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Substantial yield reduction in sweet potato due to tropospheric ozone, the dose-response function[☆]

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ABSTRACT

Impacts of tropospheric ozone on sweet potato (*Ipomoea batatas*) are poorly understood despite being a staple food grown in locations deemed at risk from ozone pollution. Three varieties of sweet potato were exposed to ozone treatments (peaks of: 30 (Low), 80 (Medium), and 110 (High) ppb) using heated solardomes. Weekly measurements of stomatal conductance (gs) and chlorophyll content (CI) were used to determine physiological responses, along with final yield. gs and CI were reduced with increasing ozone exposure, but effects were partially masked due to elevated leaf senescence and turnover. Yield for the *Erato orange* and *Murasaki* varieties was reduced by ~40% and ~50% (Medium and High ozone treatments, respectively, vs Low) whereas *Beauregard* yield was reduced by 58% in both.

The DO_3SE (Deposition of Ozone for Stomatal Exchange) model was parameterized for gs in response to light, temperature, vapour pressure deficit and soil water potential. Clear responses of gs to the environmental parameters were found. Yield reductions were correlated with both concentration based AOT40 (accumulated ozone above a threshold of 40 ppb) and flux based POD_6 (accumulated stomatal flux of ozone above a threshold of 6 nmol m^{-2} s^{-1}) metrics (R^2 0.66 $p = 0.01$; and R^2 0.44 $p = 0.05$, respectively). A critical level estimate of a POD_6 of 3 (mmol m^{-2} Projected Leaf Area^{-1}) was obtained using the relationship. This study showed that sweet potato yield was reduced by ozone pollution, and that stomatal conductance and chlorophyll content were also affected. Results from this study can improve model predictions of ozone impacts on sweet potato together with associated ozone risk assessments for tropical countries.

1. Introduction

Tropospheric (ground level) ozone (O_3) is a secondary air pollutant posing current and future risks to human health, vegetation and crops (Fleming et al., 2018; Mills et al., 2018a). It is formed from chemical reactions in sunlight between pre-cursor gases (including carbon monoxide (CO), nitrogen oxides (NO_x), methane (CH_4) and non-methane volatile organic compounds (Simpson et al., 2014; Monks et al., 2015; Tiwari and Agrawal, 2018). O_3 air pollution is a global issue that is estimated to reduce yields of major crops such as wheat (by 6%–10%, Mills et al., 2018b) and rice (by ~3%, Tai et al., 2021). Future (predicted to 2080) O_3 related yield losses are estimated to be in the range of 10.4–12.5 billion USD for wheat and 6.7–10.6 billion USD for rice (Sampedro et al., 2020). Modelled data suggests that O_3 'hotspots' are occurring in crop growing tropical regions such as equatorial and southern Africa, and parts of Asia, where 7 h, 3 month mean, concentrations can exceed 56 ppb (Emberson et al., 2018). Whilst measured data of trends in tropospheric O_3 across continents like Africa is sparse, air quality monitoring stations in South Africa have regularly measured O_3 levels above the South African air quality standard limit (8 h moving average of 61 ppb) (Laban et al., 2018). In Rwanda daily measured mean values have exceeded 70 ppb during the dry season (DeWitt et al., 2019). Long term observational data from east Asia has also revealed seasonal means of O_3 of above 50 ppb (Wang et al., 2019), and daily maximum 8 h moving average O_3 concentrations were recorded in Korea at 52 ppb in 2017 (Kim et al., 2021). Measured monthly mean ozone concentrations exceed 50 ppb for some months at several sites in countries including India (Sharma et al., 2016), China (Liu et al., 2021) and Japan (Ito et al., 2021). These concentrations are also predicted to increase, especially in rapidly developing regions (Huang et al., 2018; Turnock et al., 2018).

The primary route for O_3 damage to plants follows O_3 uptake via leaf

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stomatal pores. Within the leaf, O_3 reacting with apoplastic fluid creates reactive oxygen species (ROS) which can result in changes to cell structure and the initiation of cell defence mechanisms (Ainsworth, 2017; Emberson et al., 2018). In O_3 sensitive vegetation this can lead to impacts including visible leaf damage, early senescence, reductions in flower numbers and seed production. In crops this can result in reductions in crop yield, and crop quality (Feng and Kobayashi, 2009; Fuhrer, 2009; Ainsworth et al., 2012). The mechanisms of impact vary between species, with some impacts occurring through reduced resource availability and others through changes in resource allocation. Many major crops such as cereals, rice, potato and beans are affected, however, sensitivity to phytotoxic O_3 doses varies among species and between varieties/cultivars (Shi et al., 2009; Mills and Harmens, 2011; Mishra and Agrawal, 2015; Pandey et al., 2019). Features that can influence ozone sensitivity of different cultivars of the same species include enzyme activity (Lee et al., 2007) and stomatal conductance (Brosche et al., 2010).

Impacts of O_3 on temperate crops are well established (e.g. wheat, rice, potato, pulses, as summarised in Mills et al., 2007). However, impacts on tropical crops are less well understood. Emerging research has shown the detrimental effects of O_3 pollution on tropical crop varieties including wheat and beans (Hayes et al., 2019). Sweet potato (*Ipomoea batatas*) is a commonly grown tropical root crop (~110 countries worldwide; FAOSTAT, 2019) used in commercial as well as small scale agriculture (Low et al., 2015; Ezin et al., 2018). Requiring low inputs it is a versatile and popular crop for intercropping systems and in subsistence farming (Low et al., 2009; Nedunchezhiyan et al., 2012) and is promoted in food security, land regeneration, and climate change adaption projects (Saadu et al., 2009; Abidin et al., 2017; Iese et al., 2018). Sweet potato provides a source of iron, protein, fibre and vitamins, and the orange-fleshed varieties in particular have been identified as being helpful in addressing dietary vitamin A deficiency (Motsa et al., 2015; Laurie et al., 2018).

