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RESEARCH

Elevated Carbon Dioxide and Ozone Effects on Peanut: II. Seed Yield and Quality

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ABSTRACT

Many adverse effects of tropospheric O_3 on C_3 crop plants are ameliorated by elevated concentrations of atmospheric CO_2, but the extent of the interaction can vary, depending on the species, gas concentrations, and other experimental conditions. A 2-yr open-top field chamber experiment was conducted to examine this interaction in peanut (*Arachis hypogaea* L.) by testing the effects of O_3 and CO_2 mixtures on yield and seed quality. Treatments were ambient CO_2 (375 μmol mol^{-1}) and CO_2 additions of approximately 173 and 355 μmol mol^{-1} in combination with charcoal-filtered (CF) air (22 nmol O_3 mol^{-1}), nonfiltered (NF) air (46 nmol O_3 mol^{-1}), and NF air plus O_3 (75 nmol O_3 mol^{-1}). At ambient CO_2, pod number was suppressed 16% in NF air and 44% in elevated O_3. Pod and seed mass were not significantly affected in NF air but were lowered 33 to 37% in elevated O_3. Elevated CO_2 increased yield parameters 7 to 17% for plants grown in CF air and restored yield in NF air and elevated O_3 treatments to control or higher levels. Gas treatment effects on peanut market grade characteristics were small. No treatment effects were observed on the protein and oil contents of seeds, but there were changes in fatty acid composition. Overall results indicate that increasing concentrations of tropospheric O_3 will suppress yield of O_3–sensitive peanut cultivars, while elevated CO_2 will moderate this response. Elevated O_3 and CO_2 are not expected to have major effects on peanut seed composition and quality.

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Abbreviations: AA, ambient air; CF, charcoal-filtered air; ELK, extra large kernels; NF, nonfiltered air; OZ, 1.56 x ambient O_3; TSMK, total sound mature kernels.

Rising concentrations of atmospheric CO_2 are predicted to increase biomass production and yield of many C_3 crops (Ainsworth and Long, 2005; Jablonski et al., 2002; Kimball et al., 2002). It is expected, however, that the magnitude of these potential gains from CO_2 enrichment will be influenced by possible changes in other environmental factors such as temperature and soil water availability (Ainsworth and Long, 2005; Prasad et al., 2005). Air pollutants, most notably O_3, also influence the effect of elevated CO_2 on crop growth and yield, and vice versa (Allen, 1990; Barnes and Wellburn, 1998; Fiscus et al., 2002; Olszyk et al., 2000). Current tropospheric O_3 levels suppress crop growth and yield in many regions worldwide, and emissions of O_3 precursors and areas affected by O_3 pollution are anticipated to increase (Ashmore, 2005; Dentener et al., 2005; Fiscus et al., 2005; Fuhrer and Booker, 2003; Houghton et al., 2001; Morgan et al., 2003; Prather et al., 2003). Elevated CO_2 concentrations tend to counteract O_3 effects on plant growth and yield, but O_3 can also diminish enhancements in these parameters due to elevated CO_2 (Barnes and Wellburn, 1998; Fiscus et al., 2002; Olszyk et al., 2000). The nature of the interaction depends on the sensitivity of the crop, the gas concentrations, and the influences of other biotic and environmental factors.

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Peanut (*Arachis hypogaea* L.) production is vulnerable to current and predicted higher levels of O_3 pollution in the future. Some peanut cultivars exhibit relatively high sensitivity to O_3 (Ensing et al., 1985, 1986; Heagle, 1989; Heagle et al., 1983). For example, regression modeling based on open-top field chamber experiments indicated that yield of an O_3–sensitive peanut line (NC-6) was suppressed 7 to 14% by ambient O_3 levels (52–56 nmol mol^{-1}, 7 h daily average) relative to control treatments (25–26 nmol mol^{-1}), and even more so by higher O_3 concentrations (Heagle, 1989). Climate model projections forecast that the largest peanut producing regions in the world, located mainly in eastern China, central India, central Africa, the southern United States, and Indonesia (Rhoades and Nazarea, 2003), may experience significantly higher levels of tropospheric O_3 in the coming 50 yr (Dentener et al., 2005; Prather et al., 2003; Wang and Mauzerall, 2004). Rising levels of atmospheric CO_2 will likely moderate the effects of increasing ground-level O_3 concentrations in these regions, but eventual effects on yield in concert with other changing environmental factors are unclear.

Ozone suppresses plant growth and yield in large part by inhibiting net photosynthesis and possibly translocation processes, thus limiting photosynthate availability (Fiscus et al., 2005; Long and Naidu, 2002; Pell et al., 1997; Runeckles and Chevone, 1992). Increases in maintenance respiration and detoxification processes might curtail growth as well (Amthor, 1988). In addition, detrimental effects of O_3 on pollen germination and tube growth, fertilization, and abscission rates of flowers, pods, and seeds can contribute to suppressed yield in some crops (Ashmore, 2005; Black et al., 2000; Runeckles and Chevone, 1992).

