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 (gᵥ) 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 gᵥ 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 gᵥ 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 gᵥ that reproduce observations at low ambient O₃ concentration and maintain the positive correlation between midday gᵥ and K observed experimentally at higher O₃ concentrations. Effects mediated by reduced K may interact with more rapid responses of gᵥ 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; Olczyk 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; Olczyk 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 (gᵥ) (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 gᵥ 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.
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 (\( \psi_w \)) or epidermal (\( \psi_e \)) tissue in which the stomata are embedded (Fuchs & Livingston 1996; Shackel & Brinckmann 1985; Bunce 1996). Differences between \( \psi_e \) and \( \psi_w \) 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 \( O_3 \) (Muldau et al. 1990). White \( g_s \), 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; Lehnherr et al. 1987; Pell & Pearson 1983), attributed in part to oxidative modification of sulphhydril residues (Eckard & Pell 1995). \( O_3 \) did not reduce synthesis of Rubisco (Brendley & Pell 1998), but accelerated protoplasting in older leaves. Similar effects on gas exchange mediated by mesophyll responses to \( O_3 \) have been identified by Lehnherr 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; Ollis 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 (gₛ; 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 (ψₑᵣ; 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 gₛ 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

Acacia cotton plants (Gossypium hirsutum L.; cv. Delta Fine 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 conductance.

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 (Dyngage, 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 (Shackell et al. 1992). In this environment. The resulting data agreed (± 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 Olioso 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 (gₛ), and bulk leaf mesophyll and epidermal water potentials (ψₑᵣ, ψₑᵣ) 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:

\[ \frac{1}{K} = 0.025 + 0.30[O₃] \times [1 - 0.20[O₃]^2] \]  

(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 gₛ (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 (ψₑᵣ) 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 (ψₑᵣ) as:

\[ ψₑᵣ = ψₑᵣ - \beta V \]  

(2)

where the constant parameter, \( \beta = 0.02 \) MPa m⁻¹. This relates ψₑᵣ to transpiration (7), through its interdependence
with V, and to \( \psi_m \) through the efficiency of hydraulic connections between mesophyll and epidermis incorporated in \( \phi \). It also incorporates an implicit stomatal response to V through the interdependence of \( \psi_m \) and \( \psi_v \) incorporated in eqns 2-5, rather than the explicit response of \( \phi \) to V in many other treatments (e.g. Jarvis 1976; Grantz et al. 1987). These relationships capture the feed-forward behaviour of \( T \) and \( \psi_m \) 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 \( \psi_v \) from \( \psi_m \), predicting changes in opposite directions under some conditions. This has been considered a potential mechanism 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 (Pranks 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 \( \phi \) is related to photosynthetically active photon flux density (PPFD) and \( \psi_v \) as

\[
g_s = \frac{(a) (PPFD) / (b + PPFD)}{I / \psi_v} = \frac{1}{h_s} (\psi_v - \psi_e) \]

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 \( f(\psi_v) \) is a linear discontinuous stomatal response to epidermal water status (Lynn & Carlson 1990) as

\[
f(\psi_v) = 1 + (b_1 \psi_v) \quad \psi_v > \psi_e \]

\[
f(\psi_v) = 1 + (b_1 \psi_v) + b_2 (\psi_v - \psi_e)^{0.5} \quad \psi_e \leq \psi_v \]

where \( b_1 = -0.0001 \), \( b_2 = 0.3 \), and \( \psi_e = -1.6 \) MPa is the critical epidermal water potential.