Despite the importance of sweet potato in many developing countries, the effect of current and predicted future O_3 pollution on its production is poorly understood. Sweet potato is a highly transpiring plant with stomata on both the upper and lower (majority) side of the leaf (Saadu et al., 2009) and as such is susceptible to injury through the stomatal flux of O_3. O_3 has been found to reduce the photosynthetic activity of sweet potato leaves by 28% (Kim et al., 2007). Their study (Kim et al., 2007) showed that antioxidant enzymes in the apoplast of the sweet potato leaves were induced following exposure to elevated O_3, and its subsequent reaction with parts of the cell wall, leading to the formation of ROS. Reduction in the photosynthetic rate, due to O_3 exposure, has been shown to reduce the yield of potatoes (Vandermeiren et al., 2005). However, foliar damage not only impacts on the amount of carbon assimilation, but can also effect the translocation of reserves between above and below ground portions, in terms of quantity and quality (Kollner and Krause, 2000; Wilkinson et al., 2012; Kumari and Agrawal, 2014). In potato plants Asensi-Fabado et al. (2010) found increased callose deposits in the phloem (produced as a response to stress, or in small deposits as a normal part of senescence), in plants exposed to elevated O_3, which restricted the supply and circulation of photosynthetic assimilates from leaves to tubers.

To our knowledge, there is only one published study on the impact of O_3 on sweet potato yield. This showed that tuber yield was significantly reduced after 4 weeks of exposure to O_3 at ~65 ppb (8 h daytime mean) for plants grown in Teflon film exposure chambers within a greenhouse (Keutgen et al., 2008). Ozone exposure studies on tropical crops, and in particular studies in developing regions are somewhat scarce as ozone exposure facilities are expensive to build and run, and required a reliable electricity supply.

Due to the uptake of O_3 via stomata, plant responses are more closely related to the dose received rather than ambient O_3 concentrations (Mills et al., 2011a). Flux based metrics are commonly used in modelling as these can better reflect the risk of O_3 impacts to vegetation (Emberson et al., 2000; Anav et al., 2016). Modelling the impact of O_3 on crops in different regions of the world provides a basis for assessing the risk of O_3 air pollution and is used to develop multi-effect protocols that inform policy decisions (Ashmore, 2005; UNECE, 2017; Emberson et al., 2018). Determining O_3 critical levels (the concentration, cumulative exposure or cumulative stomatal flux above which detrimental effects on vegetation occur) for specific crops forms an important part of this. There is a lack of data relating to sweet potato stomatal conductance under varying meteorological conditions, and impacts of phytoxic O_3 doses on yield, which are required to parameterize flux based models.

The DO$_3$SE model (Deposition of O_3 for Stomatal Exchange, https://www.sei-international.org/do3se; Emberson et al., 2000) is a dry deposition model that has been used to estimate the stomatal flux of O_3 to various land-cover types and plant species including root (Pleijel et al., 2007) and tropical crops (Hayes et al., 2020). The model was developed to account for variations in stomatal opening due to meteorological, soil, and plant specific factors, and is able to provide estimates according to UNECE LRTAP (Long-Range Transboundary Air Pollution) methodologies for effects-based risk assessment (UNECE, 2017).

This study aimed to assess the sensitivity to O_3 of sweet potato. We hypothesized that sweet potato would be sensitive to O_3 due to its high stomatal conductance, and that O_3 damage would lead to chlorophyll damage and premature senescence of leaves. Therefore, in this study we recorded growth and physiological responses (e.g. stomatal conductance, chlorophyll index, and yield) of three varieties of sweet potato to ambient and elevated O_3 concentrations and in doing so provide data for the parameterization of the DO$_3$SE model and an estimation of the O_3 critical level. This will provide important information on the ozone sensitivity of this widely grown staple food crop of tropical regions to enable improved risk assessment of ozone pollution on food security in tropical regions.

2. Material and methods

2.1. Plants and treatments

The experimental work took place at the UK Centre for Ecology & Hydrology's air pollution facility at Abergwyngregyn, North Wales (53.2°N, 4.0°W). Sweet potato (*Ipomoea batatas*) plug plants (Thompson and Morgan, UK) were each potted into 25 L tubs (35 × 37 cm) filled with John Innes No. 2 (J. Arthur Bowers, UK) compost when they had 4-6 true leaves, and the plants had 6-10 true leaves at the start of the ozone exposure. Two orange fleshed varieties were grown: *Erato orange* in 2019 and *Beauregard* in 2020 and 2021 (Table 1). The white fleshed *Murasaki* variety was also grown in 2021. The pots were randomly distributed between three heated (ambient +6 °C) solardomes (dome shaped glasshouses of 3 m diameter and 2.1 m height). 6 °C was chosen to provide growing conditions suitable for this tropical/warm temperate species, which require temperatures of 21–26 °C to produce tubers.

The solardomes were ventilated at a rate of two air changes per minute with charcoal filtered air injected with controlled levels of O_3 which was generated using concentrated oxygen (G11 O_3 generator,

Table 1
Dates of planting (from plug plants into 25 L tubs), O_3 exposure treatments, and tuber harvest for each variety of sweet potato.

Variety	Potted (from plugs)	O_3 treatment start	O_3 treatment end	Harvest
Erato orange	June 11, 2019	June 13, 2019	October 10, 2019	November 19, 2019
Beauregard	June 26, 2020	August 08, 2020	October 18, 2020	November 04, 2020
Beauregard	May 17, 2021	June 03, 2021	October 25, 2021	November 23, 2021
Murasaki	May 17, 2021	June 03, 2021	October 25, 2021	November 23, 2021

Pacific O_3 USA, and AirSep NewLife Intensity 10 L Oxygen Concentrator, CAIRE Inc. USA). O_3 delivery was controlled by LabVIEW software (version 2012, National Instruments, USA). O_3 concentrations were measured every 30 min (for 5 min) using two O_3 analysers (API 400A Envirotech, UK and 49i Thermo Fisher Scientific, USA) of matched calibration. Air temperature, relative humidity and light was monitored inside the solardomes (Skye Instruments, UK).

