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Relationships between ozone exposure and yield loss in European wheat and potato—a comparison of concentration- and flux-based exposure indices

H. Pleijel[a,*], H. Danielsson[a,b], K. Ojanperä[c], L. De Temmerman[d], P. Högy[e], M. Badiani[f], P.E. Karlsson[b]

[a] *Department of Applied Environmental Science, Göteborg University, P.O. Box 464, Göteborg SE-405 30, Sweden*
[b] *Swedish Environmental Research Institute, P.O. Box 47086, Göteborg SE-402 58, Sweden*
[c] *MTT Agrifood Research Finland, Environmental Research, Jokioinen FI-31600, Finland*
[d] *VAR, Leuvensesteenweg 17, Tervuren BE-3080, Belgium*
[e] *Institute for Landscape and Plant Ecology (320), University of Hohenheim, Schloss Mittelbau (West), Stuttgart D-70599, Germany*
[f] *Dipartemento di Biotecnologie per il Monitoraggio ed AgroAlimentare ed Ambientale, Universitá Mediterranea di Reggio Calabria, Facoltá di Agraria—Loc. Feo di Vito 89124 Regio Calabria, Italy*

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Abstract

Data from open-top chamber experiments with field grown crops, performed in Sweden, Finland, Belgium, Italy and Germany, were combined to derive relationships between yield and ozone exposure for wheat (*Triticum aestivum* L.) and potato (*Solanum tuberosum* L.). Three different exposure indices were compared: AOT40 (accumulated exposure over a threshold ozone concentration of 40 nmol mol^{-1}), CUO^t (cumulative stomatal uptake of ozone, using a constant ozone uptake rate threshold of t nmol m^{-2} s^{-1}) and mAOTc_0 (conductance modified AOT using a threshold concentration for ozone of c_0 nmol mol^{-1}). The latter is essentially a combination of AOT and CUO. Ozone uptake was estimated using a Jarvis-type multiplicative model for stomatal conductance. In terms of correlation between relative yield (RY) and ozone exposure, CUO^5, the CUO index with an ozone uptake rate threshold of 5 nmol m^{-2} s^{-1}, performed best for both wheat and potato, resulting in r^2 values of 0.77 and 0.64, respectively. CUO^5 performed considerably better in terms of the correlation between RY and ozone exposure, than AOT40 for wheat, while mAOT10, the best performing mAOT index in this case, was intermediate in performance for this crop. For potato, the differences between the different ozone exposure indices AOT40, CUO^5 and mAOT20 (the mAOT index performing best for potato) in the correlation between RY and ozone exposure were relatively small. To test the assumption that the non-stomatal deposition of ozone was negligible for the uppermost, sunlit leaves, measurements of ozone uptake in relation to leaf conductance for water vapor of wheat leaves in a cuvette system were used. The non-stomatal deposition of ozone to the leaves turned out to be comparatively small. Based on the non-stomatal conductance ($g_{ns} = 15$ mmol m^{-2} s^{-1}) estimated for the wheat leaves in the cuvette system, it was concluded that the consequence of omitting the non-stomatal conductance is small. In conclusion the study indicated that the ozone uptake based approach showed a high degree of fitting along a north-south European transect of pedoclimatic conditions, and represents a better and more relevant approach to the quantification of ozone effects on crops growth than the use of ozone exposure indices purely based on ozone concentrations.

Keywords: Dose-response; Non-stomatal deposition; Ozone; *Solanum*; Stomatal conductance; *Triticum*

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*Corresponding author. Tel.: +46-31-773-2532; fax: +46-31-773-2984.
E-mail address: hakan.pleijel@miljo.gu.se (H. Pleijel).

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1. Introduction

During the last decades, the effects of ground-level ozone on plants have been among the environmental impacts considered by the European co-operation on air pollution emissions control (Borrell et al., 1997). This has lead to a request from policymakers to scientists for methods to quantify these effects, which has stimulated an intensive work aiming at the development of quantitative methods for this purpose.

For ozone effects on vegetation, it is possible to discern three generations of exposure index concepts, which have been used in the Convention on Long-Range Transboundary Air Pollution (CLRTAP) under the United Nations Economic Commission for Europe (UNECE). The initial step was taken in 1988, when the first generation of critical levels for gaseous pollutants was agreed upon (UNECE, 1988). A second step was taken in 1992–1993 when the exposure index AOT40, i.e. the accumulated exposure over a threshold concentration for ozone of 40 nmol mol^{-1}, was introduced to define critical levels for ozone. It was shown that this index provided relatively strong correlation with observed effects (Ashmore and Wilson, 1994; Fuhrer and Achermann, 1994). The AOT40 index mainly reflects the ozone concentrations in the air nearby the plants, the only aspect of ozone uptake considered being that ozone exposure is only accumulated for daylight hours. There was, however, an awareness within the scientific community that the effects of ozone are likely to be related to the ozone uptake of the plants, which lead to suggestions to move towards an ozone uptake concept to express ozone exposure (Grünhage and Jäger, 1994).

Based on the consideration that the leaf uptake of phytotoxic ozone, deposition to exterior surfaces probably not being very harmful, is strongly controlled by stomatal conductance (Kerstiens and Lendzian, 1989), a developmental work was initiated. This resulted in attempts to use stomatal conductance modelling (Grüters et al., 1995; Emberson et al., 1998; Emberson et al., 2000a), mainly based on the multiplicative principles put forward by Jarvis (1976), in order to estimate the stomatal response to different environmental variables and, in the end, ozone uptake. This was the birth of the third generation of ozone exposure indices.