Atmospheric CO_2 and O_3 co-occur in the atmosphere. Studies have shown that elevated CO_2 ameliorates the suppressive effect of O_3 on yield in a number of crop species, including cotton (*Gossypium hirsutum* L.), potato (*Solanum tuberosum* L.), rice (*Oryza sativa* L.), soybean [*Glycine max* (L.) Merr.], and wheat (*Triticum aestivum* L.) (Booker and Fiscus, 2005; Booker et al., 2005; Craigon et al., 2002; Fiscus et al., 2002, 2005; Heagle et al., 1999, 2000; Pleijel et al., 2000; Olszyk et al., 2000). Biomass production and yield are likely protected from O_3 stress at elevated CO_2 by reduced O_3 uptake and possibly increased availability of C substrates for detoxification and repair processes (Allen, 1990; Barnes and Wellburn, 1998; Booker and Fiscus, 2005; Cardoso-Vilhena et al., 2004; Fiscus et al., 2002, 2005; McKee et al., 1997b; Olszyk et al., 2000). However, stimulation of putative O_3 detoxification mechanisms by elevated CO_2 has not convincingly been observed to date (Booker and Fiscus, 2005; McKee et al., 1997b). An interaction between elevated CO_2 and O_3 is not always observed, particularly in cases where O_3 levels or crop cultivar sensitivity to O_3 were too low to result in suppressed growth and yield (Bender et al., 1999). Conversely, amelioration of O_3 effects by elevated CO_2 can be marginal in cases where cultivars are extremely sensitive to O_3 so that O_3 damage occurs despite the presence of elevated CO_2 (Heagle et al., 1993, 2002, 2003). It has been suggested that elevated CO_2 did not prevent suppression of wheat yield by O_3 due to direct effects of O_3 on reproductive organs and processes (McKee et al., 1997a; Mulholland et al., 1998).

In this study, we investigated the effects of elevated CO_2 and O_3, administered singly and in combination, on yield and quality of peanut. Because peanut is relatively sensitive to both CO_2 and O_3 when applied individually (Heagle, 1989; Prasad et al., 2005), it was unclear how yield and quality parameters would respond to various mixtures of the gases. Comparisons were also made between plants treated with nonfiltered (NF) air in open-top chambers and plants treated with ambient air in chambers without plastic sidewalls to assess effects of the chambers on yield responses to ambient levels of CO_2 and O_3.

MATERIALS AND METHODS

Plant Culture Conditions and Gas Treatments

The experiment was conducted with peanut, cultivar NC-V11, during 2002 and 2003 at a site 5 km south of Raleigh, NC (35°43′48″N, 78°40′48″W), as described by Booker et al. (2007). The soil consisted of about 30 cm of Norfolk loamy sand (fine-loamy, kaolinitic, thermic Typic Kandiudult) overlying an Appling sandy loam (fine, kaolinitic, thermic Typic Kanhapludult) (Miller et al., 1988). Plants were sown in rows with 1-m spacing and with plant spacing of 9 cm (11 plants m^{-2}). Plants were irrigated as needed to prevent visible signs of water stress. Plots were sprayed to control insects as described in Booker et al. (2007).

Plants were exposed to mixtures of CO_2 and O_3 in cylindrical open-top chambers, 3 m diameter by 2.4 m tall, beginning on 30 May 2002 and 3 June 2003, as described by Booker et al. (2007). The experimental design consisted of all combinations of three CO_2 treatments and three O_3 treatments (Table 1). The CO_2 treatments were ambient CO_2 (375 μmol CO_2 mol^{-1}), ambient plus 173 μmol CO_2 mol^{-1}, and ambient plus 355 μmol CO_2 mol^{-1}. The O_3 treatments were charcoal-filtered (CF) air, NF air, and NF plus 1.56 times ambient O_3 (OZ). Additional chambers were included to test the effects of a higher CO_2 addition, 634 μmol mol^{-1}, added to NF. Plants were also grown in ambient air (AA) within chamber frames lacking panels to assess chamber effects. All CO_2 and O_3 treatments were administered 7 d per week. The treatments continued until 30 Sept. 2002 and 5 Oct. 2003, when plants were harvested. Meteorological conditions and gas concentrations on a monthly basis are shown in Booker et al. (2007).

Harvest Procedures and Quality Analysis

Plots consisted of two 3-m rows. Plants in two 1-m row segments of each of row were unearthed independently with a digging fork.

Table 1. Elevated CO_2 and O_3 treatment concentrations and number of replicate chambers per treatment in each year of the 2-yr experiment. Gas concentrations are seasonal 12 h d^{-1} (0800–2000 h EST) means for the 2-yr experiment.†

Treatment abbreviation	Treatment	[O_3]	[CO_2]	Replicate chambers yr^{-1}
		nmol mol^{-1}	µmol mol^{-1}	
CF-375	CF + ambient CO_2	22	375	3
CF-548	CF + 173 µmol CO_2 mol^{-1}	22	548	2
CF-730	CF + 355 µmol CO_2 mol^{-1}	22	730	3
NF-375	NF + ambient CO_2	46	375	2
NF-548	NF + 173 µmol CO_2 mol^{-1}	46	548	2
NF-730	NF + 355 µmol CO_2 mol^{-1}	46	730	2
NF-1009	NF + 634 µmol CO_2 mol^{-1}	46	1009	2
OZ-375	OZ + ambient CO_2	75	375	3
OZ-548	OZ + 173 µmol CO_2 mol^{-1}	75	548	2
OZ-730	OZ + 355 µmol CO_2 mol^{-1}	75	730	3
AA	Ambient air	48	375	3

†CF, charcoal-filtered air; NF, nonfiltered air; OZ, nonfiltered air with O_3 added at 1.56 × ambient air concentration; AA, ambient air.

Pods separated from the plants during the digging process were collected from the 1-m^2 area beneath each excavated row segment and placed in mesh bags to air dry in a greenhouse. Harvested plants with attached pods were inverted on their respective row segments and left to dry in the field for 1 wk. Pods in each row segment were then collected by hand and placed in mesh bags to air dry in a greenhouse. Before drying, immature pods (<1-cm diameter) and pods of any size exhibiting symptoms of rot or disease were separated into a cull fraction that was dried in a forced air oven at 27°C and analyzed separately for each row segment. After drying, soil was removed from pods by agitation, and pod number and mass were determined. Pod numbers and masses from plants harvested for biomass determination (Booker et al., 2007) and the primary harvest plants were combined in the total value for each 1-m row segment. Pods from the individual row segments in each plot were then pooled, and two samples from each plot were analyzed for market grade characteristics using standard grading procedures for Virginia-type peanuts (USDA, 2003).

