

Observations and model simulations link stomatal inhibition to impaired hydraulic conductance following ozone exposure in cotton

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ABSTRACT

Ozone (O₃) inhibits plant gas exchange and productivity. Vapour phase (g_s) and liquid or hydraulic phase (K) conductances to water flux are often correlated as both change with environmental parameters. Exposure of cotton plants to tropospheric O₃ reduces g_s through reversible short-term mechanisms and by irreversible long-term disruption of biomass allocation to roots which reduces K . We hypothesize that chronic effects of O₃ on gas exchange can be mediated by effects on K without a direct effect of O₃ on g_s or carbon assimilation (A). Experimental observations from diverse field and exposure chamber studies, and simulations with a model of mass and energy transport, support this hypothesis. O₃ inhibition of K leads to realistic simulated diurnal courses of g_s that reproduce observations at low ambient O₃ concentration and maintain the positive correlation between midday g_s and K observed experimentally at higher O₃ concentrations. Effects mediated by reduced K may interact with more rapid responses of g_s and A to yield the observed suite of oxidant impacts on vegetation. The model extends these physiological impacts to the extensive canopy scale. Simulated magnitudes and diurnal time courses of canopy-scale fluxes of H₂O and O₃ match observations under low ambient concentrations of O₃. With greater simulated concentrations of O₃ during plant development, the model suggests potential reductions of canopy-scale water fluxes and O₃ deposition. This could represent a potentially unfavourable positive feedback on tropospheric O₃ concentrations associated with biosphere–atmosphere exchange.

Key-words: air pollution; allocation; dry deposition; evapotranspiration; oxidant; ozone flux; regional ozone concentrations; root–shoot communication; water relations

INTRODUCTION

Root response to O₃

Exposure of plants to ambient concentrations of tropospheric ozone (O₃) reduces biomass production and alters biomass allocation within the plant. Root to shoot biomass ratio is frequently reduced (Cooley & Manning 1987; Oshima *et al.* 1979), often in an allometric fashion (Reiling & Davison 1992), although in some cases the root to shoot ratio is unchanged or increased by O₃ (Reiling & Davison 1992).

Ozone reduces yields of adapted upland (*Gossypium hirsutum* L.) cotton cultivars by about 20% in the San Joaquin Valley of California (Grantz & McCool 1992; Olszyk *et al.* 1993; Oshima *et al.* 1979; Temple *et al.* 1988), despite many cycles of yield selection in this O₃-impacted environment. Yield and productivity of Pima (*G. barbadense* L.) cotton cultivars, selected in low-O₃ environments, are even more sensitive (Grantz & McCool 1992; Olszyk *et al.* 1993). In this irrigated region of high evaporative demand and high agronomic inputs of mineral nutrients, root function is a critical determinant of yield and biomass production. Exposure to O₃ has been shown to reduce both vapour phase (g_s) (Grantz & Yang 1995, 1996a; Temple 1986, 1990) and liquid or hydraulic phase (K) conductances to water flux (Grantz & Yang 1995, 1996a,b) in cotton.

Parallel declines in g_s and K may reflect independent responses to O₃. However, typically conserved allometric relationships between root and shoot biomass (e.g. Farrar & Gunn 1996) and reduced productivity of cotton plants with restricted root development (Browning *et al.* 1975) suggest that O₃-inhibited root system development could mediate reductions in long-term shoot gas exchange. Differential yield sensitivity to O₃ of two cultivars of sweet corn (*Zea mays*) has been linked to differential responses of root system development and hydraulic properties (Harris & Heath 1981). Mechanistic relationships between stomatal function and root hydraulic properties have been suggested previously (Meinzer & Grantz 1990). This could be mediated by root tip metabolism or water relations, through altered synthesis or transport to the shoot of phytohormones, mineral nutrients or other substances (e.g.

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Zhang & Davies 1990; Dodd *et al.* 1996; Muller *et al.* 1996; Puliga *et al.* 1996). Alternatively, the interaction could be mediated by effects of K on soil water acquisition and resulting water status of the leaf mesophyll (ψ_m) or epidermal (ψ_e) tissue in which the stomata are embedded (Fuchs & Livingston 1996; Shackel & Brinckmann 1985; Bunce 1996). Differences between ψ_e and ψ_m have been documented (Shackel & Brinckmann 1985), although associated stomatal control mechanisms and sensitivity to O_3 exposure have not been assessed.

Rapid reductions in shoot gas exchange following exposure to O_3 may be associated with altered phloem loading (e.g. McCool & Menge 1983; McLaughlin & McConathy 1983; Mortensen & Engvild 1995; Grantz & Farrar 1999) and end-product inhibition of carbon metabolism. Reduced root system capacity may also lead to long-term reductions in carboxylase activity and gas exchange performance. Feedback from root to shoot following chronic exposure to O_3 would necessarily be long-term and slowly reversed, and would be expressed as a limit on maximal stomatal response to other environmental parameters. The potential mediation of chronic phytotoxic effects of O_3 on gas exchange by such a mechanism has not been investigated.