3. Experimental conditions

Each solardome contained 4 replicates to undergo exposure to either Low, Medium or High O_3 exposure (daytime target maximums: ~30 ppb, ~80 ppb, and ~110 ppb, respectively). To represent the episodic nature of O_3 pollution, for two days of the week all treatment domes received the Low O_3 level. For the control treatment a mean ozone concentration of ~20 ppb (and a maximum of 30 ppb) was used rather than pre-industrial ozone concentrations as this was to represent current clean air conditions.

Due to disruption caused by Covid-19 the exposure period for the Beauregard variety grown in 2020 was shorter than for the other seasons (Table 1). O_3 exposure levels were similar over the 2019 and 2020 growing seasons, but were slightly reduced in 2021 (Table 2, mean hourly profiles for each day of the week are also shown in the supplementary information, Figure S1).

The average day time air temperature in the solardomes over the treatment periods was 29 °C (±0.1) in 2019, 25 °C (±0.1) in 2020, and 28 °C (±0.0) in 2021. Night time average air temperature was 21 °C (±0.0) in 2019, 18 °C (±0.1) in 2020, and 22 °C (±0.0) in 2021.

3.1. Plant measurements

Over the growing seasons general observations were made of leaf injury. During 2019 (9 July - 19 November) and 2020 (14 July – 14 October) weekly measurements of stomatal conductance (gs, mmol H_2O m^{-2} s^{-1}; AP4 porometer Delta-T, UK), with simultaneous non-destructive measurements of chlorophyll content index (CI; CCM200 m, Opti-Sciences, USA), and soil moisture (ML2 probe attached to HH2 Moisture meter, Delta-T, UK) were taken. During 2021 (22 June – 15 September) additional gs (and accompanying) measurements were taken on sunny days when gs was expected to be high to ensure that g_{max} (maximum gs as defined in the DO_3SE model description below) could be established. A total of 1368 stomatal conductance measurements were made, each with associated CI and soil moisture and covering all years and varieties. For all measurement periods the majority of gs measurements were taken from the lower surface of the leaf because this surface had higher stomatal conductance than the upper surface. In addition, some paired measurements were also taken from the upper and lower surface of leaves to determine the lower to upper leaf ratio in order to express gs based on projected leaf area. On the mature plants gs was recorded from leaf four or leaf five along the vine (where leaf one was the first fully unfurled leaf at the growth tip), as these were representative of fully expanded leaves of the plant canopy. Some additional sets of measurements were made from all leaves along the length of the vine. To explore any differences between the treatments and the variation in photosynthetic rates with leaf agetwo specific sets of measurements of gs (and ancillary measurements) were taken for leaves along the vine: for *Erato orange* on 21 August and 11 September (2019); and for *Beauregard* on 12 August and 15 September (2020).

Plants were harvested at the end of the growing season (November, see Table 1 for specific dates) and the fresh weight of tubers was recorded.

3.2. Statistical analysis

Data analysis was carried out using R (version 3.6.3, R Core Team, 2020) and model residuals and plots were checked for the appropriateness of each model. Data of gs and CI was analysed separately for each experimental year. The response of representative leaf gs and CI to the fixed factors of day of the year and O_3 treatment (as well as their interactions) were separately explored using linear mixed models (package 'nlme', Pinheiro et al., 2017) with the random effect of plant identification number (ID) and maximum likelihood (ML) estimation. gs (2019 & 2020) and CI (2020) data were log transformed prior to subsequent analysis. Dates were analysed using the day of the year number with a quadratic polynomial applied. The suitability of the inclusion of an autoregressive (AR) correlation term for repeated measures was determined by plots and model fit. The best model fit was assessed using comparisons of Akaike's Information Criteria (AIC). gs and CI measurements from leaves along the vine were tested against the fixed factors of leaf number, date (as a factor) and O_3 treatment (and their interactions) with the random effect of plant ID and ML estimation. Differences in the yield (fresh weight, g) were tested using a linear model with the fixed factor of O_3 treatment. Model results were summarised using ANOVA 'type 3' (package 'car', Fox and Weisberg, 2011) which performs a Wald chi-square test (χ^2). Tukey HSD post-hoc tests (package 'multcomp', Hothorn et al., 2008) and contrasts of means (package 'emmeans', Lenth, 2020) were carried out where appropriate.

3.3. DO_3SE parameterization and model run

After the removal of two outliers, all gs measurements (numbering 1356 and covering a range of times and conditions) were used to parameterize the DO_3SE model (Deposition of O_3 for Stomatal Exchange, version 3.0.5; https://www.sei-international.org/do3se) for the modification of gs by the environmental conditions light, leaf temperature, air vapour pressure deficit (VPD) and soil moisture.

Data relating to light and leaf temperature was as recorded by the porometer and measured simultaneously with the gs measurements. VPD was calculated from air temperature and relative humidity, measured at 30 min intervals, and the volumetric soil moisture measurements, measured at the same time as the gs measurements, were converted to soil water potential (SWP) using the relationships defined in Saxton and Rawls (2006). The mean gs lower:upper leaf ratio was used to calculate gs on a projected leaf area basis (PLA). g_{max} was calculated as the 95th percentile of measurements, and subsequent parameterisations were based on relative gs. Relative gs was plotted separately against light, leaf temperature, VPD and SWP. To fit the physiologically relevant curves (as described in Emberson et al., 2000) the x-axis was divided into sections, and the 90th percentile of the gs measurements in each section was calculated. The curve was then fitted based on a combination of raw datapoints and the 90th percentile points. The maximum gs on PLA basis (mmol H_2O m^{-2} PLA s^{-1}) was

Table 2
Summary of O_3 treatments over the experimental periods. Standard deviations are shown in brackets. 12 h and daily means are between 08:00 and 20:00.