Following grading, peanut seeds from the market grade assessment were combined into a single sample for each plot, and two 10-g subsamples per plot were ground into flour and analyzed for oil, protein, and fatty acid content. Oil content was determined by pulsed proton nuclear magnetic resonance using a Maran pulsed NMR instrument (Resonance Instruments, Witney, Oxfordshire, UK) by the Field Induction Decay-Spin Echo procedure of Rubel (1994). Oil and moisture content were measured, and oil percent dry mass was determined by correcting for moisture content. Protein content was determined by the Dumas combustion method using a LECO FP-425 Nitrogen determinator (LECO Corporation, St. Joseph, MI). Samples were oven-dried overnight at 80°C. Samples (0.2 g) were then prepared in tin foil packets for combustion analysis. Protein was calculated from N values using a factor: protein (%) = 6.25 × N (%). For determination of fatty acid composition, peanut flour samples (1 g) were extracted for 12 h in 3 mL of solvent (chloroform/hexane/methanol, 8:5:2 v/v/v) in stoppered glass test tubes. Fatty acid methyl esters of the lipid extracts were prepared by transesterification using sodium methoxide. The samples were analyzed by gas chromatography using an HP 6890 GC (Agilent Technologies, Inc., Wilmington, DE) equipped with a DB-23 (30 m by 0.53 mm) column (Agilent Technologies, Inc.). Operating conditions were 1 µL injection volume, a 20:1 split ratio, and He carrier gas flow of 6 mL min^{-1}. Temperatures were 250, 200, and 275°C for the injector, oven, and flame ionization detector, respectively. Chromatograms were analyzed to identify peaks and integrate unknowns relative to authentic standards using HP ChemStation software (Agilent Technologies). Calibration of fatty acids were developed using authentic fatty acid methyl esters (American Oil Chemists Society RM-3, Sigma-Aldrich, Inc., St. Louis, MO).

Statistical Analysis

The treatments consisted of all factorial combinations of three CO_2 levels and three O_3 levels. The treatments were assigned to chambers in a completely randomized design. Chamber treatment assignments were rerandomized in the second year of the experiment. There were three replicate chambers for each of the high and low CO_2 × O_3 combinations (n = 12), and two replicate chambers for each of the +173 µmol CO_2 mol^{-1} and NF air treatment combinations (n = 10) (Table 1). Yield results from individual row segments were averaged for use as a chamber replicate value. Seed biomass was calculated from pod biomass and percent total kernels measured during market grade assessment. Results from the 2-yr experiment were combined for the statistical analysis. Data were checked for homogeneity of variance. Treatment effects and means for yield, market grade characteristics, and seed chemistry assays were statistically analyzed using analysis of variance for the effects of year, CO_2, and O_3 (SAS Proc GLM, SAS System, Ver. 8.02) (SAS Institute, 2001). Results from plants grown in AA were compared with results from the NF ambient CO_2 treatment in a separate analysis using a two-factor model for the effects of year and treatment. A ln transformation was applied to the pod and cull number and biomass data before analysis.

RESULTS

Yield

Main treatment effects of elevated CO_2 and O_3 were statistically significant for all yield components measured (Table 2). Marketable pods represented 95 to 98% of total pod biomass with the remainder designated as the cull fraction consisting of immature pods (<1 cm diameter) and pods of any size showing symptoms of rot or disease. Year was significantly different for all yield variables, but there were no significant interactions of year with O_3 and CO_2. In 2003, pod number and pod and seed biomass were about 25% lower than in 2002 while cull number and biomass increased by 42 and 67%, respectively (data not shown).

Ozone had an increasingly negative effect on yield components as concentrations increased (Table 2). Pod number was reduced 16% under NF conditions (NF-375),

Table 2. Yield of NC-V 11 peanut exposed to mixtures of CO_2 and O_3. Values are means ± SE of two or three replicate chambers for each treatment combination per year (see Table 1).†

Treatment‡	Pod number	Pod mass	Seed mass	Cull number§	Cull mass
	m of row^{-1}	—— g m of row^{-1} ——		m of row^{-1}	g m of row^{-1}
CF-375	481 ± 14 (100)	790 ± 33 (100)	575 ± 26 (100)	141 ± 18 (100)	34.2 ± 6.2 (100)
CF-548	531 ± 19 (110*)	905 ± 46 (115*)	671 ± 32 (117*)	148 ± 23 (105)	36.8 ± 8.3 (107)
CF-730	514 ± 17 (107)	881 ± 41 (112)	639 ± 29 (111)	179 ± 25 (127)	46.8 ± 9.5 (137)
NF-375	405 ± 15 (84***)	712 ± 37 (90)	530 ± 32 (92)	95 ± 15 (67*)	17.8 ± 4.0 (52*)
NF-548	494 ± 18 (103)	848 ± 43 (107)	628 ± 32 (109)	171 ± 26 (121)	43.2 ± 9.7 (126)
NF-730	528 ± 19 (110)	905 ± 46 (115*)	667 ± 32 (116*)	184 ± 29 (131)	44.7 ± 10.1 (130)
NF-1009	520 ± 19 (108)	886 ± 45 (112)	646 ± 32 (112)	188 ± 29 (133)	46.0 ± 10.4 (134)
OZ-375	272 ± 8 (56***)	501 ± 21 (63***)	387 ± 26 (67***)	42 ± 5 (29***)	9.4 ± 1.7 (27***)
OZ-548	414 ± 15 (86**)	707 ± 36 (89)	525 ± 32 (91)	91 ± 14 (65*)	20.6 ± 4.6 (60)
OZ-730	483 ± 14 (100)	806 ± 34 (102)	597 ± 26 (104)	141 ± 18 (100)	39.0 ± 7.0 (114)
Source					
Year	***	***	***	**	***
CO_2	***	***	***	***	***
O_3	***	***	***	***	***
Year × CO_2	NS¶	NS	NS	NS	NS
Year × O_3	NS	NS	NS	NS	NS
CO_2 × O_3	***	**	NS	**	*
Year × CO_2 × O_3	NS	NS	NS	NS	NS

*Significance at the 0.05 probability level.