The ozone absorption that takes place upon the leaf exterior surfaces is not without importance (Fowler et al., 2001; Gerosa et al., 2003). Although not directly harmful, non-stomatal deposition complicates the calculation of stomatal ozone uptake when applying a resistance analogue model, without including a resistance for the ozone uptake by the leaf outer surface (Grünhage et al., 2000). If the non-stomatal deposition is substantial compared to the stomatal, neglecting the non-stomatal component potentially leads to significant errors in the estimation of the stomatal flux.

Nevertheless, based on the stomatal conductance modelling, further stages were taken to test if improvements in dose–response relationships could be obtained compared to the AOT40 models. By testing a series of open-top chamber (OTC) experiments with wheat (*Triticum aestivum* L.), representing rather strong year-to-year variation in weather conditions, it turned out to be the case that a substantial reduction in the inter-experimental variation in response to ozone was obtained by using estimated ozone uptake instead of AOT40 (Pleijel et al., 2000).

More recently, Pleijel et al. (2002) and Danielsson et al. (2003) used observed stomatal conductance to calibrate the multiplicative Jarvis-type conductance model for potato (*Solanum tuberosum* L.) and wheat, respectively, and to combine these models with yield response data from OTC experiments with field grown crops. In addition, in these two studies the uncertainty in the parameter estimations were discussed, and the influence of the choice of ozone uptake rate thresholds on the performance of the dose–response functions was evaluated, since there is evidence that apoplastic antioxidants can efficiently scavenge toxic ozone by-products until a certain threshold is reached (Polle and Rennenberg, 1993; Turcsányi et al., 2000).

The suggested change from AOT40 to an uptake-based concept has not been uncontroversial. For the communication of the results to policymakers and other stakeholders, as well as the implementation via integrated assessment modelling in air pollution abatement strategies, a certain degree of continuity in terms of concepts used is desirable. Thus, there have been suggestions to develop a version of the AOT exposure index, which is sensitive to one or several stomatal conductance modifying factors, in order to build on the preceding models, and to make possible the use of only a limited number of ozone uptake modifying factors for the case that certain model-driving variables are not available. Grünhage et al. (1999) suggested one concept for a modified AOT approach.

It should be noted that in North America a developmental work has been initiated to identify flux based concepts, considering also the detoxification capacity of the plant, to evaluate ozone metric and potential ambient air quality standards (Musselman and Massman, 1999; Massman et al., 2000; Panek et al., 2002), which are conceptually related to the work presented in this paper.

The aim of the present study was to present relationships between relative yield and ozone exposure in terms of AOT40, CUO^{t} (cumulative uptake of ozone based on conductance modelling, using different ozone uptake rate thresholds t), and a conductance modified AOT (mAOT) using a related but slightly different concept from that of Grünhage et al. (1999), for wheat and potato. The study was based on the empirical data included in Danielsson et al. (2003) and Pleijel et al. (2002) and seven additional data sets concerning wheat from OTC experiments performed in Belgium, Italy and Finland. A further aim was to test the importance of the non-stomatal deposition of ozone to wheat leaves, based on a series of cuvette measurements, in which the fluxes of water vapor and ozone of wheat leaves were measured in parallel.

2. Materials and methods

2.1. Experiments included

Basic information concerning the OTC experiments included in the present study, all with field-grown crops, are summarised in Table 1. Twelve different experiments with wheat from four different countries and seven different experiments with potato, representing four countries, were included. The wheat part of the study made use of data from four cultivars of *T. aestivum* and one cultivar of durum wheat, *Triticum turgidum* ssp. *durum*, while for potato all data were from a single source (in The Netherlands) of the cultivar Bintje. Basics of the studies have been published in the scientific literature and relevant references are given in Table 1. One data point (a non-filtered air treatment of the Swedish data set from 1999) was removed as an outlier from the potato data set based on statistical considerations. The durum wheat data set consisted of a CF treatment and a series of OTCs with ozone added to charcoal-filtered air, all having different ozone levels. The chambers were grouped into treatments based on whether the ozone concentration distributions differed significantly or not between the different chambers. One treatment in the data set from Sweden 1997 and one treatment in the data set from Italy 1995 were removed because ozone concentrations frequently exceeded 130 nmol mol^{-1} ozone.

2.2. Calculation of exposure indices

2.2.1. Accumulated exposure over threshold (AOT)

AOT40 has been the exposure index used for critical levels for ozone in Europe (Fuhrer et al., 1997). In the present study it was calculated for the same period as the CUO index and conductance modified AOT. For wheat, the integration period started at anthesis and continued until 700°C days (base temperature 0°C) after anthesis (Danielsson et al., 2003). Consequently, the AOT40 values used here are not directly comparable with those used by Fuhrer and Achermann (1994). These were

