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# Have ozone effects on carbon sequestration been over-estimated? A new biomass response function for wheat

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## Abstract

Elevated levels of tropospheric ozone can significantly impair the growth of crops. The reduced removal of $CO_2$ by plants leads to higher atmospheric concentrations of $CO_2$, enhancing radiative forcing. Ozone effects on economic yield, e.g. the grain yield of wheat (*Triticum aestivum* L.) are currently used to model effects on radiative forcing. However, changes in grain yield do not necessarily reflect changes in total biomass. Based on analysis of 21 ozone exposure experiments with field-grown wheat, we investigated whether use of effects on grain yield as a proxy for effects on biomass under- or over-estimates effects on biomass. First, we confirmed that effects on partitioning and biomass loss are both of significant importance for wheat yield loss. Then we derived ozone dose response functions for biomass loss and for harvest index (the proportion of above-ground biomass converted to grain) based on twelve experiments and recently developed ozone uptake modelling for wheat. Finally, we used a European scale chemical transport model (EMEP MSC-West) to assess the effect of ozone on biomass (−9 %) and grain yield (−14 %) loss over Europe. Based on yield data per grid square, we estimated above ground biomass losses due to ozone in 2000 in Europe totalling 22.2 million tonnes. Incorrectly applying the grain yield response function to model effects on biomass instead of the biomass response function of this paper would have indicated total above ground biomass losses totalling 38.1 million (i.e. overestimating effects by 15.9 million tonnes). A key conclusion from our study is that future assessments of ozone induced loss of agroecosystem carbon storage should use response functions for biomass, such as that provided in this paper, not grain yield, to avoid overestimation of the indirect radiative forcing from ozone effects on crop biomass accumulation.

## 1 Introduction

Tropospheric ozone is well known to significantly impair the growth of a wide variety of plants (Ainsworth et al., 2012), including forest trees, semi-natural vegetation and crops, e.g. the ozone sensitive species such as wheat (Feng and Kobayashi, 2009). Wheat is the most important crop in Europe and the fourth most important globally (http://faostat.fao.org/site/291/default.aspx). The reduction in net photosynthesis and biomass accumulation caused by ozone is inevitably linked to a decreased uptake of $CO_2$ and thus storage of organic carbon, leading to an enhanced radiative forcing (Ainsworth et al., 2012). Assessments of this indirect contribution to global warming by elevated tropospheric ozone have incorrectly assumed that the grain yield of wheat would represent an estimate of the biomass effect of an ozone sensitive crop represented by wheat (Sitch et al., 2007; Collins et al., 2010). This neglects the fact that a large fraction of the ozone effect on economic yield, e.g. grain yield in wheat, depends on altered partitioning of biomass between reproductive and non-reproductive parts of the plant (Pleijel et al., 1995; Leisner et al., 2012); the implications of excluding this effect are discussed and an alternative function is proposed for use in modelling indirect radiative climate forcing.

Many crops, including wheat, are monocarpic annuals, only flowering once. Their life cycle is characterised by an initial non-reproductive stage of biomass accumulation, which is followed by a reproductive phase including flowering and grain filling (Evans, 1993). When the plant has entered the reproductive stage it becomes prone to senescence, which can be enhanced by stresses such as elevated ozone (Grandjean and Fuhrer, 1989; Pleijel et al., 1998). The shortened reproductive phase results in a smaller biomass accumulation during this phase compared to the non-reproductive phase, and to a less complete redistribution of carbohydrates from the photosynthesis of non-reproductive plant parts to grain (Pleijel et al., 1997).

Formally the relationship between grain yield, biomass partitioning between reproductive and non-reproductive parts and biomass accumulation can be represented by:

$$Y_G = H_I B_A \tag{1}$$

where $Y_G$ is grain yield, $H_I$ is the harvest index (the fraction of above-ground biomass forming grain, Evans, 1993) and $B_A$ is the aboveground biomass at harvest. We can denote $Y_G$ in a situation with elevated ozone (or exposure to any other environmental factor) as $f_1 Y_{Gref}$, where $Y_{Gref}$ is the grain yield in a reference situation, e.g. a control treatment in an experiment, and $f_1$ is a factor representing the degree of influence on $Y_G$, positive if $f_1 > 1$ and negative if $f_1 < 1$. It follows from Eq. (1) that $f_1$ can be expressed as a function of the effects $f_2$ and $f_3$ by setting:

$$f_1 Y_{Gref} = f_2 H_{Iref} f_3 B_{Aref} \tag{2}$$

Here, $H_{Iref}$ and $B_{Aref}$ are the harvest index and above-ground biomass in the control treatment or reference situation. If $f_2$ is much closer to unity than $f_3$ it follows that biomass effects are dominating effects on $Y_G$, but if $f_2$ differs substantially from unity, partitioning effects are also important.