**Significance at the 0.01 probability level.

***Significance at the 0.001 probability level.

†Values in parentheses indicate percent of the control treatment (CF-375) and statistical significance of difference from the control treatment.

‡Treatments were (i) charcoal-filtered (CF) air-ambient CO_2 (CF-375); (ii) CF air plus 175 μmol CO_2 mol^{-1} (CF-548); (iii) CF air plus 355 μmol CO_2 mol^{-1} (CF-730); (iv) nonfiltered (NF) air–ambient CO_2 (NF-375); (v) NF air plus 173 μmol CO_2 mol^{-1} (NF-548); (vi) NF air plus 355 μmol CO_2 mol^{-1} (NF-730); (vii) NF air plus 634 μmol CO_2 mol^{-1} (NF-1009); (viii) 1.5 × ambient O3–ambient CO_2 (OZ-375); (ix) 1.5 × ambient O3 plus 173 μmol CO_2 mol^{-1} (OZ-548); and (x) 1.5 × ambient O3 plus 355 μmol CO_2 mol^{-1} (OZ-730).

§Culls are defined as pods of <1-cm diameter or pods of any size that show symptoms of rot or disease.

¶NS, nonsignificant.

but suppressive effects on pod and seed mass were not large enough to be statistically significant relative to the CF control (CF-375) given the experimental variability among chambers. Significant reductions in pod number (−44%), pod mass (−37%), and seed mass (−33%) were observed in plants exposed to elevated O_3 (OZ-375). Cull number and mass were lower (−33% and −48%, respectively) in the NF-375 treatment compared with the control, and strongly reduced (−73%) by added O_3 in the OZ-375 treatment.

In general, elevated CO_2 had a positive effect on yield parameters. The relative magnitude of the effect, however, was dependent on the O_3 treatment, and vice versa (i.e., the negative effect of O_3 on yield was dependent on CO_2 concentration) (Table 2). Under subambient O_3 concentrations, pod mass was 15% higher for plants in the CF-548 treatment compared with the ambient CO_2 control (CF-375), but the smaller increase in pod mass in the CF-730 treatment was not statistically significant. Similar trends were observed for seed mass and pod number. There was a tendency for increased cull number and cull biomass at elevated CO_2, but the effects were not statistically significant. In NF treatments, pod number, pod mass, and seed mass were increased up to 30% at the higher CO_2 concentrations (NF-548 and NF-730) relative to ambient CO_2 (NF-375) ($P \leq 0.05$). Cull number and mass increased approximately twofold at elevated CO_2 (NF-730) compared with ambient CO_2 in NF (NF-375) ($P \leq 0.01$). There was no additional benefit observed in the highest level of added CO_2 (NF-1009) for any yield parameter. Under elevated O_3 concentrations of 1.56 × ambient, pod number, pod mass, and seed mass were 78, 61, and 47% higher, respectively, in the elevated CO_2 treatment (OZ-730) relative to ambient CO_2 (OZ-375) ($P \leq 0.01$). Cull number and mass increased three- to fourfold by the higher level of elevated CO_2 (OZ-730) relative to ambient CO_2 (OZ-375) ($P \leq 0.01$).

There were significant O_3 × CO_2 interactions for all yield parameters except seed mass (Table 2). The relative effects of elevated CO_2 were much more pronounced in the NF air and added O_3 treatments than in the CF air treatments. Decreased pod number in the NF-375 treatment was counteracted by CO_2 enrichment. Pod and seed mass values in the NF-730 treatment exceeded control values by about 15%. Yield suppression in the OZ-375 treatment also was diminished by elevated CO_2. Pod and seed mass in the OZ-548 and OZ-730 treatments were not significantly different from the control. However, pod number in the

OZ-548 treatment was 14% less than the control, although differences between the OZ-730 and control treatments were not statistically significant for this parameter.

Market Grade Characteristics

Market value of Virginia-type peanuts is based in part on pod and seed size. Pods larger than 1.3 cm in diameter are given the term "fancy" with a greater value placed on bulk peanuts that have more than 40% fancy pods. Seed mass associated with a known mass of bulk peanuts is measured to determine percent total kernels. Seeds larger than 0.85 cm in diameter are considered extra large kernels (ELK). Extra large kernels are a subset of total sound mature kernels (TSMK), defined as seeds with a diameter of 0.6 cm or greater. There were significant year differences for percent fancy pods (3% lower in 2003) and ELK (37% lower in 2003), but not for TSMK or percent total kernels (data not shown). There were no interactions of year with any of the gas treatments (Table 3).

Fancy pods represented greater than 80% of harvested peanuts for all gas treatment combinations (Table 3). There was a tendency for added O_3 to decrease values for percent fancy pods, but the changes were small (3–5% for a given CO_2 treatment) and were not significantly different from the CF-375 control. Elevated CO_2 increased values for fancy pods up to 6%, but the CO_2–induced increases were significantly different from the CF-375 control only in the CF-730 and NF-1009 treatments.