Table 1
Basic information concerning the experiments included in the study

Country, year	Cultivar	Treatments	*n*	Reference
Wheat				
Belgium 1994	Minaret	CF, NF	3	Bender et al. (1999)
Belgium 1995	Minaret	CF, NF	3	Bender et al. (1999)
Belgium 1996	Minaret	CF, NF	3	Bender et al. (1999)
Finland 1991	Satu	CF, NF	5	Ojanperä et al. (1994) and Pleijel et al. (1997)
Finland 1992	Satu	NF, NF+	5	Ojanperä et al. (1994) and Pleijel et al. (1997)
Finland 1993	Satu	CF, NF, NF+	5	Ojanperä et al. (1994) and Pleijel et al. (1997)
Sweden 1987	Drabant	CF, NF, NF+	7	Pleijel et al. (1991)
Sweden 1988	Drabant	CF, NF, NF+, NF++	5	Pleijel et al. (1991)
Sweden 1994	Dragon	NF, NF+, NF++, NF+++	3	Pleijel et al. (1999)
Sweden 1995	Dragon	NF, NF+	5	Pleijel et al. (1998)
Sweden 1997	Dragon	CF, NF, NF+, NF++	5	Gelang et al. (2000)
Italy 1996	Duilio	CF, CF+, CF++	1–3	Badiani et al. (1996)
Potato				
Belgium 1998	Bintje	CF, NF, NF+	3	Pleijel et al. (2002) and De Temmerman et al. (2002)
Belgium 1999	Bintje	CF, NF, NF+	3	Pleijel et al. (2002) and De Temmerman et al. (2002)
Finland 1998	Bintje	NF, NF+, NF++	4	Pleijel et al. (2002) and De Temmerman et al. (2002)
Germany 1998	Bintje	NF, NF+	3	Pleijel et al. (2002) and De Temmerman et al. (2002)
Germany 1999	Bintje	NF, NF+	5	Pleijel et al. (2002) and De Temmerman et al. (2002)
Sweden 1998	Bintje	NF, NF+	6	Pleijel et al. (2002) and De Temmerman et al. (2002)
Sweden 1999	Bintje	CF, NF, NF+	4	Pleijel et al. (2002) and De Temmerman et al. (2002)

CF charcoal filtered air; CF+ charcoal filtered air with additional ozone; NF non-filtered air; NF+, NF++, NF+++ non-filtered air with additional ozone; *n* number of OTC replicates. All wheat cultivars except the Italian belonged to the species *Triticum aestivum* L. The Italian cultivar was a durum wheat, *Triticum turgidum* ssp. *durum* Desf.

based on longer time periods, which included pre-anthesis exposure and post-end of grain filling exposure. These two periods were considered redundant in the present study, based on the observation that post-anthesis ozone exposure seems to dominate the effect on grain yield (Pleijel et al., 1998), and that ozone exposure cannot influence grain yield after the end of grain filling. For potato, ozone exposure was integrated from tuber initiation (when tubers start to form on the roots) until haulm harvest and from emergence until haulm harvest for comparison.

2.2.2. Cumulative uptake of ozone (CUO)

CUO is the cumulative uptake of ozone per unit leaf area (mmol m^{-2}) based on hourly estimates of the ozone uptake rate U. Only the uppermost leaf level is considered, which receives most of the light and is most important for photosynthesis. An ozone uptake rate threshold t (nmol $m^{-2}\,s^{-1}$) can be used (CUO^t), which is similar to the cut-off concentration c_0 in the AOT concept, based on hourly averages of the ozone uptake rate. Ozone uptake by the leaves was estimated using multiplicative conductance models based on the principles suggested by Jarvis (1976):

$$g_s = \max\{g_{\min};\ g_{\max}(g_{\text{phen}}g_{O_3}g_{\text{VPD}}g_T g_{\text{PAR}}g_{\text{time}})\}, \tag{1}$$

where $g_{\min}$ and $g_{\max}$ denote, respectively, the minimum and maximum stomatal conductance allowed for a certain species by the model. The factors g_{VPD}, g_T, g_{PAR} and g_{time} represent the short-term (based on hourly averages) effects of leaf-to-air vapor pressure difference, leaf temperature, photosynthetically active radiation and time of day, respectively. The influence of time-of-day is most likely an effect of the internal water potential of the plant (Livingston and Black, 1987). The long-term influences of phenology (mainly leaf aging) and ozone are described by g_{phen} and g_{O_3}, respectively. For both crops g_{phen} was expressed in terms of thermal time accumulation, since plant development is known to be modelled more accurately using that approach than using time (Campbell and Norman, 1998; Pleijel et al., 2000; Hacour et al., 2002).

In wheat, elevated ozone after anthesis has a strong senescence-promoting effect (Ojanperä et al., 1992). This means that ordinary senescence under such conditions may have little influence on stomatal conductance. Because of that, a most limiting factor concept was used for the two factors g_{phen} and g_{O_3}in wheat (Danielsson et al., 2003):

$$g_s = \max\{g_{\min};\ g_{\max}(\min[g_{\text{phen}}g_{O_3}]g_{\text{VPD}}g_T g_{\text{PAR}}g_{\text{time}})\}. \tag{2}$$

The $g_{\max}$ values and the g functions for wheat and potato were taken from Danielsson et al. (2003) and Pleijel et al. (2002), respectively (Table 2).

The uptake rate U of ozone to a plant leaf is the product of a conductance g_{actual} and an ozone concentration c_{actual}. If the reference point is close to the leaves, the main components of g_{actual} are the stomatal conductance ($g_s = 1/r_s$; r_s is the stomatal resistance) and the leaf boundary layer conductance ($g_b = 1/r_b$; r_b is the leaf boundary layer resistance), which can be combined using the resistance analogue:

$$F = \frac{c_{\text{actual}}}{r_b + r_s} \tag{3}$$

assuming that the ozone concentration within the leaf is close to zero (Laisk et al., 1989) and that non-stomatal ozone deposition to the leaf exterior is negligible.

