Assessment of ozone impacts on vegetation in southern Africa and directions for future research

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LEVELS OF BACKGROUND OZONE IN SOUTHern Africa are high enough to cause concern, as they frequently exceed the 40 ppb threshold currently adopted by the United Nations Economic Commission for Europe. They also surpass the exposure index of 3000 ppb.h, which is intended to protect crops and natural vegetation in Europe. Natural vegetation and crops in southern Africa may be tolerant of elevated ozone concentrations because of naturally high background levels, but additional anthropogenic inputs of ozone precursors may result in exceedances of ozone damage thresholds that affect vegetation. Current impact assessment policies in Europe are shifting from an exposure approach to one based on flux. If existing European methods are to be applied in southern Africa, the flux model would be the more appropriate of the two to assess likely impacts. Besides data requirements for flux modelling, the method would need to accommodate extended growing periods, locally appropriate crops such as maize, and the frequency and extent of drought periods. In southern Africa, crop production may be more greatly affected by drought, floods, and agronomic inputs but the possible deleterious effects of elevated ozone are sufficient to merit further investigation.

Introduction

Tropospheric ozone is the most prevalent and damaging air pollutant to which plants are exposed in many parts of Europe, North and Central America and the Far East.[1–3] In the United States, estimates of the economic loss from the exposure to ozone pollution by crops exceed $3 billion per year, while ozone levels in Europe in 1990 were concluded to cause losses in crop yields of £4.3 billion.[4,5] There has been growing concern that the concentrations of ozone commonly found in the southern African troposphere may adversely affect natural vegetation, forests and crops.[6–11] Some studies on ozone effects on vegetation have been conducted in Egypt[12,13] and South Africa[6,14–16] but, generally, little research of this kind on vegetation has been done in Africa, and specifically in southern Africa.

This paper serves two purposes. First, we consider existing information on environmental ozone to decide whether its influence on vegetation is likely to pose a potential problem in southern Africa. Second, we describe two approaches, namely an exposure model and a flux model, currently used to assess ozone impacts on European vegetation, and consider their application and further research requirements in southern Africa.

Tropospheric ozone in southern Africa

Ozone is a secondary pollutant formed by the reaction of VOCs (volatile organic compounds) and nitrogen dioxide (NO_2) in the presence of the ultraviolet portion of sunlight (<420 nm wavelength). Biogenic sources are estimated to contribute 98% of VOCs, with the balance derived in equal parts from biomass burning and anthropogenic sources.[17,18] VOC emissions from natural ('biogenic') sources differ with vegetation type and are seasonal, dropping by 85% during the dry season when leaves are lost.[19] Motor vehicle emissions are the greatest source of NO_x while biomass burning contributes CO, NO and methane.[20] In spring, soil microbial processes produce a pulse of NO. With the first rains after a long, dry season, the NO flux, as well as N_2O fluxes, can increase by up to 10-fold.[21,22] The combination of the pyrogenic emissions (peaking in May to September) with the beginning of biogenic emissions (September to October) produces enough precursors to result in the high ozone levels measured at the beginning of the southern African summer.[17,23,24] The concentrations of ozone precursors, the complex production and removal processes, and the short lifespan of ozone, mean that ozone concentration in the atmosphere is highly variable[25,26] but has increased since the late 1800s as a result of anthropogenic emissions of ozone precursors.[27]

Tropospheric ozone levels in southern Africa may be high enough to damage vegetation. An ozone concentration value of 40 parts per billion (ppb) is the threshold value used by the United Nations Economic Commission for Europe (UNECE) as the critical level of the gas above which effects on vegetation may occur.[28] Over southern Africa, measurements of total ozone in the lower troposphere (surface to 500 hPa, corresponding to an altitude of about 5 km, or about 3 km above ground level over the high interior plateau) range from 75 ppb (spring 1992) to 37 ppb (autumn 1994).[18] Over rural southern Africa, surface ozone concentrations range between 20 and 40 ppb.[29,30] Mean annual ambient ozone is 22 ppb at Cape Point, South Africa, which is an unpolluted, background measuring station forming part of the Global Atmosphere Watch network.[31] In Zimbabwe, mean annual concentration at the surface was 42 ppb across 14 rural sites.[32] Hourly ozone concentrations have been continuously measured at Maun, a remote small town in a rural setting in northwestern Botswana. The hourly mean is reported to be 50 ppb with a maximum of 150 ppb. Monthly means exceeded 40 ppb in September, October and November 1999, and from July to November 2000 (Fig. 1).[33]