Added O_3 increased percent TSMK and percent total kernels up to 10%, with the largest effects observed at ambient CO_2 (OZ-375) (Table 3). Values for TSMK and percent total kernels were significantly higher than the control in the NF-375, OZ-375, and OZ-548 treatments. There was a significant $CO_2 \times O_3$ interaction for percent total kernels, probably due to the strength of the O_3–induced increase at ambient CO_2.

Seed Chemistry

There were differences between years for most seed chemistry variables, but there were no interactions between year and any of the gas treatment variables (Table 4). Neither O_3 nor elevated CO_2 had any statistically significant effect on oil or protein content of peanut seeds.

There were, however, significant O_3 and CO_2 effects on fatty acid composition (Table 4). Fatty acid analysis

Table 3. Market grade characteristics of NC-V 11 peanut as influenced by CO_2 and O_3.†

Treatment‡	% Fancy pods§	% ELK¶	% TSMK#	% Total kernels††
CF-375	82.9 ± 1.2 (100)	36.5 ± 2.8 (100)	67.8 ± 1.0 (100)	70.9 ± 0.7 (100)
CF-548	84.8 ± 1.5 (102)	41.0 ± 3.4 (112)	69.1 ± 1.3 (102)	72.0 ± 0.8 (102)
CF-730	88.1 ± 1.4 (106**)	39.0 ± 3.1 (107)	68.2 ± 1.2 (101)	71.4 ± 0.8 (101)
NF-375	81.7 ± 1.5 (99)	38.2 ± 3.4 (105)	71.5 ± 1.3 (105*)	73.3 ± 0.8 (103*)
NF-548	83.2 ± 1.5 (100)	38.2 ± 3.4 (105)	68.9 ± 1.3 (102)	71.9 ± 0.8 (101)
NF-730	86.2 ± 1.5 (104)	38.3 ± 3.4 (105)	69.4 ± 1.3 (102)	72.3 ± 0.8 (102)
NF-1009	88.0 ± 1.5 (106*)	38.0 ± 3.4 (104)	68.6 ± 1.3 (101)	71.6 ± 0.8 (101)
OZ-375	79.4 ± 1.2 (96)	47.5 ± 2.8 (130*)	74.7 ± 1.0 (110***)	76.2 ± 0.7 (107***)
OZ-548	81.7 ± 1.5 (99)	38.2 ± 3.4 (105)	71.2 ± 1.3 (105*)	73.4 ± 0.8 (104*)
OZ-730	84.0 ± 1.2 (101)	37.7 ± 2.8 (103)	69.4 ± 1.0 (102)	72.2 ± 0.7 (102)
Source				
Year	**	***	NS‡‡	NS
CO_2	***	NS	NS	NS
O_3	*	NS	**	**
Year × CO_2	NS	NS	NS	NS
Year × O_3	NS	NS	NS	NS
$CO_2 \times O_3$	NS	NS	NS	*
Year × $CO_2 \times O_3$	NS	NS	NS	NS

*Significance at the 0.05 probability level.

**Significance at the 0.01 probability level.

***Significance at the 0.001 probability level.

†All values are expressed as percent of pod biomass. Values in parentheses indicate percent of the control treatment (CF-375) and statistical significance of difference from the control treatment. Values are means ± SE of two or three replicate chambers for each treatment combination per year (see Table 1).

‡Treatments were (i) charcoal-filtered (CF) air-ambient CO_2 (CF-375); (ii) CF air plus 175 μmol CO_2 mol^{-1} (CF-548); (iii) CF air plus 355 μmol CO_2 mol^{-1} (CF-730); (iv) nonfiltered (NF) air-ambient CO_2 (NF-375); (v) NF air plus 173 μmol CO_2 mol^{-1} (NF-548); (vi) NF air plus 355 μmol CO_2 mol^{-1} (NF-730); (vii) NF air plus 634 μmol CO_2 mol^{-1} (NF-1009); (viii) 1.5 × ambient O_3–ambient CO_2 (OZ-375); (ix) 1.5 × ambient O_3 plus 173 μmol CO_2 mol^{-1} (OZ-548); and (x) 1.5 × ambient O_3 plus 355 μmol CO_2 mol^{-1} (OZ-730).

§Fancy pods are large pods that will not pass through a 1.3 by 7.6 cm screen.

¶Extra large kernels (ELK) are sound, whole kernels that will not pass through a 0.8 by 2.5 cm screen.

#Total sound mature kernels (TSMK) are all whole kernels not passing through a 0.6 by 2.5 cm screen including ELK and sound split kernels.

††Total kernels include TSMK and all other kernels, including nonmarketable pieces.

‡‡NS, nonsignificant.

showed that the major constituents in the peanut seeds were palmitic (16:0), oleic (18:1), and linoleic (18:2) acids, which together accounted for approximately 90% of the total. Added O_3 increased stearic acid (18:0) and decreased lignoceric acid (24:0) concentrations about 10% compared with the control. Elevated CO_2 decreased palmitic acid (16:0) values up to 3% with the largest declines observed in the OZ-730 and NF-1009 treatments. Elevated CO_2 increased oleic acid (18:1) values up to 4% at all of the high CO_2 concentrations (CF-730, NF-730, NF-1009, and OZ-730). The increase in oleic acid (18:1) at elevated CO_2 was associated with a decline in linoleic acid (18:2) of the same magnitude.