Year	24 h mean (ppb)			12 h mean (ppb)			Mean daily maximum (ppb)			AOT40 (ppm)[a]		
	Low	Medium	High	Low	Medium	High	Low	Medium	High	Low	Medium	High
2019	19.1 (10)	42.0 (26)	53.1 (39)	25.0 (8)	59.5 (25)	77.9 (40)	32.6 (11)	74.1 (26)	111.1 (46)	0.03	33.41	60.26
2020	15.0 (12)	33.6 (33)	42.3 (42)	25.5 (9)	59.8 (27)	71.8 (40)	33.3 (4)	70.5 (26)	95.4 (41)	0.01	21.79	32.93
2021	22.2 (7)	38.7 (24)	46.3 (29)	23.2 (6)	55.8 (24)	66.2 (30)	29.8 (16)	67.5 (27)	79.8 (35)	0.18	36.39	52.57

[a] Sum of the differences between the hourly O_3 concentration exceeding 40 ppb, and 40 ppb (between 08:00 and 20:00).

converted to g_{max} O_3 (mmol O_3 m^{-2} PLA s^{-1}) using a conversion factor of 0.663 (UNECE, 2017).

Hourly means of the meteorological and O_3 concentrations from the experiment were used to run the DO_3SE model. The required constants were obtained from a mixture of the experimental data and literature (as detailed in the Results section, Table 3).

DO_3SE outputs the modelled stomatal conductance (of O_3, g_s) on an hourly basis therefore a direct comparison between the modelled and 'point in time' observed gs data is not possible. However, to provide an indication of the performance of the model, the individual gs measurements (mmol H_2O m^{-2} PLA s^{-1}) were first converted to mmol O_3 m^{-2} PLA s^{-1} and a mean hourly value (from observations made within each hour and treatment) was calculated. The final g_s output was compared to the observed data, and the root mean square error (RMSE) and normalized RMSE (using the data maximum and minimum values) were calculated.

Species (sweet potato) specific relationships between yield and AOT40 (accumulated O_3 above a threshold of 40 ppb in daylight hours), and between yield and threshold Y values for POD_Y (Phytotoxic O_3 Dose instantaneous flux threshold of Y nmol m^{-2} s^{-1}) from 0 to 6 were obtained (POD_0SPEC toPOD_6SPEC). The significance of the relationships between the DO_3SE modelled outputs for AOT40 and POD_Y and yield were determined using a linear model.

Estimations of critical levels for sweet potato were made using the method outlined in Hayes et al. (2021) (Figure S9) using an accumulated O_3 flux value calculated at a constant 10 ppb (Ref10 POD_y) as the reference value, and calculating the O_3 flux for a 5% reduction in yield compared to this (UNECE, 2017). The use of Ref10 POD_y is designed to provide a more realistic baseline value by accounting for background O_3 levels representing an estimated pre-industrial mean O_3 concentration (UNECE, 2017).

4. Results

4.1. Plant growth and yield

Some foliar injury attributed to O_3 was observed on *Erato orange* within a few days of the start of the ozone treatments (Figure S2). However throughout the exposure period, the higher O_3 treatments generally resulted in fewer leaves due to early senescence rather than leaf damage following visible ozone injury symptoms on the leaves (Figure S3- S5; Sharps et al., 2021). In the higher ozone treatments many senesced leaves were observed on the surface of the pots and the floors of the solardomes. Although the majority of leaves that remained on the plants in the higher O_3 treatments appeared healthy visually, there was still a reduction in stomatal conductance and chlorophyll content for these leaves.

In a comparison between O_3 treatments using healthy leaves, for *Erato orange* the stomatal conductance around August/September was significantly lower in the High treatment (χ^2 (4) = 18.27, p = 0.001 (for year day*ppb), Fig. 1a). Whereas, overall stomatal conductance for *Beauregard* was significantly lower in both the Medium and High treatments compared to the Low treatment ($p < 0.001$, for both treatment levels, TukeyHSD, Fig. 1c).

Erato orange chlorophyll content varied as senesced leaves were replaced. Compared to the Low treatment, CI in the Medium treatment was lower during September but increased to a peak in early October, whereas CI in the High treatment was higher in late August before dropping to follow a corresponding level and pattern as the plants in the Medium treatment (χ^2 (4) = 10.08, p = 0.04 (for year day*ppb), Fig. 1b). *Beauregard* leaf CI was also significantly lower in the Medium treatment ($p < 0.001$, TukeyHSD) with levels in the High treatment reducing on occasions (χ^2 (4) = 18.88, $p < 0.001$ (for year day*ppb), Fig. 1d).

Table 3

Number of harvested tubers for each sweet potato variety and ozone treatment. Standard deviations are shown in brackets.

Treatment	*Erato orange*	*Murasaki*	*Beauregard*
Low	4.75 (0.96)	10.25 (1.26)	9.50 (1.91)
Medium	4.25 (2.63)	10.25 (2.06)	7.00 (3.46)
High	4.25 (1.50)	11.00 (5.10)	6.25 (1.50)

DO_3SE flux model.

For *Erato orange* gs and CI remained similar with leaf age (along the vine) with no significant differences found between the treatments. In the August measurement, when there were only 5 leaves on the vine, gs was maintained in the higher O_3 treatments to a similar level as that in the Low treatment. In September, when there were 13 leaves on the vine in the Low treatment compared to 6 and 7 in the Medium and High treatments (respectively), gs varied more and reached higher levels in the Medium treatment. However, this trend was not significant with wide variation in the data (Figure S6).

Beauregard generally had fewer leaves along the vine than *Erato orange* (6 vs. 13, Low treatment) and showed greater variation in gs along the vine. In the August measurement, taken shortly after the O_3 treatments started, gs increased with leaf age in the high treatment in contrast to the reduction shown with age in the Low and Medium treatments (χ^2 (2) = 6.79, p = 0.03 (for leaf*date*ppb), Fig. 2a and b). However, this trend was not seen in September where gs tended to reduce with age of leaf along the vine and gs levels in all treatments were greatly reduced (compared to the August values). Although there was no significant influence of O_3 on the CI measurements, CI did reduce more with leaf age in September compared to August (χ^2 (1) = 13.11, $p < 0.001$ (for leaf*date), Fig. 2c and d).