In the heavily industrialized mining and energy generation region of the South African highveld, maximum hourly means of 77 and 110 ppb have been measured at Verkykkop and Elandsfontein, respectively. Maximum daily means over 40 ppb were recorded at four out of five highveld monitoring stations in 1994.[33,34] These ozone records stem from a variety of sources with different measurement methods, and so comparison is not possible. Nevertheless, the various data show that elevated ozone levels occur frequently, and over a wide area of southern Africa. Regional model outputs also indicate that hourly ozone concentrations exceeding 40 ppb commonly occur over large parts of the subcontinent.[35]

Ozone effects on vegetation

Most of our understanding of the effects of ozone is based on agricultural crops and selected forest species. Crops, in particular, are well suited to defining the quantitative relationships between ozone exposure and the effects of interest. The following discussion focuses on crop plants, and annual crops in particular, as existing knowledge on ozone effects on commercial crops can be readily applied

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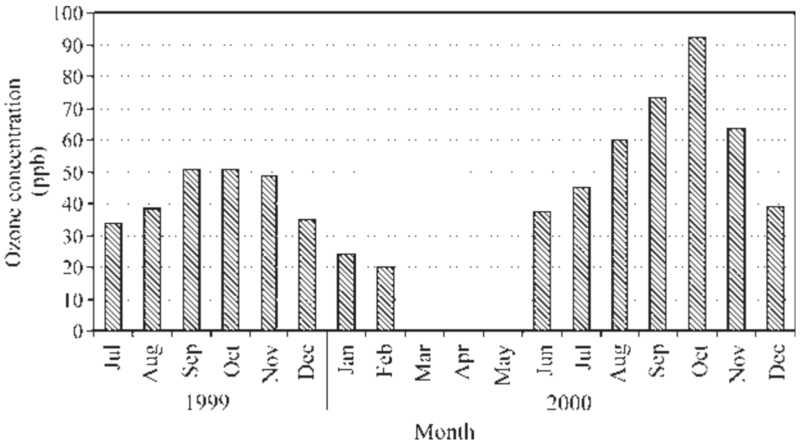

Fig. 1. Mean monthly ozone concentrations measured at Maun from July 1999 to December 2000.

to southern Africa, whereas this is not the case for northern hemisphere trees and natural vegetation. Ozone impacts on natural ecosystems are only recently being investigated in any depth in Europe[36,37] and there is no record of experimental work on the consequences of ozone on natural vegetation in southern Africa.

Ozone damage may occur even if visible symptoms are not evident, as the gas reduces plant growth and changes the distribution of assimilates within the plant.[2,3,38–40] Visible ozone injury commonly appears as small flecks or stipples on the interveinal areas of the upper leaf surface. The flecks may be white, red, black or bronze, depending on species and may join to form extensive areas of chlorosis as the leaf ages. Damage to foliage can be extensive enough to cause complete loss of leafy crops such as lettuce and chicory.[39] Visible symptoms of ozone effects must be interpreted with caution, particularly in field studies where interactions with other pollutants and stresses may confuse results.

Reduced yields are the most commonly reported measures of ozone exposure for crops, whereas growth parameters are used for trees and herbaceous plants.[5] Hypotheses to explain how ozone suppresses growth and yield include mechanisms of membrane damage, reduced photosynthetic capacity, changes to carbohydrate allocations, hypersensitive responses and accelerated senescence.[41–44] Plants may respond by compensatory or defensive reactions, such as avoidance of exposure through stomatal closure, detoxification of ozone by chemical reaction, adjustment by changing metabolic pathways, or repair of damaged tissue.[45] Ozone may erroneously trigger the pathogen-defence pathway, resulting in a hypersensitive response.[46] Local experiments have shown that this is a likely response for *Zea mays* (maize) to moderate levels of ozone exposure (120–150 ppb) that may have significant effects on crop yields (J.U. Grobbelaar, pers. comm.).[16] As shown earlier, such ozone concentrations occur over parts of southern Africa.