Open-Top Chamber Effects

The comparison between plants grown in NF air with those grown in AA (chamber frames without plastic side panels) suggested that any chamber effects on yield components and market grade characteristics were minor. Values were higher for pod number and mass, seed mass, and percent fancy pods, and lower for cull number and mass in AA, but these differences were not statistically significant (Table 5). Seed oil and protein concentrations were not significantly different in the two treatments, but there was some variation in fatty acid composition between AA and NF treatments. There was significantly less palmitic acid (3%) and linoleic acid (6%) in seeds from plants grown in AA versus NF conditions. Conversely, there was significantly more stearic acid (9%) and oleic acid (5%) in seeds from the AA treatment (Table 5).

DISCUSSION

The NC-V11 peanut cultivar used in this study was found to be sensitive to elevated O_3 and CO_2. Pod number was

Table 4. Seed oil and protein content and fatty acid composition of NC-V 11 peanut exposed to mixtures of CO_2 and O_3.†

Treatment‡	Oil	Protein	Fatty acid composition							
	—% seed mass—		weight %							
			Palmitic 16:0	Stearic 18:0	Oleic 18:1	Linoleic 18:2	Arachidic 20:0	Gadoleic 20:1	Behenic 22:0	Lignoceric 24:0
CF-375	51.8 ± 0.4 (100)	29.1 ± 0.4 (100)	10.4 ± 0.1 (100)	2.0 ± 0.0 (100)	47.0 ± 0.4 (100)	34.0 ± 0.3 (100)	1.2 ± 0.0 (100)	1.5 ± 0.0 (100)	2.6 ± 0.1 (100)	1.5 ± 0.0 (100)
CF-548	51.8 ± 0.5 (100)	29.3 ± 0.4 (101)	10.2 ± 0.1 (98)	2.0 ± 0.0 (100)	47.8 ± 0.5 (102)	33.5 ± 0.4 (98)	1.3 ± 0.0 (107)	1.4 ± 0.1 (94)	2.5 ± 0.1 (99)	1.4 ± 0.0 (97)
CF-730	51.7 ± 0.4 (100)	29.9 ± 0.4 (103)	10.2 ± 0.1 (98)	2.0 ± 0.0 (102)	48.4 ± 0.5 (103*)	32.9 ± 0.4 (97*)	1.2 ± 0.0 (103)	1.4 ± 0.0 (95)	2.4 ± 0.1 (95)	1.4 ± 0.0 (95)
NF-375	51.3 ± 0.5 (99)	28.9 ± 0.4 (99)	10.3 ± 0.1 (100)	2.1 ± 0.0 (104)	47.4 ± 0.5 (101)	33.7 ± 0.4 (99)	1.2 ± 0.0 (103)	1.4 ± 0.1 (97)	2.5 ± 0.1 (96)	1.4 ± 0.0 (96)
NF-548	51.2 ± 0.5 (99)	29.4 ± 0.4 (101)	10.2 ± 0.1 (99)	2.0 ± 0.0 (104)	47.3 ± 0.5 (101)	33.9 ± 0.4 (100)	1.2 ± 0.0 (99)	1.4 ± 0.1 (95)	2.5 ± 0.1 (98)	1.4 ± 0.0 (97)
NF-730	51.3 ± 0.5 (99)	29.9 ± 0.4 (103)	10.1 ± 0.1 (98)	2.0 ± 0.0 (102)	48.7 ± 0.5 (104*)	32.6 ± 0.4 (96*)	1.2 ± 0.0 (100)	1.5 ± 0.1 (98)	2.5 ± 0.1 (97)	1.4 ± 0.0 (97)
NF-1009	51.8 ± 0.5 (100)	29.6 ± 0.4 (101)	10.0 ± 0.1 (97*)	2.1 ± 0.0 (106)	48.9 ± 0.5 (104*)	32.5 ± 0.4 (96**)	1.2 ± 0.0 (103)	1.4 ± 0.1 (96)	2.4 ± 0.1 (95)	1.4 ± 0.0 (94)
OZ-375	51.8 ± 0.4 (100)	29.0 ± 0.4 (99)	10.4 ± 0.1 (100)	2.2 ± 0.0 (110***)	47.5 ± 0.4 (101)	33.8 ± 0.3 (100)	1.2 ± 0.0 (100)	1.3 ± 0.0 (85**)	2.3 ± 0.1 (91*)	1.3 ± 0.0 (90**)
OZ-548	51.4 ± 0.5 (99)	29.9 ± 0.4 (103)	10.3 ± 0.1 (100)	2.0 ± 0.0 (103)	47.4 ± 0.5 (101)	33.9 ± 0.4 (100)	1.2 ± 0.0 (99)	1.4 ± 0.1 (94)	2.4 ± 0.1 (93)	1.4 ± 0.0 (93*)
OZ-730	52.5 ± 0.4 (101)	28.5 ± 0.4 (98)	10.0 ± 0.1 (97*)	2.1 ± 0.0 (107*)	48.5 ± 0.4 (103*)	32.9 ± 0.3 (97*)	1.2 ± 0.0 (103)	1.4 ± 0.0 (93)	2.5 ± 0.1 (96)	1.4 ± 0.0 (95)
Source										
Year	*	***	NS§	***	NS	*	***	**	***	***
CO_2	NS	NS	*	NS	**	**	NS	NS	NS	NS
O_3	NS	NS	NS	**	NS	NS	NS	NS	NS	*
Year × CO_2	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Year × O_3	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
CO_2 × O_3	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Year × CO_2 × O_3	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS

*Significance at the 0.05 probability level.

**Significance at the 0.01 probability level.

***Significance at the 0.001 probability level.

†Values are means ± SE. Values in parentheses indicate percent of the control treatment (CF-375) and statistical significance of difference from the control treatment.