Rapid shoot response to O_3

In contrast, rapid gas exchange responses to O_3 have been well documented. In bean plants (*Phaseolus vulgaris* L.), stomatal conductance (g_s) was reduced within 6–12 min by 0.3–0.5 ppm O_3 (Moldau *et al.* 1990). While g_s declined by about 50% within 3 h, the mesophyll conductance to CO_2 was unaffected. Similar apparent direct effects of O_3 on g_s have been identified by Hill & Littlefield (1969) and by Amundson *et al.* (1987).

Light-saturated carbon assimilation declined by about 25% in winter wheat (*Triticum aestivum* L.; Farage *et al.* 1991) and 40% in pea and oak (*Pisum sativum* L. and *Quercus robur* L.; Farage & Long 1995), while g_s declined by about 40% (wheat, pea) and about 80% (oak) following 4 h of exposure to 0.4 ppm O_3 . This was associated with minimal effect on photosynthetic light reactions assayed as variable chlorophyll fluorescence and as quantum yield. Carboxylation capacity was reduced by about 30% (wheat, oak) to 45% (pea), consistent with O_3 -induced reductions in Rubisco protein and activity (Eckard & Pell 1995; Lehnher *et al.* 1987; Pell & Pearson 1983), attributed in part to oxidative modification of sulphhydryl residues (Eckard & Pell 1995). O_3 did not reduce synthesis of Rubisco (Brendley & Pell 1998), but accelerated proteolysis in older leaves. Similar effects on gas exchange mediated by mesophyll responses to O_3 have been identified by Lehnher *et al.* (1988) and Myhre *et al.* (1988).

In cotton we observed rapid stomatal and mesophyll responses to O_3 in older leaves that required several days to reverse in O_3 -free air (unpublished observations) while young leaves exhibited substantially enhanced g_s and A. This potentially compensatory gas exchange in young leaves exposed to O_3 ameliorates whole-plant impacts of

O_3 on gas exchange (e.g. Pell *et al.* 1994) and reflects nitrogen remobilization from older leaves undergoing accelerated senescence (e.g. Brendley & Pell 1998). These short-term, often reversible (e.g. Guidi *et al.* 1997), effects of O_3 on gas exchange may reflect parallel impacts on both g_s and mesophyll function, with reduced Rubisco activity restricted to older leaves and longer time frames (e.g. in wheat; Grandjean Grimm & Fuhrer 1992).

Present approach

Use of model simulations may reveal mechanistic relationships when experimental manipulations have proven inconclusive, and may elucidate effects at larger scales of biological organization than can be readily manipulated. Here we use a comprehensive simulation model of stomatal conductance (Lynn & Carlson 1990; Olioso *et al.* 1996; Taconet *et al.* 1986) to explore the role of O_3 -inhibited root system development on gas exchange performance at leaf and canopy scales. The model as modified for this study describes single leaf g_s and canopy-scale fluxes of energy, water and O_3 between the bulk soil, the plant, and the atmospheric mixed layer. The single-day simulations invoke a partial dependence of g_s on epidermal water status, but exclude chemical root signals, direct effects of O_3 on photosynthesis or guard cell metabolism, and longer-term feedbacks on canopy transport associated with O_3 -reduced growth and leaf area development. The model incorporates a direct O_3 effect on K as the only physiological impact of O_3 . Secondary effects of K on g_s , leaf water relations, and energy and mass balances at the canopy scale are simulated from the single physiological impact on K . This is in contrast to previous simulations of growth and gas exchange responses to O_3 (e.g. Constable & Taylor 1997) in which a direct impact of O_3 on leaf gas exchange (maximal carboxylation capacity) is an input parameter.

We investigate the gas exchange and water relations behaviour of mature, individual cotton plants embedded in an extensive cotton canopy, following chronic exposure to O_3 during plant development. We begin with experimental observations obtained under a variety of conditions and attempt to reproduce them using the mechanistic simulation model. The simulated values reproduce observed gas exchange behaviour without invoking any direct effect of O_3 on leaf gas exchange.

MATERIALS AND METHODS

Experimental observations

Field exposure chambers

Cotton plants (*Gossypium hirsutum*; cv. Acala SJ-2 and *G. barbadense*; cv. Pima S-6) were grown in 1992 from seed in closed-top field exposure chambers as described by Musselman *et al.* (1986) located in Riverside, California. Seeds were planted in rows 1 m apart with approximately 13 seeds/m. Plants received drip irrigation daily and complete fertilization monthly. Yield and stomatal responses to

O₃ of similar plants in 1991 were substantial (Grantz & McCool 1992). Data from the 1992 season have not previously been published.