The aim of this investigation was to elucidate the role of biomass partitioning for ozone effects in crops to understand the magnitude of the error caused by using grain yield loss as a proxy for biomass yield loss from ozone in investigations of the indirect radiative forcing from ground-level ozone. More specifically we (1) quantify the relative contribution of biomass accumulation and biomass partitioning for the ozone effects on wheat grain yield, (2) derive dose response functions for effects of ozone on biomass accumulation and harvest index in wheat, and (3) assess the magnitude and geographical distribution of the effect of ozone on biomass loss and grain yield loss in wheat over Europe using the EMEP MSC-West model (Simpson et al., 2013). Our hypothesis was that the ozone effect on wheat grain yield is significantly larger than the effect on biomass accumulation, and that studies which ignored this difference have likely substantially overestimated the indirect radiative forcing from ozone caused by effects on crop growth.

## 2 Materials and methods

Data on wheat grain yield, above-ground biomass and harvest index from experiments using field-grown wheat were extracted from peer-reviewed literature for 21 experiments, representing eight countries and three continents (Table 1). The non-filtered air treatment of each experiment was used as a reference to which treatments with elevated ozone or reduced ozone by charcoal filtration were compared on a relative scale by dividing the value of the biological variables for a certain treatment with that of the reference treatment in each experiment. The deviation of the regression line from a hypothetical 1 : 1-relationship in Figs. 1 and 2 was tested according to Underwood (1997).

Dose-response functions were derived for the relative effect of ozone on above-ground biomass and harvest index, respectively, based on the Phytotoxic Ozone Dose (representing the stomatal ozone uptake by the sunlit leaves) above a threshold of $6\,\mathrm{nmol\,m^{-2}\,s^{-1}}$ based on hourly values ($\mathrm{POD_6}$) (Mills et al., 2011a). Stomatal conductance was estimated from air humidity (vapour pressure deficit), temperature, solar radiation and the influence of phenology (Grünhage et al., 2012). Effects were related to the effect estimated at zero $\mathrm{POD_6}$ for each experiment. At zero $\mathrm{POD_6}$ exposure, the biological variables were set to unity on a relative scale, i.e. it was assumed that there was no ozone effect associated with zero $\mathrm{POD_6}$. The details of the methodology for the calculations, including the regression method for defining relative yields for individual experiments, have been described earlier (Mills et al., 2011a; Grünhage et al., 2012). A sub-set of twelve (performed in Sweden, Finland and Belgium) out of the 13 experiments on which the response function for ozone effects on grain yield in wheat was derived (Mills et al., 2011a; Grünhage et al., 2012) were used to derive functions for harvest index and above-ground biomass as these data were lacking for one of the 13 experiments. The experiments included in the dose–response relationships have been described in the scientific literature (Table 1). One experiment included in Figs. 3 and 4 was not included in Figs. 1 and 2 because it lacked a non-filtered air reference treatment, but adds valuable data to Figs. 3 and 4 which are not sensitive to existence of a non-filtered treatment.

Percentage yield loss (response function in Mills et al., 2011a) and biomass loss (response function in Fig. 3 of the present paper) were calculated for the EU27+CH+NO countries in Figs. 5 and 6 using 50 × 50 km (approximately) grid square $\mathrm{POD}_6$ values determined for year 2000 using the EMEP MSC-W Eulerian model, version rv 3.7 (Simpson et al., 2012) that simulated the emissions, transport, transformation and removal of pollutants, including calculation of ozone fluxes using the Deposition of Ozone for Stomatal Exchange ($\mathrm{DO_3SE}$) model (Emberson et al., 2001; Simpson et al., 2006; Tuovinen et al., 2007). Impacts of ozone on total above ground biomass were calculated from the total yield per 50 × 50 km grid square (see Mills and Harmens, 2011, for method) using the following relationship, derived from the published experimental data included in the current analysis:

$$B_\mathrm{A} = (1.371 Y_\mathrm{G}) + 4.705 \tag{3}$$

Units are tonnes per hectare for biomass and grain yield. Total effects for Europe (in million tonnes) were calculated by summing effects on biomass or yield in every grid square where wheat is grown. Figure 6 show effects for the 50 × 50 km grid squares where total wheat yield exceeded 6000 tonnes.