‡Treatments were (i) charcoal-filtered (CF) air–ambient CO_2 (CF-375); (ii) CF air plus 175 μmol CO_2 mol^{-1} (CF-548); (iii) CF air plus 355 μmol CO_2 mol^{-1} (CF-730); (iv) nonfiltered (NF) air–ambient CO_2 (NF-375); (v) NF air plus 173 μmol CO_2 mol^{-1} (NF-548); (vi) NF air plus 355 μmol CO_2 mol^{-1} (NF-730); (vii) NF air plus 634 μmol CO_2 mol^{-1} (NF-1009); (viii) 1.5 × ambient O_3–ambient CO_2 (OZ-375); (ix) 1.5 × ambient O_3 plus 173 μmol CO_2 mol^{-1} (OZ-548); and (x) 1.5 × ambient O_3 plus 355 μmol CO_2 mol^{-1} (OZ-730).

§NS, nonsignificant.

reduced 16% in NF while O_3 at 1.56 times ambient concentrations suppressed yield components by 33 to 44% (Table 2). This supported previous research that identified peanut as an O_3–sensitive crop (Heagle et al., 1983; Ensing et al., 1985, 1986). When elevated CO_2 was combined with elevated O_3, most yield parameters were restored to the same or greater values as the CF-375 control treatment, demonstrating an amelioration of the negative effects of O_3 by elevated CO_2 (Table 2). Elevated CO_2 concentrations in CF increased yield parameters up to 17% (Table 2), evidence for CO_2 stimulation of yield under conditions where O_3 stress was minimal. A stimulation of yield with elevated concentrations of CO_2 along with a protective effect of elevated CO_2 against O_3 reductions in yield have been found in a number of experiments with other crop plants (Booker and Fiscus, 2005; Booker et al., 2005; Craigon et al., 2002; Fiscus et al., 2002; Heagle et al., 1998, 1999, 2000; Olszyk et al., 2000). Other studies, in contrast, did not find that elevated CO_2 attenuated O_3–induced yield losses, possibly due to toxic effects of O_3 on pollen tube growth and fertilization in wheat (Black et al., 2000; McKee et al., 1997a; Mulholland et al., 1998) or high sensitivity of certain snap bean (*Phaseolus vulgaris* L.) and potato cultivars to O_3 (Heagle et al., 2003; Heagle et al., 2002). In this study, the elevated CO_2 protective effect was associated with increased net photosynthesis and reduced leaf O_3 uptake in peanut plants (Booker et al., 2007) leading to an enhanced physiological status to support reproductive growth. Increased availability of C skeletons with elevated CO_2 also might enhance defense and repair mechanisms that contribute to the protective effect (Allen, 1990; Barnes and Wellburn, 1998; Booker and Fiscus, 2005; Cardoso-Vilhena et al., 2004; McKee et al., 1997b).

Table 5. Open-top chamber effects on yield, market grade characteristics, and seed quality of NC-V 11 peanut. Plants were exposed to non-filtered air (NF-375) and ambient air (AA; chamber frames without side panels) in ambient concentrations of CO_2.†

Parameter	Treatment	
	NF-375	AA
Yield		
Pod number, m of row^{-1}	411 ± 12	420 ± 10
Pod biomass, g m of row^{-1}	722 ± 25	757 ± 20
Seed biomass, g m of row^{-1}	530 ± 21	552 ± 17
Cull number, m of row^{-1}	100 ± 10	72 ± 8
Cull biomass, g m of row^{-1}	21.2 ± 2.3	16.7 ± 1.9
Market grade characteristics		
% fancy pods	81.7 ± 1.4	84.7 ± 1.2
% extra large kernels	38.2 ± 1.5	38.6 ± 1.2
% TSMK	71.5 ± 1.1	71.7 ± 0.9
% total kernels	73.3 ± 1.0	73.3 ± 0.8
Seed quality		
Oil, % seed mass	51.3 ± 0.3	51.8 ± 0.3
Protein, % seed mass	28.9 ± 0.4	29.3 ± 0.3
Fatty acids, weight %		
Palmitic (16:0)	10.3 ± 0.05	10.1 ± 0.04 (97**)
Stearic (18:0)	2.1 ± 0.03	2.2 ± 0.03 (109**)
Oleic (18:1)	47.4 ± 0.2	49.6 ± 0.1 (105***)
Linoleic (18:2)	33.7 ± 0.1	31.7 ± 0.1 (94***)
Arachidic(20:0)	1.2 ± 0.01	1.2 ± 0.01
Gadoleic (20:1)	1.4 ± 0.05	1.3 ± 0.04
Behenic (22:0)	2.5 ± 0.04	2.4 ± 0.04
Lignoceric (24:0)	1.4 ± 0.02	1.4 ± 0.02

**Significance at the 0.01 probability level.

***Significance at the 0.001 probability level.

†Values are means ± SE of two (NF) or three (AA) replicate chambers for each treatment per year. Values in parentheses indicate percent of the NF-375 treatment.

Peanut is generally considered to be highly responsive to elevated atmospheric CO_2 concentrations (Prasad et al., 2005). However, there was a limit to yield stimulation by elevated CO_2 for this peanut cultivar because no further yield increase was observed in the CF-730 treatment compared with the CF-548 treatment as well as in the NF-1009 treatment compared with the NF-730 treatment. Stanciel et al. (2000) also found that 'Georgia Red' peanut seed mass of hydroponically grown plants increased only marginally at 1200 μmol CO_2 mol^{-1} compared with 800 μmol CO_2 mol^{-1}. Further, plant biomass at harvest was not significantly different in the NF-730 and NF-1009 treatments (Booker et al., 2007). Thus, there is a maximum genetic potential for growth and yield stimulation by CO_2 in these peanut cultivars at 548 to 800 μmol mol^{-1} depending on the experimental conditions used.