A significant reduction in yield with increased O_3 was recorded with each variety (Fig. 3). Tubers were not properly formed for the *Beauregard* variety grown in 2020 (Figure S7), however a yield was obtained from this variety in 2021. Compared to the Low treatment, yields for the Medium and High treatments were significantly lower (*Erato orange*: $p > 0.01$ and $p > 0.001$; *Murasaki*: $p < 0.05$ and $p < 0.01$; *Beauregard*: $p < 0.01$ and $p < 0.01$, respectively, TukeyHSD; Fig. 3). Reductions in the higher O_3 treatments were similar for *Erato orange* and *Murasaki* (*Erato orange*: 36% and 47%; *Murasaki*: 38% and 50%, for the Medium and High treatments respectively), whereas for *Beauregard* they were 58% lower in both. The *Beauregard* variety also showed a greater variation in the number of tubers with a trend (not significant) for fewer, as well as smaller, in the higher O_3 treatments (Table 3).

Data from all growing seasons was used to obtain specific DO_3SE model input values for sweet potato. g_{max} was 790 mmol H_2O m^{-2} s^{-1} and 355 mmol O_3 m^{-2} PLA s^{-1} on a projected leaf area basis. There was no significant difference in g_{max} between the different varieties. The subsequent curves for the initial parameterization of gs in response to light, temperature, VPD and soil water potential are shown in Fig. 4. The soil moisture function has a very high proportion of data at the non-limiting end and has been set at a weak level of response, which has a good fit to the strong reduction in tuber growth at decreasing soil moisture shown by Gajanayake et al. (2013). The constants obtained from this parameterization and subsequently used in the DO_3SE model runs are shown in Table 4 (along with some additional values obtained from literature, as per sources listed) that are required to run the model. For this study we used data on maximum LAI from the published literature and scaled this over the growing season to peak at the time of flowering. Model performance was good with a normalized RMSE value of 0.16 (see also Figure S8). The RMSE value (between the modelled hourly g_s and corresponding observed data) was 51 (mmol O_3 m^{-2} PLA s^{-1}; observation mean 152; maximum value 374; and minimum value 45).

Using the model outputs the relationship between yield and the concentration based AOT40 metric, and O_3 flux thresholds (ranging from POD_0 to POD_6) were explored using yield data from this study. Correlations varied in strength, but significant relationships were found within both concentration and flux metrics (AOT40 R^2 0.66, p = 0.01;

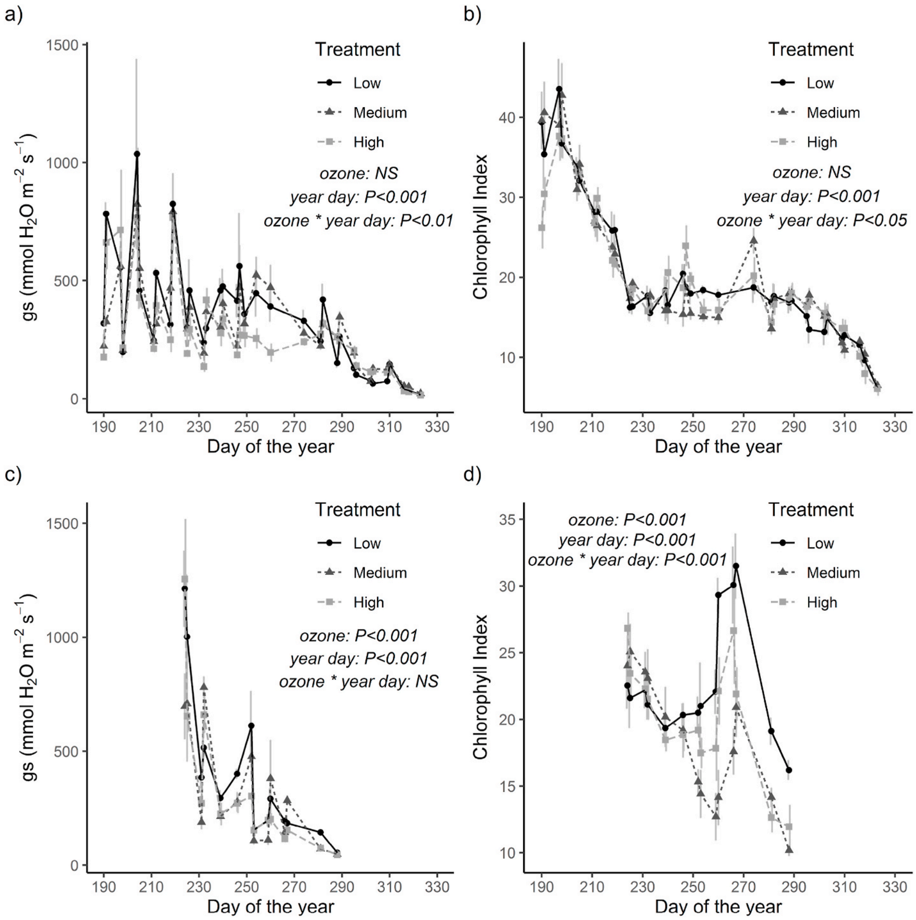

Fig. 1. *Stomatal conductance (gs, taken from the lower side of the leaf) and the chlorophyll content index (CI, of representative canopy leaves) for both sweet potato varieties in each ozone treatment (Low, Medium and High) with statistical significance indicated: a)* Erato orange *gs recorded from* 9th *July*-19th *November 2019; b)* Erato orange *CI taken at the same time as gs; c)* Beauregard *gs recorded from* 11th *August*-14th *October 2020; and d)* Beauregard *CI taken at the same time as gs.*

POD_0 R^2 0.35, $p = 0.10$; POD_3 R^2 0.47, $p = 0.04$; and POD_6 R^2 0.44, $p = 0.05$, Fig. 5). In accordance with parameterizations for other crops (e.g. potato (Pleijel et al., 2007) and beans (Hayes et al., 2020)), together with the benefits of POD_YSPEC over AOT40 when combining data from multiple years and differing environmental conditions (Pleijel et al., 2022) the POD_6SPEC relationship was used in the critical level calculation. This resulted in a critical level estimate of a POD_6 of 3 mmol m^{-2} PLA^{-1} (as a 5% reduction in the yield from that modelled with a background of 10 ppb O_3 (REF10 POD_6SPEC).