## 3 Results

### 3.1 Effect of ozone on $Y_\mathrm{G}$ in relation to effects on $B_\mathrm{A}$ and $H_\mathrm{I}$

From Fig. 1 it can be inferred that effects of ozone, in relation to near-ambient ozone treatments using non-filtered air, on wheat $Y_\mathrm{G}$ are strongly correlated ($R^2 = 0.93$) to the effects on $B_\mathrm{A}$. Effects on $Y_\mathrm{G}$ are, however, larger than on $B_\mathrm{A}$ as shown by the strong and statistically significant deviation of the regression line from the hypothetical 1 : 1 relationship, which represents a situation where $Y_\mathrm{G}$ effects would be entirely explained by effects in $B_A$. Correspondingly, Fig. 2 shows that effects on $Y_G$ are correlated to effects on $H_I$ ($R^2 = 0.85$), however with an even larger deviation from the 1 : 1 line than in Fig. 1, indicating that ozone effects on $H_I$ is of significant but smaller importance, than effects on $B_A$, for ozone effects on $Y_G$. In both Figs. 1 and 2 the deviation of the regression line from the hypothetical 1 : 1-realtionship was strongly significant ($p < 0.001$ in both cases).

Obviously, effects of ozone on both $B_A$ and $H_I$ are important for the effect on grain yield. Over the range of all elevated ozone treatments the average value of $f_1$ in Eq. (2) was 0.808, while $f_2$ was 0.904 and $f_3$ was 0.880. It can be noted in Figs. 1 and 2 that filtered air treatments, having reduced ozone concentrations compared to current ambient levels, mostly had a positive effect on wheat growth and yield. This strongly indicates that improved $Y_G$ can be expected if emissions of ozone precursors, and thus ozone concentrations, are reduced.

### 3.2 Dose-response functions for ozone effects on $B_A$ and $H_I$ in wheat

Figures 3 and 4 represent $\mathrm{POD}_6$ based response functions for the ozone effects on $B_A$ and $H_I$, respectively, based on the twelve experiments for which complete datasets are available. The POD index, which is sensitive to the ozone uptake by the plants as influenced by ozone concentrations, air humidity (vapour pressure deficit), temperature, solar radiation and phenology, has been shown to correlate strongly with ozone effects in several plants (Mills et al., 2011b).

The relationships shown in Figs. 3 and 4 use the most recent calibration of the stomatal conductance model for wheat developed under the ICP Vegetation of the Convention on Long-Range Transboundary Air Pollution. It is thus directly comparable with the response function for wheat grain yield using the stomatal conductance model published earlier (Mills et al., 2011a; Grünhage et al., 2012) and is based on a sub-set of the data for which both biomass and yield effects are available. $B_A$ (Fig. 3) and $H_I$ (Fig. 4) were both significantly and negatively related to $\mathrm{POD}_6$, but the negative slopes were smaller (−0.024 for $B_A$ and −0.017 for $H_I$) compared to $Y_G$ (−0.038; Mills et al., 2011a).

### 3.3 Modelled ozone effects on $B_A$ and $Y_G$ for Europe

With the purpose of studying the relationship between the estimates of ozone effects on wheat $Y_G$ and $B_A$, the EMEP model results for the year 2000 were combined with response functions for $Y_G$ and $B_A$. Figure 5 shows the average and variation of the estimated ozone induced loss of wheat $B_A$ and $Y_G$. The comparison reflects the substantial variation in $POD_6$ ozone exposure over Europe and shows an average reduction of biomass loss of 9 % compared to 14 % for grain yield loss, suggesting a ratio of ∼ 0.64 between the effects on $B_A$ and $Y_G$.

The geographical distribution over Europe of the effects on wheat biomass estimated with the EMEP model for year 2000 is presented in Fig. 6. The largest percentage effects (Fig. 6a) are indicated for parts of the Mediterranean, but also major parts of central Europe exhibit effects above 10 %. In peripheral parts of Europe, where wheat is still grown (i.e. not in the areas with the coldest climates), effects are mostly in the range between 5 and 10 %. However, when the quantity of wheat above-ground biomass per grid square was considered (Fig. 6b) the impact on above ground biomass was highest in central and northern areas where wheat is the dominant crop and climatic conditions are highly conducive to ozone uptake. In total, this analysis suggests that ozone pollution in 2000 accounted for lost biomass weighing over 22.2 million tonnes in the wheat growing areas shown in Fig. 6b. Applying, incorrectly, the grain yield response function to the biomass data instead of the biomass response function of this paper would have indicated above ground biomass losses totalling 38.1 million tonnes (i.e. overestimating effects by 15.9 million tonnes). The median value for the above ground biomass losses shown in Fig. 6b was 7.2 tonnes per grid square whilst applying the grain loss function would have indicated a median loss of 12.2 tonnes per grid square.