The intensity and duration of ozone exposure may produce plant responses which differ in both mechanism and effect. Stomatal response to ozone requires biochemical reactions with a time delay before the stomata close. Since closure may lag, short-term exposures to high concentrations may be more damaging than longer exposures at lower concentrations, where ozone uptake is limited by stomatal closure. Exposure of local rust-resistant and susceptible cultivars of *Helianthus annus* (sunflower) to 230 ppb ozone for a short period resulted in stress symptoms in several photosynthetic properties, with the resistant plant showing faster recovery.[15] Under short-term diurnal exposures, plants can react defensively against the ozone stress and produce compensatory growth. Under chronic low concentration exposure to ozone, the constant stress may inhibit defence reactions. The defence capacity of plants may thus be induced by ozone exposure or exhausted by long-term exposure to high concentrations.[45,47]

The influence of ozone on plants may be measured at the physiological level by investigating photosynthetic criteria such as yield of photosystem II and electron transport rate,[16] perioxidase activity, ascorbate content[48] and chlorophyll *a* and *b* content,[40] and water use, yield and biometric parameters.[49] At the community or ecosystem scale, ozone exposure may select against sensitive individuals and species and may result in more ozone-tolerant populations that change the floristic composition of the plant community.[36,50–52] Furthermore, exposure may also lead to increased incidence of fungal infection and disease pests.[53–55]

Southern African data indicate that ozone levels may be high enough, and of sufficient duration, for vegetation to be affected. Before more rigorous investigation of ozone impacts in the subcontinent, however, it is useful to examine the methods of assessment adopted elsewhere. In the following section, we consider two such approaches and indicate future research needs.

The European approaches to ozone impact assessment

The ozone exposure approach

The United Nations Economic Commission for Europe currently uses the AOT40 concept as the basis for mitigation and reduction strategies to prevent ozone pollution damage to plants. The AOT40 index refers to accumulated ozone exposure above a threshold of 40 ppb (the sum of daytime hourly ozone concentrations minus 40 ppb, if the concentration is more than 40 ppb). Accumulation is performed only over daylight hours because of stomatal closure at night, when ozone is not taken up. A standard growing season of three months is assumed for crops[28,56] and natural vegetation.[57] The units of the AOT40 index are ppb.h. The AOT40 threshold is strongly correlated with reduced crop yields under European conditions.[28] Data on species-specific dose responses to ozone are scarce, so models and assessments are often based on a single representative species determined under test conditions.[2,3,58–60] The current critical level for crops and sensitive herbaceous natural ecosystems (AOT40 of 3000 ppb.h) is based on an exposure-response function derived for grain yield of wheat grown in open-top field chamber studies in northern and central Europe.[2,28,58] For trees, the critical level for significant growth reduction is currently set at an AOT40 of 10 ppm.h or 10 000 ppb.h.[47] Recent European studies suggest that adverse effects on trees are possible below 25 ppb, which is near to the pre-industrial background concentrations of ozone,[47] and it may be appropriate to reduce the AOT40 index value to 5000 ppb.h for sensitive tree species.[61]

Calculated AOT40 values in southern Africa

Monthly AOT40 values were calculated for the growing seasons of 2000 and 2001 using continuously monitored ozone values for Maun (Table 1). The growing season lasts from October to March each year, several months longer than the

Table 1. Monthly AOT40 values calculated for Maun, Botswana, using daylight hours (10:00–17:00).

Month (ppb.h)	Monthly AOT40(ppb.h) (ppb.h)	Accumulation over growing season
October 2000	13 770	
November	8 850	22 620
December	2 400	25 020
January 2001	5 210	30 230
February	N.D.	–
March	N.D.	–

N.D., not determined.

corresponding period in Europe. Ozone data were only available for the first four months of this period. The UN ECE threshold of 3000 ppb.h over three months, set for the protection of crops and natural vegetation in Europe, is exceeded in three of the four months at Maun.