Table 2
Functions and constants used in the multiplicative conductance models for wheat and potato. PAR, photosynthetically active radiation, μmol $m^{-2}\,s^{-1}$

	Wheat	Potato
$g_{\max}$[a]	414 mmol H_2O $m^{-2}\,s^{-1}$	685 mmol H_2O $m^{-2}\,s^{-1}$
$g_{\min}$	$0.01g_{\max}$	$0.001g_{\max}$
g_{PAR}	$y = (1 - e^{-0.012\text{PAR}})$	$y = (1 - e^{-0.0090\ \text{PAR}})$
g_{VPD}	$y = (1 + (\text{VPD}/2.7)^8)^{-1}$	$y = (1 + (\text{VPD}/3.5)^6)^{-1}$
g_T	If $T \leqslant 27°\text{C}$ then $y = ((1 + (T/17)^{-10})^{-1}) \times 1.01$	If $T \leqslant 29°\text{C}$ then $y = (1 + (T/18)^{-10} + 0.001)^{-1}$
	If $T > 27°\text{C}$ then $y = (1 + (T/35)^{25})^{-1}$	If $T > 29°\text{C}$ then $y = (1 + (T/37)^{20} + 0.002)^{-1}$
g_{time}	$y = (1 + (\text{time}/0.72)^{15})^{-1}$	$y = (1 + (\text{time}/0.7)^{10})^{-1}$
g_{phen}	If $\text{DDA} \leqslant 0$ then $y = 1$	$y = (1 + (\text{DDE}/1250)^5)^{-1}$
	If $\text{DDA} > 0$ then $y = (1 + (\text{DDA}/740)^8)^{-1}$	
g_{O_3}	$y = (1 + (\sum \text{CUO}^0/6.48)^{10})^{-1}$	$y = (1 + (\text{AOT0}/40)^5)^{-1}$

VPD, leaf-to-air vapor pressure deficit of the air, kPa. T, leaf temperature, °C. SWP, soil water potential, MPa. *time*, time of day is expressed as hour/24. DDA, number of 0°C days after anthesis in wheat, using a base temperature of 0°C. DDE, number of 0°C days after emergence in potato, using a base temperature of 2°C. CUO^0, estimated uptake of ozone, mmol m^{-2}, cumulated from 14 days before anthesis. AOT0, sum of all hourly ozone concentrations starting from emergence and onwards (μmol mol^{-1} h).

[a] Expressed on a total leaf area basis, recalculated for O_3 when used to calculate CUO.

Constant values for r_b were used for the calculation of the dose–response functions. They were taken from Pleijel et al. (2000) for wheat ($g_b = 1138\,\text{mmol}\,\text{m}^{-2}\,\text{s}^{-1}$ O_3) and from Pleijel et al. (2002) based on Unsworth et al. (1984) for potato ($g_b = 1073\,\text{mmol}\,\text{m}^{-2}\,\text{s}^{-1}$ O_3) to represent the air movement situation in the OTCs. The conversion factor for molecular diffusivity from water vapor to ozone was 0.61.

2.2.3. Conductance modified AOT

Eq. (3) can also be modified to:

$$U = g_{\text{actual}} c_{\text{actual}}. \tag{4}$$

Here g_{actual} represents the total conductance for ozone uptake by a leaf from a reference point near the leaf as above.

A theoretical modified ozone concentration c_{mod} is now introduced in Eq. (5). This is the ozone concentration, which results in the same uptake of ozone as in Eq. (4), if the conductance were at its maximum:

$$g_{\text{actual}} c_{\text{actual}} = g_{\max} c_{\text{mod}}. \tag{5}$$

This can be used to modify observed or modelled ozone concentrations if $g_{\max}$ is known and an accurate measure of the actual conductance is available, such as based on the kind of multiplicative model used in the present study:

$$c_{\text{mod}} = \frac{g_{\text{actual}}}{g_{\max}} c_{\text{actual}}. \tag{6}$$

c_{mod} can be viewed as a bioavailable ozone concentration, since the ratio $g_{\text{actual}}/g_{\max}$ in Eq. (6) determines the relative bioavailability of ozone. The concentration c_{mod} can be converted to a corresponding conductance modified concentration for ozone and can be used to calculate a conductance modified mAOT c_0 index, using any cut-off concentration c_0.

2.3. Estimation of the non-stomatal flux of ozone and of its importance

If we assume the non-stomatal resistance ($r_{ns} = 1/g_{ns}$) to be in parallel with the stomatal resistance, and the resulting resistance of these to act in series with the boundary layer resistance, the stomatal ozone flux by the leaf, according to Kirchhoff's current laws, is

$$U_{\text{stomatal}} = \frac{c_{\text{actual}}}{r_b + r_s + (r_b r_s / r_{ns})}. \tag{7}$$

In order to evaluate the influence of the non-stomatal flux of ozone, a series of cuvette measurements performed in the laboratory, in which the ozone flux and the water vapor flux of wheat leaves were measured in parallel, was used. The temperature of the cuvette was 20°C, the maximum photosynthetically active radiation $950\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$ and the relative humidity 45–55%. The air flow rate through the system was $0.61\,\text{min}^{-1}$ and the air residence time in the cuvette 20 s. The air of the cuvette was continuously stirred by the fan. This was assumed to completely remove the leaf boundary layer resistance. The ozone concentration of the cuvette during the measurements was kept at $65 \pm 10\,\text{nmol}\,\text{mol}^{-1}$. Measurements were made in darkness, in intermediate light, in full light, and in full light after cutting the leaf from the rest of the plant. Measurements of the empty cuvette were also made both in darkness and in light. The cuvette and gas exchange system has been described in detail by Wallin et al. (1990).