5. Discussion

5.1. Plant growth and yield

In this study we have shown impacts of O_3 on three sweet potato varieties where foliage was affected, and stomatal conductance and yield reduced. These effects occurred at O_3 concentrations already found in tropical areas. For example in Rwanda, DeWitt et al. (2019) recorded highs of around 80 ppb (15 min average), and concentrations of O_3 in South Africa have also been measured at levels up to 80 ppb (hourly average over a month, Laban et al., 2018).

The plants responded to the O_3 treatments quickly, with each variety showing signs of impact (foliar and gs) within a week. The foliar damage we observed was similar to instances of leaf bleaching (attributed to the O_3 pollution) found on sweet potato grown in fields in Taiwan (Sun, 1994). There is a risk of episodic peaks in O_3 pollution in tropical areas due to wind direction and other atmospheric conditions, as well as seasonal human activities such as biomass burning (Permadi and Oanh, 2008; DeWitt et al., 2019; Maji and Sarkar, 2020), and our findings suggest that sweet potato would be susceptible to the increase in ozone concentration caused by these. However, it is not known whether (or how quickly) they would recover after any short term exposure to extreme peaks. Whilst the observations of foliar damage were infrequent in this study, the shortened leaf life span on the plants in the Medium and High treatments inevitably impacted on their ability to photosynthesise at a whole-plant level because of the large reduction in the number of leaves per plant.

There were some differences in the response of the varieties to the O_3 treatments. Although there were fewer leaves in the higher O_3 treatments, *Erato orange* maintained levels of gs and CI in the Medium treatment (compared to the Low treatment) and had higher levels of CI towards the end of the season, suggesting that plant resources continued to be deployed to the canopy to the likely detriment of tuber development. However, *Beauregard* was impacted to a greater extent than *Erato orange* showing an overall decline in both the Medium and High treatments where gs was not maintained (this was the case only in the High treatment for *Erato orange*). *Beauregard* yield was also reduced in the Medium treatment (−58%) to a greater extent than was found with the *Erato orange* (−36%) and *Murasaki* (−38%) varieties suggesting a greater sensitivity to O_3 pollution. O_3 is known to reduce photosynthetic activity in sweet potato (Kim et al., 2007) and the lower number of leaves and reduced gs impact on carbon assimilation, and hence yield (Kays, 1985; Bhagsari and Ashley, 1990; Haimeirong and Kubota, 2003).

This is comparable to the findings in Keutgen et al. (2008) where there was a difference in sensitivity between two varieties of sweet potato exposed to O_3 with one variety maintaining canopy biomass at

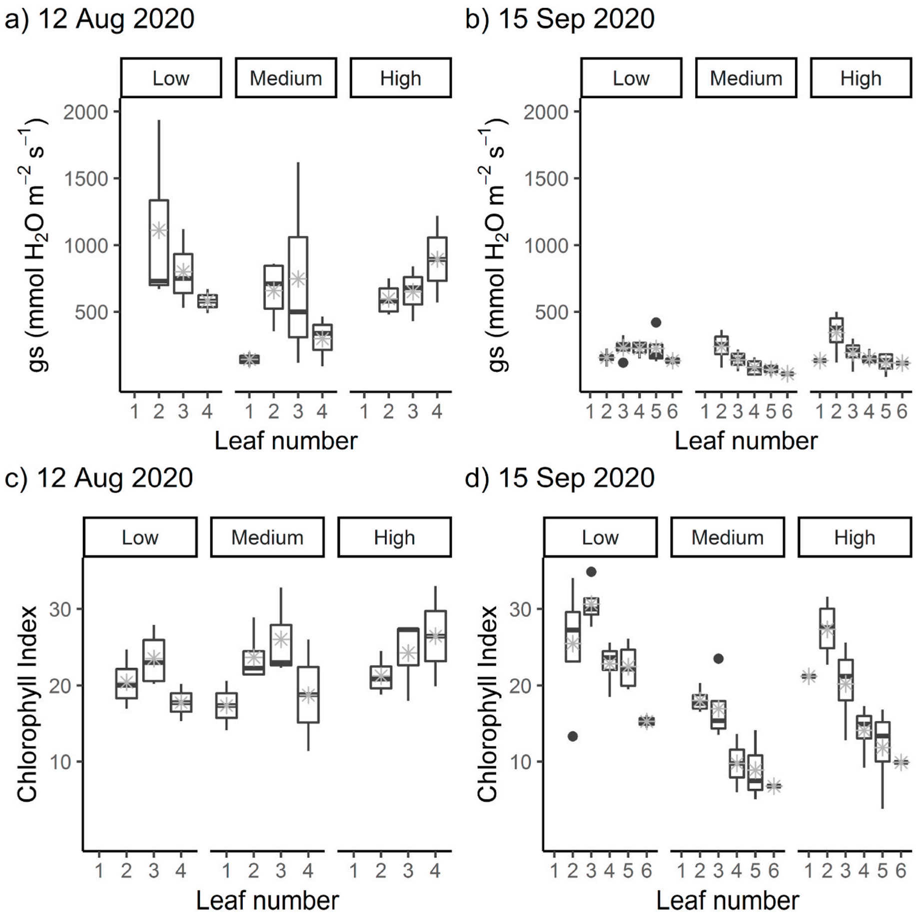

Fig. 2. *Distribution (with the data mean denoted by an asterisk) of stomatal conductance (gs) and chlorophyll index (CI) of* Beauregard *leaves, along the vine, taken at two time points: a) gs on* 12th *August; b) gs on* 15th *September; c) CI on* 12th *August; d) CI on* 15th *September.*

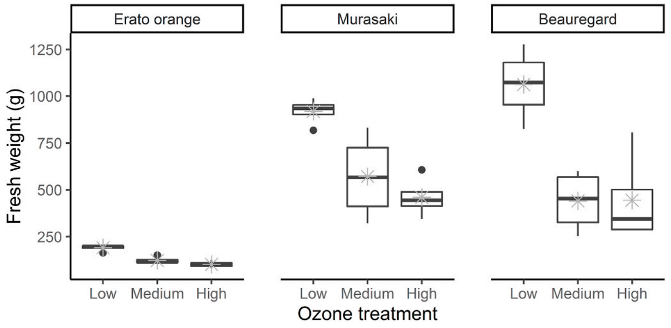

Fig. 3. Yield (fresh weight of tubers) for each variety and ozone treatment (Low, Medium and High). The centre line in the box shows the median of the data and the mean value is denoted by an asterisk.