AOT40 values were also calculated using continuously monitored hourly ozone data from a monitoring network on the South African highveld where concentrations over 40 ppb were frequent throughout the year.[6,7] Palmer is a site at 2000 m above mean sea level, 100 km east (downwind) of the main centres of industrial emissions, whereas Rivulets is at 800 m above mean sea level, about 150 km east of the main emission sources. Both sites are located within commercial forests of pines (*Pinus* species) and gum trees (*Eucalyptus* species). AOT40 values were calculated over daylight hours (06:00 to 18:00) and accumulated over the entire year, whereas the UN ECE calculation uses a shortened daylight period and only three months. At the Palmer site, the 10 000 ppb.h critical level for trees was exceeded every year and concentrations over 40 ppb occurred for at least 6–8 hours each day (Table 2).

Although comparison with the UN ECE guideline is not valid because the calculation methods differ, these values nevertheless reflect that ozone exposure is high on the highveld. It should also be noted that ozone concentrations are lowest near the earth's surface and generally increase with altitude. Ozone measuring equipment is seldom sited at the height of the surrounding vegetation, and so ambient ozone measurements may be inappropriate for crops. Mean daytime concentration has been shown to be 15–25% lower at the level of short vegetation (crops, grass) than that of ozone sensors at a typical height of 5–10 m.[62] Although these AOT40 values may overestimate the actual exposure of plants, some effect of ozone exposure on tree growth or functioning may be expected.

General limitations of the AOT40 concept

The limitations of the AOT40 concept are well acknowledged and debated,[58] but the approach has nevertheless been considered a fair compromise between sophistication, existing experimental data (at least for Europe) and practical needs.[62] Currently, AOT40 values are used to identify geographical areas in Europe where there is some risk of damage to vegetation from ozone,[47,56] but the approach cannot be used to derive actual yield loss.[63,64] Accurate estimates of yield loss must consider biological and climatic factors that influence the dose and response at a specific site for a particular period.[63]

Ozone exposure at a particular site may be dominated by either the frequency or intensity of the exceedance of 40 ppb, but this distinction is not reflected in the AOT40 concept.[62] Differences in growth responses and visible plant injury were evident in birch trees exposed to the same AOT40 value (14 000 ppb.h) but three different ozone exposure profiles. High peak concentrations produced visible symptoms of injury, and may have coincided with periods of maximum stomatal conductance, but were not important in reducing growth trajectories, suggesting that there was sufficient recovery time to activate defence reactions.[47]

The method and period of calculation is also a weakness of the AOT40 index as it is highly sensitive to relatively small changes in concentration near the threshold of 40 ppb.[62,64] The defined accumulation period may not coincide with the growing period of selected vegetation receptors as growing period varies with climate. Plant phenology may also strongly influence plant responses to ozone.[62] The use of daylight hours only for calculating AOT40 has also been questioned, as nocturnal stomatal conductance has been confirmed at least for several tree species. Plants may be more sensitive to ozone at night because their detoxifying capacity is diminished.[47]

Accommodating all these factors has led to a shift from the exposure concept, as exemplified by the use of the AOT40 criterion, to a flux-based approach.

The ozone flux approach

Ozone flux is here defined as the rate at which plant surfaces absorb ozone.[45] A flux concept, rather than a general risk assessment which is based on exposure to ambient concentrations, is biologically more acceptable. Plants respond to the stomatal ozone flux, or internal dose, rather than ambient concentrations, so the biological response should be expressed in terms of a relevant flux-based parameter rather than a measure such as the AOT40 index.[62] Flux-based ozone exposure models provide a more consistent relationship between relative yield loss and ozone exposure than the AOT40 approach.[56,63] Phenology (growth stage), and factors influencing the transport of ozone from the atmosphere to plant level such as wind speed and heat flux, and the stomatal uptake of ozone (radiation, vapour pressure deficit, temperature and soil moisture) all influence ozone uptake.[49,56,63,65] The timing of plant exposure to ozone, whether during periods of rapid or minimal photosynthesis, may also be critical in determining how plants respond to the pollutant.[45]

Flux modelling has demonstrated that, in many cases, high ozone fluxes occur

Table 2. Extent of exceedance of the 40 ppb limit during daylight hours (06:00–18:00) at two rural sites in South Africa.