2.3.1. Yield–response regressions

The regression analysis of yield in relation to ozone exposure was based on the principles suggested by Fuhrer and Achermann (1994). First, regression for each individual experiment was made. The grain yield treatment means were then divided by the intercept for each experiment. Thus, zero exposure was always associated with no effect at the individual experiment level, and relative yield (RY) from different experiments become comparable on a common, relative scale.

For the calculations of ozone uptake by the plants in the different experiments, leaf temperature and leaf-to-air vapor pressure difference was replaced by air temperature and vapor pressure deficit nearby the canopy, respectively. For sensitivity analysis of this simplification, see Pleijel et al. (2002) and Danielsson et al. (2003).

3. Results

3.1. Comparison of different ozone exposure indices

For potato the strongest correlation between relative yield and ozone exposure was obtained using CUO^5 and the ozone exposure integration period from tuber initiation until haulm harvest ($r^2 = 0.64$). Therefore, the regressions for potato shown in Figs. 1–3 were all based on that exposure period. The corresponding regressions using the period from emergence until haulm harvest were: $y = 0.98 - 0.0086 * \text{AOT40}$ ($r^2 = 0.57$), $y = 0.98 - 0.018 * \text{CUO}^5$ ($r^2 = 0.58$), and $y = 0.98 - 0.062 * \text{mAOT20}$ ($r^2 = 0.56$). In the data sets used here, the average duration of the period from emergence until haulm harvest was 1553°C days above 2°C (Pleijel et al., 2002), whereas the average period between emergence and tuber initiation was 298°C days above 2°C.

The response functions based on AOT40 for potato and wheat are presented in Fig. 1. The r^2 values for the two regressions were 0.57 and 0.41, respectively. The best performing AOT indices were AOT30 for potato

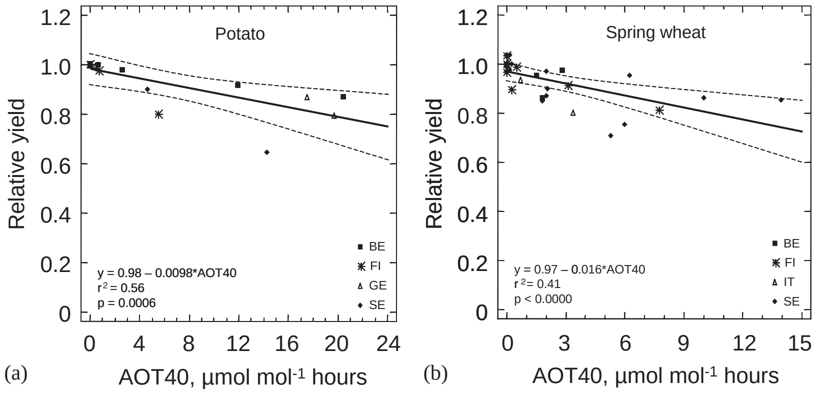

Fig. 1. Relationships between relative yield and AOT40 (a) from anthesis until 700°C days after anthesis for spring wheat and (b) from tuber initiation until harvest for potato.

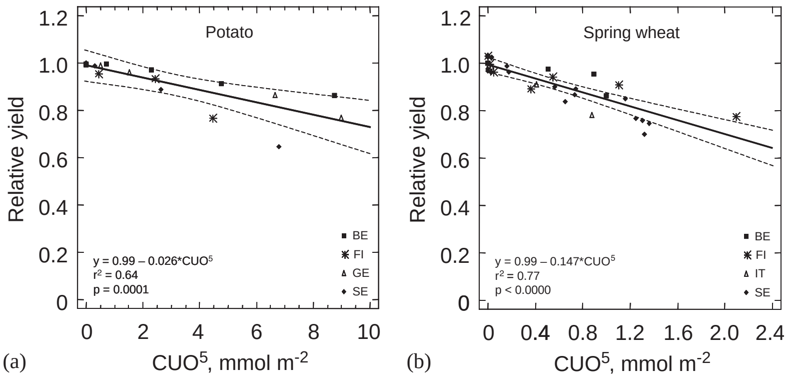

Fig. 2. Relationships between RY and the calculated cumulative uptake of ozone with an ozone uptake rate threshold of 5 nmol m^{-2} s^{-1}, CUO^5 (a) from anthesis until 700°C days after anthesis for wheat and (b) from tuber initiation until harvest for potato.

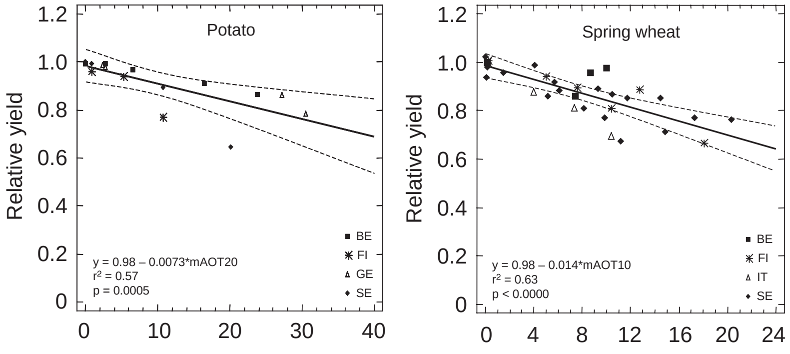

Fig. 3. Relationships between relative yield and (a) mAOT10 (conductance modified AOT10) from anthesis until 700°C days after anthesis for wheat and (b) mAOT20 (conductance modified AOT20) from tuber initiation until harvest for potato.