Stomatal conductance (g_s ; mol m⁻² s⁻¹) was determined on both surfaces simultaneously of the youngest fully expanded leaf, at midday using a transient gas exchange system (LI 6200; LiCor Inc., Lincoln, Nebraska, USA) and expressed relative to projected leaf area. Measurements were obtained on four replicate plants per chamber under natural sunlight and as near as practical to ambient humidity. The water potential of these leaves (ψ_m ; MPa) was determined at midday with a pressure chamber. Leaves were sealed in foil-covered zip-lock bags prior to excision at the base of the petiole. Sealed bags were stored in an insulated, dark container prior to measurement (< 30 min).

Hydraulic conductance (K ; mol m⁻² MPa⁻¹ s⁻¹) was determined using the gradient in water potential between the soil and the transpiring leaf, water flux during periods of high transpiration, and leaf area of the plant. Soil water potential was determined as pre-dawn leaf water potential, which was always approximately 0 MPa. These values were confirmed using the water potential of de-topped stems as described by Grantz & Yang (1996a). Water flux was approximated as the product of g_s and total plant leaf area, and leaf to air vapour pressure difference (V ; defined in the within-canopy air space and taken as a representative value of 1.5 kPa inside the chambers). Alternative methods of determining K in these studies have yielded similar values, as described by Yang & Grantz (1996).

Commercial field

Acala cotton plants (*Gossypium hirsutum* L.; cv. Delta Pine 6166) were grown in the field in 1991 (as described by Grantz *et al.* 1997) and again in the same field in 1994, under commercial conditions in the San Joaquin Valley near Firebaugh, California (36°48'50"N, 120°40'38"W).

Data were obtained in 1994 during a lengthy period including 23 August (day of year (DOY) 235, the date of our simulations). The canopy was 1 m in height and fully covered the ground, with a leaf area index of 2.52. The roughness length was determined experimentally to be 0.13 m. The field was furrow-irrigated, with the interval between irrigations lengthened to induce early reproductive development. This periodic soil water deficit allowed measurements to be obtained at different soil water contents and resulting soil-root hydraulic conductances.

Stomatal conductance of both surfaces of representative leaves at each of six insertion levels on four plants was determined near midday with a steady state porometer (LI 1600; LiCor Inc.). Hydraulic conductance was determined as in the field exposure chambers with water flux measured directly using sap flow gauges (Dynagage, Inc., Houston, Texas, USA). These were installed above the ground surface, insulated with closed-cell foam and plastic bubble wrap, and shielded from radiation with aluminium foil, to avoid the radiation-induced errors encountered previously (Shackel *et al.* 1992) in this environment. The result-

ing data agreed ($\pm 12\%$) with canopy-scale measurements of water vapour flux at midday obtained with the Bowen ratio energy balance technique (not shown).

Maximal ozone concentration at 50 m measured at this site in 1991 was about 0.08 ppm (Delany *et al.* 1992), and that at the ground surface measured in 1994 was about 0 ppmv. Ozone deposition (F) was measured at 5 m using an eddy covariance protocol (Delany *et al.* 1992).

Model simulations

Model background

The simulation model used in this study is a further development of the soil/plant/canopy/atmosphere model described by Taconet *et al.* (1986), Lynn & Carlson (1990) and Oliosio *et al.* (1996). Following modification for the current analyses, this model simulates daily courses of atmospheric, soil and plant parameters including single leaf stomatal conductance and leaf water potential, and canopy fluxes of momentum, heat, water vapour, carbon dioxide and O₃. The modelling domain extends from the bulk soil through the rhizosphere, plant canopy, surface layer, and well into the atmospheric mixed layer, the height of which develops with model iteration. The model is exercised over single diurnal periods when net radiation is positive, from initial conditions in the early morning.

Stomatal conductance (g_s), and bulk leaf mesophyll and epidermal water potentials (ψ_m , ψ_e) are interactive functions of modelled and input local environmental parameters including root hydraulic conductance (K), an input variable in the original model (Lynn & Carlson 1990), but here a function of input [O₃] during simulated plant development, as:

$$1/K = 0.025 + 0.30[\text{O}_3] - 1.20[\text{O}_3]^2 \quad (1)$$

where [O₃] is the 12 h mean O₃ concentration. This relationship is derived from observations in field and greenhouse exposure chambers (previously unpublished results; Fig. 1a; and Grantz & Yang 1996a). A similar O₃-induced reduction in K has been observed in red spruce (*Picea rubens* (Sarg.)) by Lee *et al.* (1990). While many environmental variables may alter root development and hydraulic properties (e.g. nitrogen; Grantz & Yang 1996b) and others may affect g_s (e.g. humidity; Aphalo & Jarvis 1991; Grantz 1990), these are not explicitly considered except as they vary interactively over the single day of simulation. Over longer time periods such factors will alter plant growth and development and would require parameterization in the model.