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

\[
T = \phi \rho \frac{1}{P (n + \tau_o)} \]

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

\[
E = T + E_s \]

where \( \tau_o \) is leaf resistance and \( \tau_{bl} \) is leaf boundary layer resistance (to water vapour), \( \rho \) is air density, \( P \) is atmospheric pressure, and \( L_0 \) is the latent heat of vaporization of water. Leaf resistance to water vapour (\( \tau_l \)) is composed of the stomatal resistance (\( \tau_s \)) and the cuticular resistance (\( \tau_c = 10 \) s cm\(^{-1}\)), in parallel. \( E_s \) 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 (\( C_o \)) is calculated as

\[
C_o = \frac{C_o}{1 + \frac{\tau_s}{\tau_{tot}}} \]

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

\[
\frac{1}{\tau_{tot}} = \frac{1}{1.32(\tau_{bl} + \tau_c)} + \frac{1}{1.32 \tau_s + 1.66 \tau_c} \]

where \( \tau_{bl} \) is the aerodynamic resistance to water vapour between the ground and the top of the canopy, and \( \tau_{bl} \) is leaf area index corrected by a shelter factor (Lynn & Carlson 1990; Taconet et al. 1986; Olisco 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
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 ($\psi_m$), 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 $\psi_m$ 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 $\psi_m$ have been observed on different days in the same study (Olszyk et al. 1991). In cotton, $\psi_m$ exhibits little consistent response to ozone exposure in 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 homostasis of leaf water status (Fig. 1b) despite the 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 (Farrage & Long 1995; Farrage 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 $y_s$ (Fig. 4b) thus reflects the parallel declines of simulated midday $g_s$ and $K$ (cf. Fig. 4a, c), much as actual $y_s$ (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. 4d), 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 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 $y_s$. 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 1400 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...
elevated O₃ during plant development. The increase in V reflected reductions in both evaporative cooling of leaves and in canopy humidification, as gₑ 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 gₑ reflects the occurrence of feedback between gₑ and V in the canopy that is not observed at the single leaf level (Jarvis & McNaughton 1986).

The O₃ concentration within the canopy air space (O₃c) increased with decreasing K (Fig. 7a) and consequent decreasing gₑ (Fig. 3). While K was modelled as a function of O₃ concentration during simulated plant development, the regional values of tropospheric O₃ (C₃, 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 O₃c within the canopy with decreasing K reflect the reduced uptake of ambient ozone by individual leaves within the canopy associated with reduced gₑ and the reduced sink strength of the cotton canopy for O₃.

The ozone flux (F) predicted by the model under conditions of high hydraulic conductance (0.032 μmol m⁻² s⁻¹ near midday; Fig. 7b; outermost curve with K > 9.4) agreed well with field observations (0.031 μmol m⁻² s⁻¹ near midday; squares, Fig. 7b; Delany et al. 1992) obtained with the eddy covariance technique. This deposition of O₃ to cotton, and to other crop surfaces, makes a substantial contribution to O₃ removal from the atmosphere in this environment (Grantz et al. 1994).

Canopy O₃ flux (Fig. 7b), including plant and soil components, declined with decreasing K despite the greater driving force for plant uptake represented by the greater O₃ 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 O₃ concentrations may exhibit positive feedback, as increasing O₃ concentration leads to reduced vegetative removal of O₃ from the atmospheric mixed layer.

CONCLUSIONS

Experimental exposure to O₃ 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 wₑ was observed in spite of the reduced K because of a concomitant reduction in gₑ, the resulting correlation between liquid phase (gₑ) 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 O₃ exposure, and parameterized gₑ partially as a function of leaf epidermal water potential (ψₑ), itself a partial function of K, reproduced these systemic effects of ozone exposure on gas exchange performance. Simulated diurnal time courses of gₑ agreed well with observations in a low O₃ field environment. Increasing exposure to O₃ 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 gₑ and K, maintaining the homeostasis of simulated ψₑ. The model reproduced canopy-scale fluxes of O₃ under low O₃ field conditions, indicating that these simulations scale appropriately to the extensive canopy level where quantification of O₃ effects has proven difficult. The canopy simulations indicate that deposition of O₃ to vegetated surfaces may decline with increasing concentration of tropospheric O₃, an unwelcome positive feedback in biosphere–atmosphere exchange.

We conclude that observed effects of chronic O₃ exposure on leaf and canopy gas exchange do not require postulation of a direct physiological impact of O₃ on stomatal or mesophyll photosynthetic function. Rather, O₃-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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