($r^2 = 0.59$) and AOT10 ($r^2 = 0.63$) for wheat. For wheat, also AOT20 and AOT30 had r^2 values >0.6.

In Fig. 2, the best CUO indices for wheat and potato are shown. In both cases the ozone uptake rate threshold, t, of 5 nmol m^{-2} s^{-1} provided the best correlation between RY and ozone exposure, using steps of 1 nmol m^{-2} s^{-1} for testing t (Table 3). The intercept of the CUO^5 regression for both crops (0.99)

Table 3
R^2 values for linear regressions between relative yield and the cumulative uptake of ozone (CUO) using different cut-off values (t) for wheat and potato

Uptake rate threshold, t	Potato	Spring wheat
0	0.38	0.03
1	0.50	0.002
2	0.57	0.61
3	0.61	0.69
4	0.64	0.75
5	0.64	0.77
6	0.64	0.73
7	0.62	0.64
8	0.59	0.53
9	0.56	0.44
10	0.53	0.37

deviated very little from 1, which is a desirable property of the dose–response function, since zero exposure should be associated with no effect if an appropriate exposure index is used. The r^2 values for potato and wheat were 0.64 and 0.77, respectively. Using instead a t value of zero, much weaker correlations were obtained (Table 3), indicating the biological relevance of using an ozone uptake rate threshold.

The overall (pooling the information for both crops) best performing mAOT index was mAOT20, reflecting that the actual stomatal conductance (g_{actual}) exerts a relatively strong limitation in Eq. (6). In the case of wheat mAOT10 performed somewhat better than mAOT20, which was best for potato. In the data sets used in the regressions for wheat and potato the average $g_{\mathrm{actual}}/g_{\mathrm{max}}$ during daylight hours was 0.41 and 0.30, respectively. Consequently, the mean bioavailable ozone concentration was much lower than the actual ozone concentration. The relationships between RY and mAOT20 and mAOT10, for potato and wheat, respectively, are shown in Fig. 3. A pattern similar to that of CUO^5 was obtained. The r^2 values of the regressions, 0.57 and 0.58 for potato and wheat, respectively, were however lower than for CUO^5. For AOT40, the x-values tended to be log-normally distributed, while for CUO^5 and mAOT20 the x-values were much closer to a normal distribution.

3.2. *Evaluation of the non-stomatal ozone deposition by wheat leaves*

In Fig. 4, the leaf conductance for ozone, and the leaf uptake of ozone at an ozone concentration of $40\,\mathrm{nmol\,mol^{-1}}$ (the two parameters are autocorrelated), of wheat leaves in the cuvette, are plotted against the leaf conductance for water vapor. The $40\,\mathrm{nmol\,mol^{-1}}$ was chosen since it is the cut-off concentration of AOT40. A strong correlation ($r^2 = 0.97$) was obtained. In order to estimate the non-stomatal leaf conductance to ozone deposition, the cuticular (non-stomatal) transpiration has to be taken into account. This represents the potential for leaf transpiration when the stomata are closed. Typical values for the cuticular conductance for water vapor loss for soft leaves have been suggested to be $10–15\,\mathrm{mmol\,m^{-2}\,s^{-1}}$ (Larcher, 2003) or $13 \pm 4\,\mathrm{mmol\,m^{-2}\,s^{-1}}$ (Körner, 1994), both expressed on a projected area basis. Thus, rather than using the intercept with the y-axis to identify the non-stomatal conductance to ozone deposition, an x-value of approximately $6–7\,\mathrm{mmol\,m^{-2}\,s^{-1}}$ (expressed on a total leaf area basis, used in the present study) should be used in the linear equation, since at approximately this level of transpiration the stomata can be expected to be closed. The value for the non-stomatal leaf conductance for ozone deposition thus found was $g_{\mathrm{ns}} = 15\,\mathrm{mmol\,m^{-2}\,s^{-1}}$.

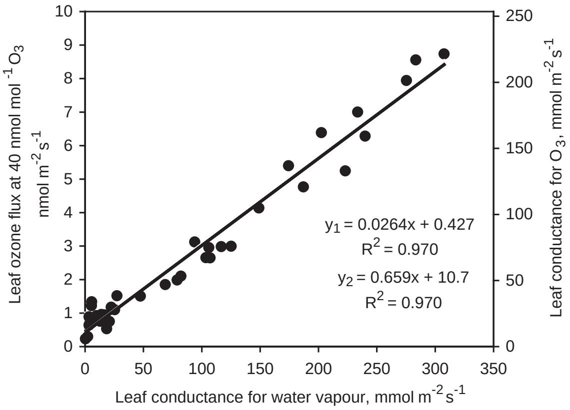

Fig. 4. Calculated ozone flux at a concentration of $40\,\mathrm{nmol\,mol^{-1}}$ (y_1), and leaf conductance for ozone (y_2), in relation to the leaf conductance for water vapor for wheat leaves enclosed in a cuvette, exposed to varying light intensity and cut from the plant at the end short before the end of the measurements.

