nutrient recycling from leaves, since this would have implications for the following year's growth.

There was no significant effect of O_3 on the photosynthetic rate in cv. Elsanta, which agrees with the observations made by KEUTGEN & al. 1997, 1999, 2001 and DROGOUDI & ASHMORE 2002. However, gas exchange measurements were not made on the older leaves, which were exposed to O_3 for a longer time, may have shown a significant reduction in response to O_3, particularly since an altered carbon allocation pattern was evident in these leaves.

In conclusion, O_3 has the potential to decrease yield in strawberry. When exposure started at the beginning of fruiting in cv. Bogota, yield was preferentially decreased in O_3 but there were no negative effects on growth and biomass. Instead an increase in the ^{14}C assimilates in young expanding leaves was found in O_3

treated plants. When O_3 exposure started at the end of fruiting in Elsanta, O_3 decreased the root biomass, and would probably affect the amount of stored carbohydrate available for the next year's growth and yield. An accumulation of ^{14}C assimilates in old senescent leaves was also found in O_3 treated plants.

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