Site (elevation*)	Year	Number of days with at least 1 hour with ozone >40 ppb	Mean number of daylight hours with ozone >40 ppb	Accumulated exposure exceeding 40 ppb for the year (ppb.h)
Palmer	1990	218	7.9	20 500
(2000 m)	1991	150	8.0	13 150
	1992	232	7.6	19 180
	1993	134	6.7	9 890
Rivulets	1992	91	6.5	4 810
(800 m)	1993	60	3.6	1 450

*Metres above mean sea level.

with only moderate AOT40 values.[56,63] Vapour pressure deficit (VPD) is considered to be the most important factor influencing ozone uptake, as high VPDs that limit conductance tend to occur with high ozone concentrations. Soil moisture deficit, phenology and temperature effects also affect stomatal conductance and so limit ozone uptake.[56,63] In southern Africa, where high temperatures and low relative humidity are typical during the frequent droughts, ozone uptake may be reduced because of stomatal closure caused by low soil moisture availability.

Assessing ozone impacts on vegetation in southern Africa

At several southern African sites, estimates of AOT40, an indicator of cumulative ozone exposure, are well above the 3000 ppb.h critical level set in Europe to ensure protection of crops and natural vegetation. The deleterious effects of ozone exposure on both natural vegetation and crops would therefore seem likely but, apart from controlled experimental work,[14–16] there are no reports of such damage in southern Africa.

A likely explanation for this absence of evidence from the field is the lack of awareness of potential ozone effects and the signs and symptoms of damage. Visible symptoms may be mistaken for any number of diseases or nutritional deficiencies and reduced yield may be accounted for by numerous factors, particularly drought, that influence crop productivity. An equally plausible explanation is that local vegetation may already have evolved tolerance to high ozone levels. Elevated ozone levels may be a 'natural' background condition in southern Africa because of frequent and widespread grass and bush fires. Local vegetation has had millennia to respond to elevated ozone with ozone-tolerant plants; ozone-sensitive crops simply would not perform well and would not be replanted.

To resolve the uncertainty, a number of issues need investigation. Both the AOT40 and flux models must be reconsidered before regionally appropriate assessments can be undertaken.[66] The flux-based approach is biologically more appropriate, but it requires a considerable amount of data compared to the AOT40 index. The flux approach requires species-specific parameters to calculate stomatal conductance as a function of phenology, and environmental conditions such as irradiance, soil moisture, leaf temperature and vapour pressure deficit. Stomatal function, soil data, meteorology and ozone exposure can then be used to calculate the instantaneous flux of ozone experienced by leaves in the upper canopy.[56]

Selection of appropriate species for further research

Future research on ozone impacts in southern Africa should ideally focus on local varieties of maize, wheat or sunflowers. Maize is the most widely grown crop in southern Africa, with about three million hectares planted in South Africa alone. Not only is maize commercially important, it also serves as a cruicial source of nutrition for both rural and urban farmers across the region.[67] Wheat (*Triticum aestivum*) was used to define the AOT40 limit considered to protect all crops and natural vegetation in Europe. It is grown in southern Africa in the Western and Eastern Cape and Free State provinces of South Africa and in the north of Zimbabwe. In all cases it is a winter crop, raised between May and September. In South Africa, about a million hectares are planted to wheat, of which about 15% is under irrigation. Sunflowers are also widely planted in South Africa (about 500 000 hectares) and have already been used in local impact studies.[15] Of these crops, maize is our choice as the most appropriate indicator species for ozone impacts in the subcontinent.