Epidermal water potential (ψ_e) is calculated as a function of the edaphic, atmospheric and physiological inputs embedded in the canopy-scale model (see Lynn & Carlson 1990 for details) and linked to bulk leaf mesophyll water potential (ψ_m) as

$$\psi_e = \psi_m - \beta V \quad (2)$$

where the constant parameter, $\beta = 0.02$ MPa kPa⁻¹. This relates ψ_e to transpiration (T), through its interdependence

with V , and to ψ_m through the efficiency of hydraulic connections between mesophyll and epidermis incorporated in β . It also incorporates an implicit stomatal response to V through the interdependence of g_s , ψ_c and V incorporated in eqns 2–5, rather than the explicit response of g_s to V in many other treatments (e.g. Jarvis 1976; Grantz *et al.* 1987). These relationships capture the feed-forward behaviour of T and ψ_m with respect to V , with both increasing and then decreasing in absolute magnitude as V increases with changing leaf temperature, air humidity and transpiration. They also capture the uncoupling of ψ_c from ψ_m , predicting changes in opposite directions under some conditions. This has been considered a potential mechanistic control feature underlying the feed-forward stomatal responses to humidity (Aphalo & Jarvis 1991; Bunce 1996; Grantz 1990; Maier-Maercker 1983), although this concept may require reconsideration in light of recent evidence (Franks *et al.* 1997; Monteith 1995; Mott & Parkhurst 1991).

Stomatal responses to interacting environmental variables are treated as multiplicative functions (simplified after Jarvis 1976; Grantz *et al.* 1987), so that g_s is related to photosynthetically active photon flux density (PPFD) and ψ_c as

$$g_s = [(a)(\text{PPFD})/(b + \text{PPFD})][1/f(\psi_c)] \quad (3)$$

where $a = 2.94$ and $b = 1000$. The hyperbolic stomatal response to PPFD is that derived for similar field-grown cotton by Grantz *et al.* (1997). The function $f(\psi_c)$ is a linear discontinuous stomatal response to epidermal water status (Lynn & Carlson 1990) as

$$f(\psi_c) = 1 + (b_1)(\psi_c) \quad \psi_c > \psi_c \quad (4a)$$

$$f(\psi_c) = 1 + (b_1)(\psi_c) + b_2(\psi_c - \psi_c)^{0.8} \quad \psi_c \leq \psi_c \quad (4b)$$

where $b_1 = -0.0001$, $b_2 = 0.3$, and $\psi_c = -1.6$ MPa is the critical epidermal water potential.

Canopy transpiration (T) and O_3 flux (F) are calculated (e.g. for T) as

$$T = 0.622 \rho L_e \frac{1}{P} \frac{V}{(r_l + r_{af})} \quad (5a)$$

and the total flux from the surface, including that from the soil (e.g. for water vapour, E_g) as

$$E = T + E_g \quad (5b)$$

where r_l is leaf resistance and r_{af} is leaf boundary layer resistance (to water vapour), ρ is air density, P is atmospheric pressure, and L_e is the latent heat of vaporization of water. Leaf resistance to water vapour (r_l) is composed of the stomatal resistance (r_s) and the cuticular resistance ($r_c = 10 \text{ s cm}^{-1}$), in parallel. E_g is the evaporative flux from the ground, a function of temperature and moisture of both the soil and the air near the surface (Lynn & Carlson 1990).

Ozone and water vapour fluxes follow similar paths, in opposing directions. The O_3 concentration in the canopy (C_t) is calculated as

$$C_t = \frac{C_a}{1 + \frac{r_a}{r_{\text{tot}}}} \quad (6a)$$

where C_a is O_3 concentration at 50 m, modelled as a diurnal course increasing from 0.02 ppmv at dawn to 0.08 ppm at 16:00 Pacific Daylight Time (PDT) followed by a plateau in accordance with field observations at this site in 1991, r_a is the aerodynamic resistance above the canopy, and r_{tot} is the sum of parallel resistances for cuticular, stomatal and soil fluxes, expressed as

$$\frac{1}{r_{\text{tot}}} = \frac{1}{\frac{1.32(r_{af} + r_c)}{2\text{LAI}}} + \frac{1}{\frac{1.32r_{af}}{\text{LAI}} + \frac{1.66r_s}{\text{LAI}}} + \frac{1}{1.32r_{ag}} \quad (6b)$$

where r_{ag} is the aerodynamic resistance to water vapour between the ground and the top of the canopy, and LAI is leaf area index corrected by a shelter factor (Lynn & Carlson 1990; Taconet *et al.* 1986; Oliso *et al.* 1996). Resistances to water vapour are converted to resistances to O_3 by the factors 1.32 and 1.66, for non-stomatal and stomatal resistances, respectively (Jones 1992).