the expense of belowground development. This is common response found across species including, for example, potato (Asensi-Fabado et al., 2010), wheat, and watermelon (Grantz et al., 2006). The reductions in yield we found were within the wide range of yield reductions (−14% to −81%, at exposure levels of ~65 ppb 8hr mean compared to the control group grown in filtered air) previously observed by Keutgen et al. (2008). Similar responses of decreases in canopy cover and yield, as well as reduced gs have been recorded for sweet potato varieties in connection with other environmental stresses causing oxidative damage, such as drought (Lewthwaite and Triggs, 2012; Laurie et al., 2015).

The reason for the lack of fully formed *Beauregard* tubers in 2020 is uncertain. It is possible that the slightly lower air temperatures (−4 °C (day) and −3 °C (night) compared to 2019 treatment period mean) resulted in poorer growth for this variety. The seasonal average daytime temperature of 25 °C in 2020 was marginally short of the optimum temperature determined for gs in the DO$_3$SE model (28 °C). Typically sweet potato requires hot days and warm nights (Motsa et al., 2015) especially during early tuber development (Gajanayake et al., 2014). However, there are differences between varieties with some, for example, successfully grown in the cooler climate of the Indian 'rabi' season and some clones are adapted for the different abiotic stresses across regions (Nedunchezhiyan et al., 2012; Low et al., 2015). Both saturated or drought conditions, particularly in the period 10–20 days after transplanting, can adversely affect yield (Villordon et al., 2012), but the plants in this study were kept without these stresses. There were no visible signs of plant pathogens or virus infection, and the plant material came from known commercial stock. However, Clark and Hoy (2006) found that *Beauregard* plants infected with '*Sweet potato leaf curl virus*' resulted in mean yields of 26% less than control plants, even though there were no foliar symptoms (as could be expected by the virus name). The plants were started later than in the other years which may also have affected growth, and the O$_3$ treatment was also commenced later (early August compared to June) which may have had an impact at the tuber growth stage (although there was also poor tuber production even in the Low treatment). Plants were not tested for pathogens during the course of the study as there were no signs of any problems until the point that the tubers were harvested. Yield results from *Beauregard* grown again in 2021 suggest that this variety may be particularly susceptible to O$_3$, and further work could confirm this with an additional filtered air (no O$_3$) as a control and a variation in the timing of exposure

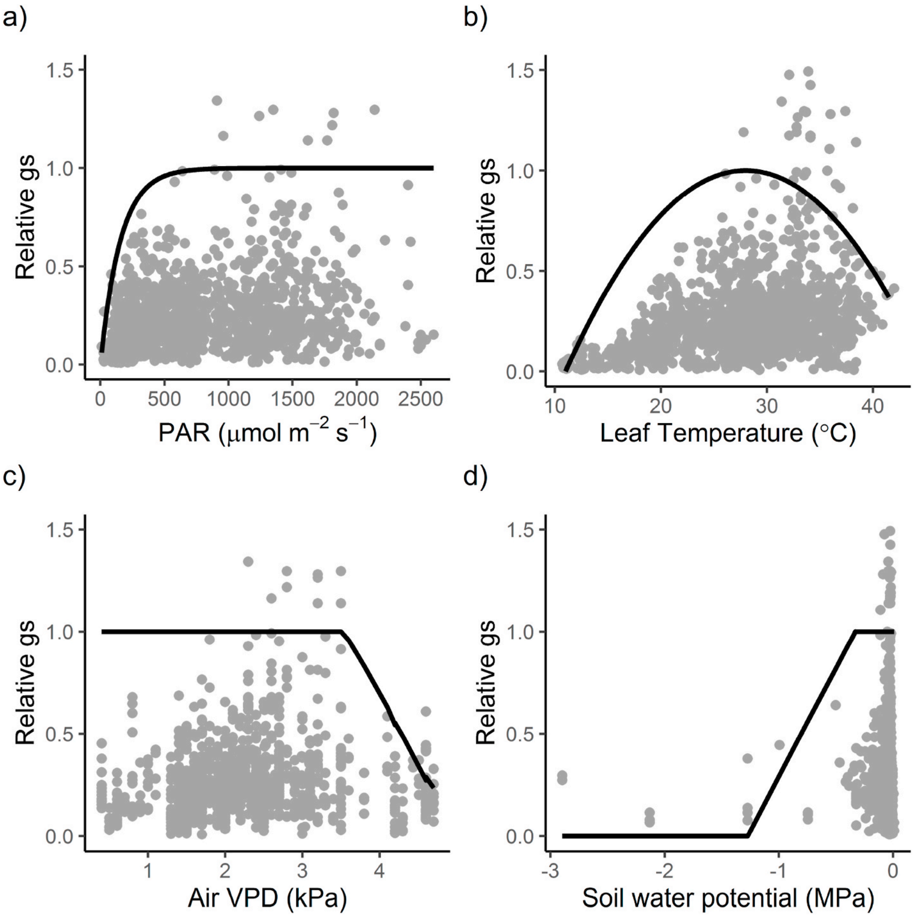

Fig. 4. Parameterizations of the DO_3SE model inputs for sweet potato in relation to: a) light (Photosynthetic Active Radiation, PAR); b) leaf temperature; c) air vapour pressure deficit (VPD); and d) soil water potential. Data points represent observed data and the black lines show the physiologically relevant curve derived from the functions (based on 90th percentiles of the observed data).

Table 4

Values used for the DO_3SE model inputs. Data was obtained from both growing seasons and the references where shown.