Elevated O_3 and CO_2 concentrations did not impact market grade characteristics of peanut as much as yield (Table 3). Small increases in fancy pods were observed under elevated CO_2. Percent TSMK and percent total kernels increased under elevated O_3, suggesting either earlier maturity or higher yield potential. Given that elevated O_3 reduces yield, the results suggest that O_3 stress accelerated development. Further evidence for O_3 stress on plant development can be seen in the cull data (Table 2). The lower numbers and masses of culls in elevated O_3 treatments suggests that energy available to initiate new pod structures is limited compared with elevated CO_2 even though the additional pods in the elevated CO_2 plots did not mature by the end of the growing season. Even though the additional culls in elevated CO_2 plots did not mature by the end of the growing season, they represented additional reproductive potential that was not available under elevated O_3.

The elevated O_3 and CO_2 treatments used in this study did not affect the oil and protein contents of peanut seeds (Table 4). Similar results have been reported in some cases for soybean (Heagle et al., 1998; Thomas et al., 2003). Heagle et al. (1998) compared three soybean cultivars and found that elevated O_3 did not affect the seed protein content and

had only small effects on seed oil content. Double ambient CO_2 did not affect soybean seed protein content (Heagle et al., 1998; Thomas et al., 2003) and had either small, variable effects (Heagle et al., 1998) or no effect (Thomas et al., 2003) on soybean seed oil content. In contrast, Mulchi et al. (1992) found that soybean grain oil content was increased and protein content decreased by elevated CO_2.

The most significant effects of elevated O_3 and CO_2 on seed quality were on fatty acid composition. In peanut, stearic acid (18:0) increased under elevated O_3 and palmitic acid (16:0) declined under elevated CO_2 (Table 4), effects that were not observed for soybean (Heagle et al., 1998). Lignoceric acid (24:0), a long-chain fatty acid found in peanut but not soybean oil, also declined in response to elevated O_3. Peanut and soybean oil composition share one common feature involving monounsaturated versus polyunsaturated 18-C fatty acids. In peanut seeds, oleic acid (18:1) content increased under elevated CO_2 and was associated with a decrease of the same magnitude in linoleic acid (18:2) (Table 4). Heagle et al. (1998) observed this same pattern for soybean grown in open-top chambers under elevated CO_2. In contrast, Thomas et al. (2003) found a similar oleic acid–linoleic acid dynamic associated with temperature, but not elevated CO_2. In soybean grown to maturity under different temperature regimes, oleic acid (18:1) increased and linoleic acid (18:2) declined in soybean oil as growth temperature increased from 28 to 44°C with no effect of elevated CO_2 at any temperature tested (Thomas et al., 2003). A potential resolution to this apparent contradiction involves the effect of elevated CO_2 on leaf temperature. Elevated CO_2 lowered stomatal conductance in our plants (Booker et al., 2007), which can lead to slightly higher leaf temperatures due to decreased transpiration and cooling ability (Long et al., 2004). Thus for soybean, elevated temperature within the canopy associated with elevated CO_2 may explain the effects on oleic acid–linoleic acid dynamics. However, a distinction between peanut and soybean is that peanut pods develop underground so that seed development temperature is modulated by soil temperature. Rising soil temperature has been shown to increase oleic acid (18:1) and lower linoleic acid (18:2) in peanut seeds (Golombek et al., 1995). Soil temperature was not measured during this study, but it seems unlikely that elevated CO_2 would affect it. An alternative, and much more speculative hypothesis, is that a high temperature signal generated in peanut leaves then regulates oil synthesis in developing peanut seeds located underground.

The open-top chamber approach for exposing plants to gaseous pollutants has advantages and limitations. Chambers allow for subambient O_3 controls where CF treatments can be used as a reference point for interpreting effects of elevated CO_2 and O_3. For example, the inclusion of a CF control in this study revealed that CO_2 stimulation of peanut yield under NF conditions was attributable to amelioration of ambient O_3 effects. However, open-top chambers are known to alter environmental conditions (increased temperature, lower light levels, and constant air turbulence) that can affect plant growth (Kimball et al., 1997; Long et al., 2004; Manning and Krupa, 1992). In this study, such chamber effects were not significant for peanut yield and quality parameters because the NF-375 and AA treatments were not statistically different, small changes in fatty acid composition being the only exception (Table 5). Free air exposure systems provide an alternative approach that alleviates some concerns regarding chamber effects, but do not include a subambient O_3 control. The two approaches, open-top chambers versus free air exposure, have shown similar relative effects of elevated CO_2 (Ainsworth and Long, 2005; Kimball et al., 1997). A comparison of the two approaches for elevated O_3 is more difficult because assessment of O_3 effects on crop yield using free air exposure systems is limited to one recent soybean study by Morgan et al. (2006). In this case, the observed yield reductions under the free air exposure conditions were generally consistent with open-top chamber studies (Morgan et al., 2006).

CONCLUSIONS

Peanut cultivar NC-V 11 yield was found to respond to both O_3 and CO_2 with a significant interaction observed between the two gases. Yield losses in the presence of elevated O_3 were largely ameliorated by addition of CO_2. Yield was also stimulated by elevated CO_2 under CF air conditions where O_3 stress was minimal, evidence that rising CO_2 should have a direct effect on peanut production as well. Market grade characteristics and seed protein and oil contents were not affected by elevated O_3 and CO_2, suggesting the major impacts of rising atmospheric O_3 and CO_2 will be on productivity, not product quality. Given the strong interaction between O_3 and CO_2, it would seem important to include CO_2 as a factor in O_3 flux-yield models and to consider O_3 effects in projections of yield stimulations from elevated CO_2.

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