Simulations

The model was initialized with canopy characteristics, meteorological soundings, ozone concentrations, and approximate soil type (loamy sand) and crop species (cotton) observed at this site on or around DOY 235 during the two years of intensive measurements (1991 and 1994). Day length and incoming shortwave radiation were calculated as functions of geographic coordinates and date. Shortwave radiation was used to calculate PPFD using an empirical regression developed at this site. Simulated values of PPFD agreed well with measurements (not shown).

Data presentation

The model was run in Microsoft Fortran PowerStation (version 4.0; Microsoft Inc., Redland, Washington, USA) with output exported to Sigma Plot (SPSS Inc.; Chicago, Illinois, USA) for statistical analyses and preparation of figures. All measured and simulated conductances are converted to molar units using appropriate temperature and pressure, for compatibility with the plant physiology literature.

RESULTS AND DISCUSSION

Experimental data

Effects of ozone

Mature cotton plants grown in field exposure chambers under chronic exposure to realistic concentrations of O_3 exhibited a progressive reduction in plant hydraulic conductance with increasing O_3 concentration. This was the case on a per plant basis (not shown) and when expressed relative to transpiring leaf area as leaf area-specific hydraulic conductance (K ; Fig. 1a). The functional parameter, K (Grantz & Yang 1996a; Yang & Tyree 1993) overcomes the confounding effects of differing plant size between ozone exposures, experiments and locations, and

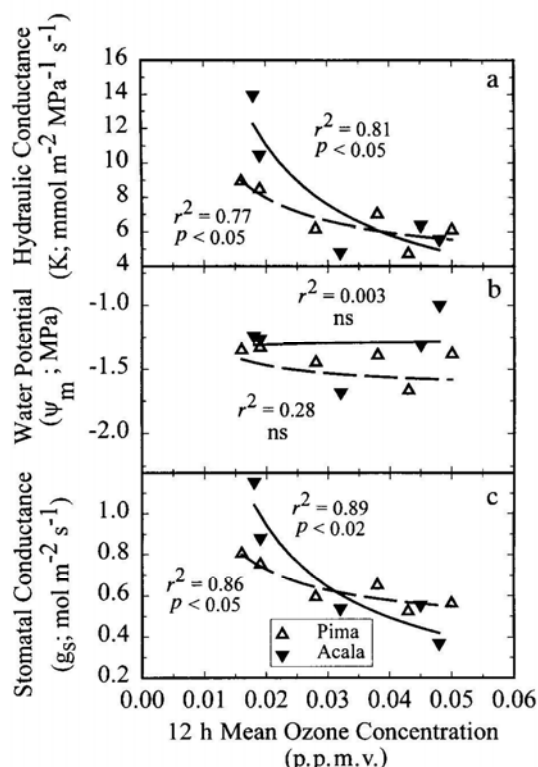


Figure 1. Measured individual relationships for two species of cotton, between 12 h seasonal mean O_3 concentration imposed in field exposure chambers and (a) leaf area-specific plant hydraulic conductance (K), (b) water potential of exposed, transpiring leaves (ψ_m), and (c) stomatal conductance to water vapour of exposed, transpiring leaves (g_s). Data are means of four plants obtained near solar noon on one representative day. Curves are fit by non-linear regression of the form $y = a + b/x$.

relates root capacity to the water and nutrient requirements of the foliage.

The response of K to O_3 was similar in Acala and Pima cottons (Fig. 1a) although sensitivity was higher in Acala. Similar effects of O_3 on K have been reported for younger Pima cotton plants in greenhouse exposure chambers (Grantz & Yang 1996a) and for seedlings of red spruce (Lee *et al.* 1990). This reduction in K (Fig. 1a) could result in a substantial reduction of the mesophyll water potential of transpiring leaves (ψ_m), particularly during the midday period when evaporative demand and transpirational fluxes are maximal. This has been observed (e.g. Heggestad *et al.* 1985; Roberts & Cannon 1992) but is not generally the case. Often ψ_m is unaffected or improved slightly (e.g. Grantz & Yang 1996a; Lee *et al.* 1990; Temple 1986, 1990; Temple *et al.* 1988) reflecting a tight coordination of stomatal and hydraulic conductance. In citrus trees, both positive and negative effects of O_3 on ψ_m have been observed on different days in the same study (Olszyk *et al.* 1991). In cotton, ψ_m exhibits little consistent response to ozone exposure in