Consequences of omitting non-stomatal resistance were evaluated by using a value of $g_{\mathrm{ns}} = 25\,\mathrm{mmol\,m^{-2}\,s^{-1}}$, which was applied to the NF++ treatment of the Swedish study of 1988. The CUO^5 value was $1.36\,\mathrm{mmol\,m^{-2}}$ when the non-stomatal conductance was neglected and $1.33\,\mathrm{mmol\,m^{-2}}$ when it was included.

Fig. 4 can be used to compare the ozone exposure indices AOT40 and CUO^5. In the cuvette situation, where the leaf boundary layer is removed, the total leaf conductance for ozone is the sum of the non-stomatal and the stomatal conductance. Thus, a stomatal flux of ozone of $5\,\mathrm{nmol\,m^{-2}\,s^{-1}}$ (the threshold ozone uptake rate of CUO^5) can be estimated to be associated with a total leaf ozone flux of $5.6\,\mathrm{nmol\,m^{-2}\,s^{-1}}$. At an ozone concentration of $40\,\mathrm{nmol\,mol^{-1}}$ (the cut-off concentration of AOT40), this leaf ozone flux corresponded to a leaf conductance for water vapor of 196 mmol m^{-2} s^{-1}. At higher stomatal conductance than this, in combination with lower ozone concentrations, there may be additions to CUO^5, but not to AOT40. At lower stomatal conductance, but higher ozone concentrations, there will be contributions to AOT40 but not necessarily to CUO^5.

4. Discussion

For potato, the integration period from tuber initiation until haulm harvest, the period during which growing tubers are present on the stolons, resulted in a slightly better regression between RY and CUO^5 compared to the integration period from emergence until haulm harvest. This is in accordance with the response pattern in wheat, in which species exposure after anthesis, the period during which growing grains are present seem to be most important for effects on grain yield (Pleijel et al., 1998; Soja et al., 2000). The difference between the two periods for potato was, however, not very large. A disadvantage in using the period starting at tuber initiation until haulm harvest is that this period is likely to be harder to identify in mapping and modelling exercises. In potato, the period of tuber growth comprises a substantial part of the total life cycle of the plant, 81% in the present study, while the grain filling period in wheat comprises of a much shorter part of the life cycle (Pleijel et al., 1998).

Three different types of exposure indices for ozone effects on crops were tested in the present study. The best performance was obtained with CUO^5, but also the mAOT20 index performed better than the presently used AOT40, in particular for wheat. From a mechanistic point of view it seems to be a step forward to use a CUO approach, where the bioavailability of ozone comes into play, as suggested earlier by i.e. Massman et al. (2000). The distribution of the x-values of the regressions favor the choice of CUO^5 compared to AOT40, the latter having log-normally distributed x-values. It should be kept in mind that the use of a constant value to represent the detoxification capacity, the t value of 5 nmol m^{-2} s^{-1}, represents a simplification. However this approach is likely to be more biologically realistic than using no quantitative representation of detoxification capacity. In the future, more advanced dose–response relationships are likely to incorporate diurnal and seasonal variation in the detoxification capacity (Massman et al., 2000).

There was a clear difference between wheat and potato in that the difference in correlation between the different exposure indices was small for potato but large for wheat. Although a larger genetic and climatic difference was present in the data set for wheat, the best correlation obtained for wheat had a much higher correlation coefficient than for potato. In part, this is likely to be an effect of the larger variability of a potato field, where a few tenths of plants fit into an OTC having a ground area of 1–10 m^2, while the number of wheat ears in an OTC plot varies from hundreds to thousands. Also, the smaller number of experiments included for potato (seven) compared to wheat (12) may have influenced the outcome of the investigation in terms of the difference in correlation between RY and ozone exposure.

The regression between RY and CUO^5 for wheat revealed a relatively large degree of consistency among different varieties of wheat in different climates. Compared to AOT40, it is likely that large site-to-site and year-to-year variability in ozone uptake is eliminated by using stomatal conductance modelling, as was the case also in the earlier study by Pleijel et al. (2000). From the results in Fig. 2b, different cultivars tended to show different sensitivity to ozone. For instance, the cultivar Minaret seems to be slightly less sensitive than the durum wheat cultivar from Italy. Possibly, such differences would diminish if different cultivar specific $g_{\max}$ values were used for the wheat varieties. Such information was not available for the present study. As a matter of fact, using only Swedish data, obtained from two genetically related cultivars, yielded a correlation coefficient as high as 0.90 (Danielsson et al., 2003). The limited range of cultivars of wheat (five, only one of which a winter grown crop) and especially of potato (only one cultivar) is of course a limitation of the present study. Another limitation is that no drought-stressed plants were used in the experiments and for the calibrations of the conductance model. In reality crops may experience soil water shortage if not irrigated or grown in humid climates. In order not to overestimate ozone uptake soil water effects should be included in further developments of the models presented in this study.

In the study by Pleijel et al. (2000), the best correlation between RY and CUO was obtained when using no cut-off value t for the ozone exposure index. The difference from the present study, in which a cut-off value of 5 nmol m^{-2} s^{-1} was adopted, is due to changes in the stomatal conductance model, i.e. the use of a lower $g_{\min}$, inclusion of g_{time} and g_{O_3} factors and a change of the g_{vpd} function. Since these changes were based on actual conductance measurements performed in the field (Danielsson et al., 2003), they are likely to represent improvements of the stomatal conductance model.