Constant	Unit	Value	Reference
g_{max}	mmol O_3 m^{-2} PLA s^{-1}	355	
T_{min}	°C	11	
T_{opt}	°C	28	
T_{max}	°C	45	
$light_a$	–	0.006	
VPD_{max}	kPa	3.5	
VPD_{min}	kPa	5.0	
SWP_{min}	MPa	−1.27	
SWP_{max}	MPa	−0.33	
Canopy height	m	0.8	
Root depth	m	1.0	Gregory and Wojciechowskic (2020)
Leaf dimension	m	0.05	
Leaf Area Index (max)	m^2/m^2	6.0	Laurie et al. (2009); Saitama et al. (2017)

to O_3.

Along with the yield quantity, the nutritional quality is also important and this can be affected by environmental stresses. For example, protein and carbohydrate contents in sweet potato can be altered by water stress (Ekanayake and Collins, 2004; Gouveia et al., 2020), and O_3 pollution has been found to impact starch, free amino acids, and macronutrient contents (Keutgen et al., 2008) with outcomes varying with variety. Yield quality was not covered in this study, however, this would be a useful parameter to consider in further work on the effects of O_3 on different cultivars to enable better selection for planting in areas at risk of high O_3 and where the crop is vital part of nutrition.

5.2. DO_3SE model inputs and critical level estimation

Using stomatal conductance data from our experiment we have presented a number of sweet potato relevant constants required by the DO_3SE model. This will enable more accurate risk assessments of the impact of O_3 on sweet potato yields through mapping and modelling of ‘at risk’ regions (e.g. Mills et al., 2018c). This study was conducted in solardomes, which have a constant windspeed that can favour ozone uptake compared to still air conditions that might occur in field conditions. However, an additional advantage of the stomatal conductance based approach to risk assessment is that windspeed is accounted for in the parameterisations and calculations.

In comparison to the more established critical levels (Mills et al., 2011b) for wheat (POD_6 of 1 mmol m^{-2}) and potato (POD_6 of 5 mmol m^{-2}) the estimated critical level we provide (POD_6 of 3 mmol m^{-2}) suggests that sweet potato is less sensitive to O_3 than wheat, but more sensitive than potato.

Even a 5% reduction in yield could represent a substantial loss, especially for subsistence farmers. In West Africa in 2018, 5.58 Mt of sweet potato were produced, with a gross production value of 780 million USD. A 5% change in this value would equate to 39 million USD. Currently it is not known whether O_3 pollution is already reducing current yields for this important crop. Further assessments on the susceptibility to O_3 of different sweet potato varieties commonly used in

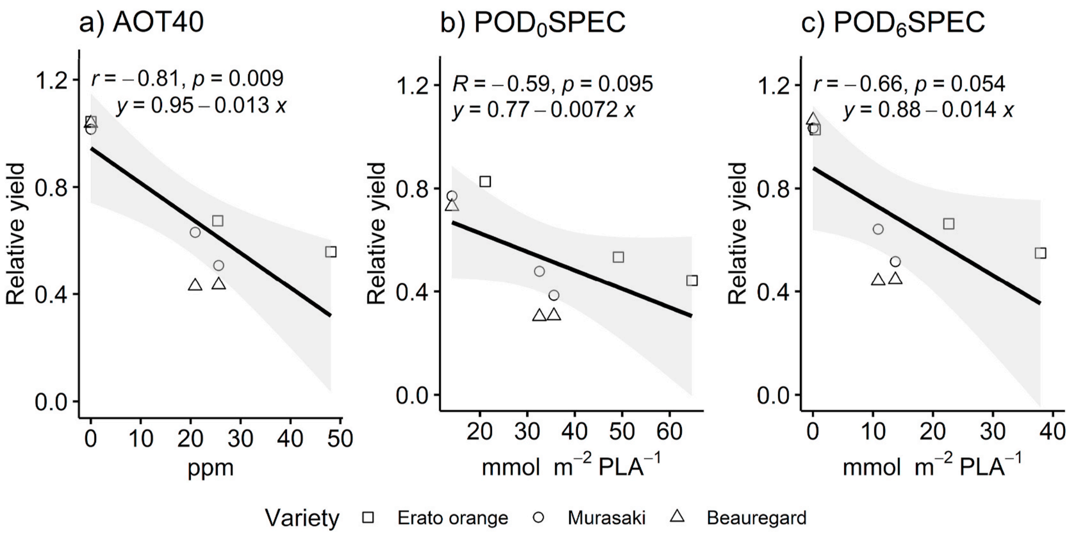

Fig. 5. Sweet potato species specific ozone concentration and flux based relationships with yield: a) concentration based AOT40 (accumulated O_3 above a threshold of 40 ppb); b) flux based POD_0; and c) flux based POD_6 (instantaneous flux threshold of 6 nmol m^{-2} s^{-1}). Black lines represent the model fit with the 95% confidence interval shown by the shaded area.

tropical regions (preferably in as close to in field conditions as possible) is required to provide more information in the setting of a critical level. The ability of cultivars to cope with multiple stresses such as O_3 and drought would also be of use in determining the most appropriate cultivars for future climate conditions.

6. Conclusions

This study showed that each of the three sweet potato varieties tested were sensitive to O_3 pollution, with a large decrease in yield. We show that this yield reduction is related to an O_3-induced leaf loss, resulting in reduced carbon assimilation by the plants, whilst the photosynthetic capacity (based on the chlorophyll index) of the remaining leaves is maintained. Given the importance of sweet potato as a staple food crop in tropical regions, yield losses are important to quantify, and we found reductions of a similar magnitude to known O_3-sensitive crops including wheat and potato. An O_3 critical level based on ozone-uptake for this species is suggested, and a number of parameters are quantified that could be used for the improvement of atmospheric exchange models. This will enable more accurate risk assessments of the impact of O_3 pollution on tropical crop yields in 'at risk' regions, which will in turn highlight regions were efforts are needed to improve air quality and/or crop tolerance to ozone to ensure continued food security.

Credit author statements

Amanda J Holder: Conceptualization, Methodology, Investigation, Formal analysis, Writing – Original Draft, Visualization. **Felicity Hayes**: Conceptualization, Methodology, Investigation, Writing – Review & Editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2022.119209.

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