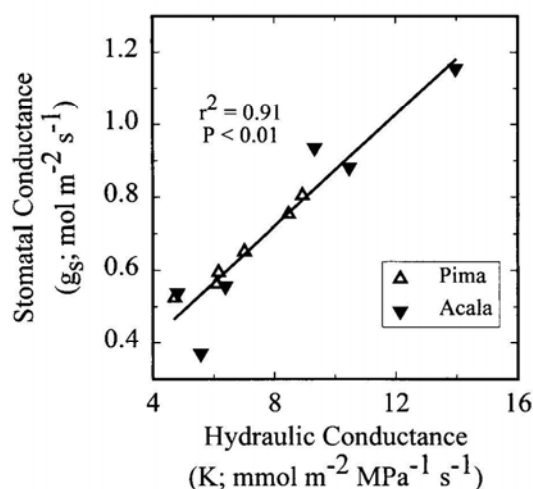


Figure 2. Measured combined relationship for two species of cotton between midday stomatal (g_s ; vapour phase) and hydraulic (K ; liquid phase) conductances to water transport. Data are taken from Fig. 1(a,c). The line is obtained by regression.

mature, field chamber-grown plants (Fig. 1b). Similar results were obtained with other field chamber-grown mature plants (Temple 1986, 1990), and with greenhouse chamber-grown seedlings (Grantz & Yang 1995, 1996a,b).

This homeostasis of leaf water status (Fig. 1b) despite degraded root (Grantz & Yang 1996a) and resulting plant (Fig. 1a) hydraulic capacity indicates that water loss is reduced by declining g_s with increasing O_3 concentration. Reductions in g_s parallel to the declines in K were observed in the present study (Fig. 1c), and in previous studies with Pima cotton seedlings (Grantz & Yang 1996b). In general, a reduction in g_s is observed in response to ozone exposure, although changes in K are infrequently evaluated.

Relationship between stomatal and hydraulic properties

A potential functional relationship between vapour phase (stomatal; g_s) and liquid phase (hydraulic; K) conductances is suggested by the similarity in the responses to O_3 concentration shown in Fig. 1(a,c). Similar relationships were also observed in sugarcane (*Saccharum* spp. hybrid; Meinzer & Grantz 1990) as K and g_s varied with plant age and soil moisture. A strong linear relationship between g_s and K was apparent in sugarcane (Meinzer & Grantz 1990). A similar linear relationship between g_s and K was observed in cotton (Fig. 2) as both declined with increasing exposure to O_3 .

Exposure to O_3 may reduce stomatal conductance in the short term. This may involve direct impacts on guard cell metabolism and indirect effects mediated by inhibition of mesophyll photosynthetic function and resulting increases in intercellular CO_2 concentration (Farage & Long 1995; Farage *et al.* 1991; Moldau *et al.* 1990). However, O_3 may

exposure (Fig. 3; successively lower lines and smaller K). The simulated midday stomatal closure began earlier in the day and persisted longer with decreasing K (Fig. 3). The resulting midday values of simulated g_s (Fig. 4c) described an O_3 dose-response relationship similar to the observed relationship (cf. Fig. 1c). The near homeostasis of simulated ψ_m (Fig. 4b) thus reflects the parallel declines of simulated midday g_s and K (cf. Fig. 4a,c), much as actual ψ_m (Fig. 1b) reflects the parallel declines in actual g_s and K (cf. Fig. 1a,c).

A strong correlation (Fig. 5; solid crosses, solid line) was apparent between these simulated midday values of g_s (Fig. 4c) and K (Fig. 4a), similar to that observed (cf. Fig. 2). The data obtained in field exposure chambers (triangles; from Fig. 2) were well described by the model regression (Fig. 5, triangles). The data obtained from a commercial cotton field with contrasting soil moisture were also well described by the relationship (Fig. 5; squares), particularly at low values of K and g_s , although g_s was higher than predicted immediately following irrigation (Fig. 5; upper squares). Deviations of experimental observations from the model relationship (Fig. 5; cf. triangles and squares, solid line) are well within expected levels of experimental variability (cf. Fig. 2). Yet this simulated relationship developed from model iteration in the absence of any direct modelled impact of O_3 on leaf gas exchange.