It is worth noting that Grünhage et al. (2001), using a different approach for estimating risks for negative effects of ozone on plants, came to the conclusion that concentrations of ozone down to approximately 20 nmol mol^{-1} may cause toxic effects on plants. This is in agreement with the present study, where concentrations down to approximately 20 nmol mol^{-1} may contribute to ozone damage if the leaf conductance is close to its maximum value.

Another type of thresholds or cut-off value has also been used in establishing the critical levels for ozone. A least significant effect associated with a certain exposure to get a critical value was suggested by the critical level meeting in Kuopio (Kärenlampi and Skärby, 1996). Since the least significant effect according the regressions between RY and ozone exposure was around 5%, the ozone exposure associated with that damage level was used to identify the critical level (Pleijel, 1996). Consequently, the statistical uncertainty associated with the regressions used formed a basis for quantitatively taking that uncertainty into account. In the present study the 5% yield loss level was associated with a CUO^5 of approximately $0.3\,\mathrm{mmol\,m^{-2}}$ for wheat. The corresponding figures for potato were $1.6\,\mathrm{mmol\,m^{-2}}$ if the period from tuber initiation until haulm harvest was used, and $1.7\,\mathrm{mmol\,m^{-2}}$ if the period from emergence until haulm harvest was used. For wheat the 5% damage level corresponded well with the least significant effect according to the regression in Fig. 2b, but for potato the least significant RY loss was around 5.5% associated with a CUO^5 exposure of $1.7\,\mathrm{mmol\,m^{-2}}$ using tuber initiation until haulm harvest as the integration period, and a 6.5% RY loss from $2.5\,\mathrm{mmol\,m^{-2}}$ if emergence until haulm harvest was used. When comparing the critical CUO^5 values for wheat and potato, it has to be kept in mind that the duration of the period of integration of ozone exposure is much longer for potato, that the stomatal conductance of potato is larger than for wheat and that potato seems to be less sensitive to ozone than wheat according to the present study.

It is essential to view CUO and mAOT as exposure indices, which are sensitive to the same set of factors which influence the stomatal conductance of the uppermost, sunlit leaves of the crop canopy. Hence, the bioavailability of ozone to the leaves which are most important for the ozone impact on photosynthesis is mirrored by the exposure index. Consequently, CUO does not represent the total flux of ozone per unit ground area. The total flux has a number of other components: uptake by soil and organic litter on the soil surface, and shaded, often partly or fully senescent leaves with low stomatal conductance, which scarcely contribute to the production of grain and of tubers. For upscaling of ozone flux to canopy level see Emberson et al. (2000b).

There are both advantages and disadvantages using either the total flux or the uppermost leaf approach. The uppermost leaves receive most of the sunlight and are least senescent. This means that they are most important for the photosynthesis on which grain and tuber production is based. Furthermore, the flux per unit ground area is not of direct importance for yield loss estimations, but indirectly it is important to be able to estimate ozone concentration gradients, which is needed to estimate the ozone concentration at canopy height. However, for the toxicological evaluation of potential yield loss it seems more relevant to base it on the most productive leaves and to avoid the ozone uptake by the soil and parts of the canopy which may consume substantial amounts of ozone without influencing yield to any considerable extent. More specifically, an advantage of the sunlit leaf approach is that the ratio $g_{\mathrm{ns}}/g_{\mathrm{s}}$ is the smallest for that leaf category. As illustrated in Fig. 4, the $g_{\mathrm{ns}}/g_{\mathrm{s}}$ ratio of a green wheat leaf exposed to saturating radiation is around 1:20 if other factors are not strongly limiting stomatal conductance. As a consequence of this high ratio, the difference in CUO^5 for the NF++ treatment of 1988 in Sweden was very small. For older leaves in the depth of the canopy, receiving much less solar radiation levels than sunlit leaves, the $g_{\mathrm{ns}}/g_{\mathrm{s}}$ ratio is likely to be much higher. When using the results of Fig. 4, however, it should be kept in mind that the measurements were made in the laboratory. Field grown plants may differ in non-stomatal conductance from greenhouse grown, and the literature on this point is scanty.

A point to note is that there exists a systematic and transparent way of omitting or adding stomatal conductance modifying factors using the multiplicative approach, simply by setting that factor to one. This holds for both the CUO and the mAOT approaches. It is essential that the dose–response function used is calibrated using the same multiplicative factors that are used in the application, e.g. mapping or other estimations of yield loss. This allows, if required, to move successively from concentration based to ozone uptake based ozone exposure indices. A soil moisture factor, g_{swp}, which was omitted in the present study, could be added to the model using a relationship describing the influence of soil moisture on stomatal conductance in wheat or potato.

5. Conclusions

The main conclusions of the present study were: (1) Using conductance modelling and assuming one common $g_{\max}$ for European wheat, a consistent relationship between RY and CUO^5 with strong correlation was obtained for OTC grown wheat from climates ranging from Finland, over Sweden and Belgium to Italy. (2) Although the range of climatic conditions in Europe covered was smaller for potato than for wheat, the relationship between RY and CUO^5 was weaker, and the improvement using CUO^5, compared to using AOT40, was smaller. (3) The use of a flux modified AOT (mAOT) approach resulted in yield–response relationships similar to those with CUO^5. Accuracy in the response-relationship for wheat was however lost using mAOT20, which reflects the closer relationship between yield effect and ozone uptake above a threshold, compared to the flux modified ozone concentration. (4) In wheat, non-stomatal deposition of ozone was indicated to be small compared to the stomatal uptake and hence to be of little importance for the derivation of the dose–response relationship between RY and CUO^5 in wheat.

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