Determining vegetation impacts

To date, no reports of crop yield reductions or visible symptoms of foliage damage have been attributed to ozone anywhere in southern Africa. It must be cautioned, however, that the recognition of ozone effects and demonstrating cause-and-effect requires a considerable and sophisticated investigation involving locally appropriate dose–response functions derived under controlled conditions. Although such relationships have been derived for maize,[68–70] they are not available for southern African varieties. Furthermore, ozone tolerance differs between and within species.[15,47,49,71]

Interactions with other stresses

Interactions with other stressors, such as other pollutants and drought, must be considered in any southern African ozone impact assessment. As global levels of CO_2 rise, plant growth and yield are anticipated to increase in response. With higher atmospheric CO_2 concentrations, plants may be protected from ozone uptake because of reduced stomatal conductance. Similarly, under drought conditions, stomatal closure to prevent water loss serves to prevent ozone uptake and so protects the plant. Plant species and cultivars vary in response to elevated ozone and CO_2 singly and to mixtures of both. Experiments on maize and wheat demonstrated that CO_2 enrichment benefited the latter but not maize, whereas ozone exposure reduced the grain yield of both maize and wheat.[68] With mixtures of both gases, growth stimulation by CO_2 enrichment was greater when O_3 concentration was also high although the mechanism of protection offered by elevated CO_2 is not known.[72]

Timing of assessment

The timing of pollution exposure episodes over the lifespan of a plant can determine their effect on plant growth and productivity. Plants may be sensitive at some growth stages and tolerant at others.[65] The leaves of seedlings are particularly sensitive to ozone exposure, but young leaf tissue has a higher concentration of anti-oxidants than older leaves. Higher ascorbate content in young leaves protects them from visible leaf injury.[73,74]

Ozone sensitivity in seed crops is greatest during the period between anthesis (flowering) and seed maturity, with sensitivity lower before and after.[75] Both wheat and bean were less sensitive to ozone in the pre-flowering period than at subsequent stages of growth. Ozone exposure between anthesis and end of grain filling decreased the grain yield of wheat by 11% compared with exposure before anthesis.[40] Even in plantain, which has an indeterminate growth pattern, ozone effects were most pronounced when plants were exposed halfway through their development.[65]

Ozone-induced declines in leaf longevity are considered the main factor responsible for the negative effects of the pollutant on grain yield. This is because the flag leaf, the uppermost leaf of a reproductive cereal shoot, situated immediately below the ear, has a shorter lifetime and reduced chlorophyll content after ozone exposure.[40,65] In wheat, and probably in other cereal crops, it is the most important source of photosynthate for grain filling. Maximum conductance in flag leaves of wheat also occurs just before the beginning of grain fill, so ozone exposure after anthesis is more important than during establishment.[40] At higher ozone exposures, the senescence of flag leaves accelerates.[40,65] Between 60% and 70% of assimilates transported to the developing wheat grain is derived from current photosynthesis and about 30–40% is retranslocated from storage pools. Lower leaves receive less direct sunlight, are older and more senescent, so they contribute less to grain filling than the upper leaves. The lower leaves also tend to have a lower conductance and so take up less ozone per unit of leaf area.[63]

In wheat, anthesis is essentially completed within one week, although the geographical spread of wheat across Europe means that anthesis spans a six-week period from the Nordic to Mediterranean countries.[65] Similarly, maize flowering is differentially spread across southern Africa. The seed is typically planted in southern Africa in October but, depending on the date of first rains in a given year, this could be as late as January. Planting dates also take into account the likelihood of a midsummer drought, during which pollination and fertilization are reduced. Anthesis is reached 60–90 days after planting, and the crop is harvested after about 120 days. Regional assessments of ozone exposure would need to take both the geographical and temporal differentiation of maize production into account.

Conclusions

The abundance of naturally occurring ozone precursors in the southern African atmosphere elevates ozone levels in the lower troposphere. Additional contributions of these precursors from anthropogenic sources could raise ozone concentrations to levels beyond the natural tolerance of native plants and locally adapted crops. Approaches to assessing the effects of ozone on vegetation in southern Africa, should differ from those in Europe and must take into account local conditions, such as extended growing seasons, and that soil moisture is frequently a growth limiting factor. Flux-based modelling, rather than the AOT40 approach, should be attempted using available site-specific data. Importantly, locally derived dose–response functions are needed for local crop cultivars. Crop production in southern Africa may be more dramatically affected by drought, floods, and agronomic inputs, but the potential influence of elevated atmospheric ozone should not be ignored.

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