The model (Lynn & Carlson 1990) was developed independently of the plant species (cotton) and region (high radiation and evaporative demand; Grantz *et al.* 1997) to which we have applied it. The correspondence between

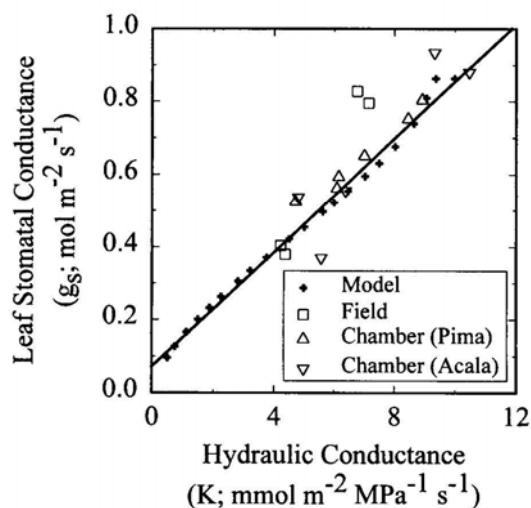


Figure 5. Modelled and measured relationships between midday stomatal (g_s ; vapour phase) and hydraulic (K ; liquid phase) conductances to water transport. Data are from field exposure chambers (Δ , ∇ ; from Fig. 2) or from a commercial Acala field in which hydraulic conductance varied with soil moisture (\square). Model output values (+) are obtained as in Fig. 3 (means 14:00–14:30 PDT) with discrete input values of O_3 concentration during plant development. The line is obtained by regression through the model output only.

simulated and measured relationships at the single leaf level supports the hypothesis that chronic O_3 -induced reductions in g_s could be mediated by reduced carbon allocation to roots, reduced K , and a decline in midday ψ_m . A similar relationship between historic air pollution and K observed in Scots pine (*Pinus sylvestris* L.; Rust *et al.* 1995) was also accompanied by a parallel decline in gas exchange.

Canopy fluxes of water vapour and ozone

It is difficult to observe effects of ambient ozone on extensive canopies, yet these are hypothesized to lead to ecosystem-scale effects on productivity, species diversity, crop yield and forest decline (MacKenzie & El-Ashry 1989). Simulations from the present model over a range of O_3 exposures allowed these effects to be investigated.

Midday values of leaf to air vapour pressure difference in the canopy (V ; Fig. 6a) increased with increasing O_3 concentration and decreasing K . The peak value of V at 14:00 PDT nearly doubled from 1.75 to 3.25 kPa when K decreased from its non-limiting value of 9.4 to 2.2 mmol m⁻² MPa⁻¹ s⁻¹ in response to simulated exposure to

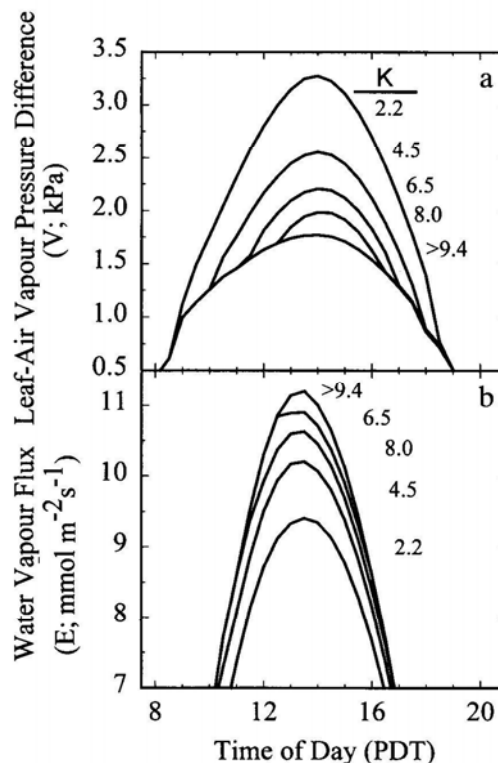


Figure 6. Modelled diurnal courses in a commercial cotton field of (a) leaf to air vapour pressure difference (V) and (b) evapotranspirational water vapour flux (E) under non-limiting hydraulic conductance (inner line in (a); outer line in (b)) and under increasing simulated exposure to O_3 (lower K ; as in Fig. 3).

elevated O_3 during plant development. The increase in V reflected reductions in both evaporative cooling of leaves and in canopy humidification, as g_s declined with K . The substantial midday stomatal closure at the single leaf scale (Fig. 3) led to a substantial reduction in daily water vapour flux at the canopy scale (E ; successively lower lines with lower K , Fig. 6b), although not to a corresponding midday depression of simulated E (e.g. Tenhunen *et al.* 1984) even at very small values of K . This uncoupling of midday E from g_s reflects the occurrence of feedback between g_s and V in the canopy that is not observed at the single leaf level (Jarvis & McNaughton 1986).

The O_3 concentration within the canopy air space ($O_{3,c}$) increased with decreasing K (Fig. 7a) and consequent decreasing g_s (Fig. 3). While K was modelled as a function of O_3 concentration during simulated plant development, the regional values of tropospheric O_3 (C_a ; eqn 5a) over the simulated measurement day were independent of these values and varied diurnally with the same time course and magnitude for all values of K . The increasing values of $O_{3,c}$ within the canopy with decreasing K reflect the reduced uptake of ambient ozone by individual leaves within the canopy associated with reduced g_s and the reduced sink strength of the cotton canopy for O_3 .

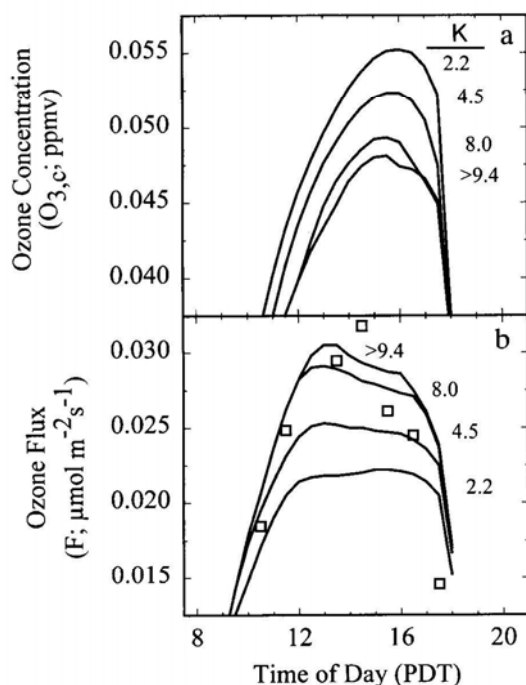


Figure 7. Modelled diurnal courses in a commercial cotton field of (a) canopy-level concentration of O_3 and (b) canopy ozone depositional flux (F) under non-limiting hydraulic conductance (inner line in (a); outer line in (b)) and under increasing simulated exposure to O_3 (lower K ; as in Fig. 3). The squares in (b) are measurements obtained in a well-irrigated commercial field as in Fig. 3.

The ozone flux (F) predicted by the model under conditions of high hydraulic conductance ($0.032 \mu\text{mol m}^{-2} \text{s}^{-1}$ near midday; Fig. 7b; outermost curve with $K > 9.4$) agreed well with field observations ($0.031 \mu\text{mol m}^{-2} \text{s}^{-1}$ near midday; squares, Fig. 7b; Delany *et al.* 1992) obtained with the eddy covariance technique. This deposition of O_3 to cotton, and to other crop surfaces, makes a substantial contribution to O_3 removal from the atmosphere in this environment (Grantz *et al.* 1994).

Canopy O_3 flux (Fig. 7b), including plant and soil components, declined with decreasing K despite the greater driving force for plant uptake represented by the greater O_3 concentration near the leaves (Fig. 7a). This represents a negative physiological feedback at the canopy scale that complicates efforts to predict ozone phytotoxicity in the field from exposures in well-stirred chambers, or from flux-response relationships obtained with individual leaves. This interaction also suggests an additional undesirable consequence of potential climate change. Tropospheric O_3 concentrations may exhibit positive feedback, as increasing O_3 concentration leads to reduced vegetative removal of O_3 from the atmospheric mixed layer.

CONCLUSIONS

Experimental exposure to O_3 caused a reduction in K , restricting water availability to transpiring leaves. This reduction in whole-plant K is attributed to reduced biomass allocation to roots and consequent reduction in root hydraulic capacity. Only minimal reduction in transpiring leaf ψ_m was observed in spite of the reduced K because of a concomitant reduction in g_s . The resulting correlation between liquid phase (g_s) and vapour phase (K) conductances to water transport was highly significant.

Application of a soil/plant/canopy/atmosphere flux model that reduced K realistically with O_3 exposure, and parameterized g_s partially as a function of leaf epidermal water potential (ψ_e), itself a partial function of K , reproduced these systemic effects of ozone exposure on gas exchange performance. Simulated diurnal time courses of g_s agreed well with observations in a low O_3 field environment. Increasing exposure to O_3 during simulated plant development led to reduced simulated K and increasingly severe simulated midday stomatal closure. The model reproduced the significant linear correlation observed experimentally between midday g_s and K , maintaining the homeostasis of simulated ψ_m . The model reproduced canopy-scale fluxes of O_3 under low O_3 field conditions, indicating that these simulations scale appropriately to the extensive canopy level where quantification of O_3 effects has proven difficult. The canopy simulations indicate that deposition of O_3 to vegetated surfaces may decline with increasing concentration of tropospheric O_3 , an unwelcome positive feedback in biosphere-atmosphere exchange.

We conclude that observed effects of chronic O_3 exposure on leaf and canopy gas exchange do not require postulation of a direct physiological impact of O_3 on stomatal or mesophyll photosynthetic function. Rather, O_3 -induced

reduction of root hydraulic function mediated by altered carbohydrate allocation at the whole-plant scale is sufficient to mediate these chronic oxidant effects.

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