## 4 Discussion

By reducing plant photosynthesis and growth, elevated tropospheric ozone will result in decreased carbon storage in vegetation and thus in an indirect radiative forcing as a consequence of the $CO_2$ that remains in the atmosphere due to impaired ecosystem carbon storage (Sitch et al., 2007; Collins et al., 2010; Ainsworth et al., 2012). However, using the loss in $Y_G$ of an ozone-sensitive crop like wheat in large-scale vegetation models, without considering the ozone effect on biomass, will lead to a substantial overestimation of the contribution of tropospheric ozone to this kind of indirect radiative forcing. Overestimation can be avoided by using a response function for $B_A$ instead of $Y_G$, such as that shown in Fig. 3, instead of response functions for $Y_G$.

The negative effect of ozone on $H_I$ can be explained by the post-anthesis high sensitivity to ozone in monocarpic crops such as wheat (Pleijel et al., 1998). After anthesis plants become prone to ozone induced senescence (Grandjean and Fuhrer, 1989; Pleijel et al., 1997). This leads to a shorter period of post-anthesis grain filling duration (Gelang et al., 2000), which results in a smaller grain biomass in relation to total biomass.

Estimates of the percent change in $B_A$ were more than one third lower than effects on $Y_G$, leading to over-estimations of effects on carbon storage if yield alone is the determining factor in analysis. There are of course uncertainties in extrapolating our results to all crops on a global basis, and also in calculations of $POD_6$ itself (Tuovinen et al., 2007). Nevertheless, mean ozone effects on $B_A$ of 9 % are relatively large, and as wheat is the most important crop in Europe, and 4th most important in the world (http://faostat.fao.org/site/339/default.asp), it is highly relevant to further investigate the extent to which ozone-induced biomass loss in wheat as well as other plants contributes to radiative forcing. Also, our results show that ground-level ozone has the potential to substantially affect the grain yield of wheat with important consequences for human nutrition. The positive effect on yield obtained from ozone being reduced by filtration of the air as evident from Figs. 1 and 2, emphasises the potential to improve yield by reducing current ozone levels, in line with the analysis of Pleijel (2011).

Although the effects showed non-negligible variation over Europe (Fig. 6), the analysis resulting from the use of the EMEP model suggests a substantial ozone effect on wheat biomass over much of the area where wheat is actually grown. The largest effects on total above ground biomass were predicted to be in central and northern Europe where wheat is most extensively grown and climatic conditions are highly conducive to ozone uptake. It should be kept in mind that in most cases the effects of ozone on belowground biomass accumulation is not or incompletely known, but there is evidence to suggest that below-ground biomass in many plants, including crops, can be more strongly affected by ozone than above-ground biomass (Cooley and Manning, 1987). Thus, the full reduction of biomass accumulation may be larger than that suggested by the effects on $B_A$, although the magnitude of the below-ground effect remains uncertain and requires further study.

The main conclusion of this study is that biomass partitioning is important to consider in crops like wheat, especially when assessing effects of ozone on indirect carbon sequestration. Previous studies using effects on relative grain yield loss from ozone are likely to have resulted in overestimates. This paper provides an alternative function based on ozone effects on biomass instead of grain/seed yield. When further considering this aspect in any analysis of the quantitative effect of ozone on carbon sequestration of crops it has to be recognized that standing biomass is not a measure of the effect on the net carbon balance. Comprehensive understanding of carbon cycling responses depends on models which take into consideration downstream effects, especially heterotrophic respiration and soil organic matter build up/decomposition in the agroecosystems, but also the further use and longevity of agricultural products.

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**Table 1.** References used to extract data for Figs. 1–2 and Figs. 3–4 as well as the number of experiments used deriving from each reference.

| Reference | Figs. 1 and 2 | Figs. 3 and 4 |
|---|---|---|
| Fuhrer et al. (1989) | 3 | |
| Fuhrer et al. (1992) | 2 | |
| Gelang et al. (2000) | 1 | 1 |
| Mortensen and Engvild (1995) | 1 | |
| Mulchi et al. (1995) | 1 | |
| Mulholland et al. (1998) | 1 | |
| Ojanperä et al. (1998) | 2 | 2 |
| Piikki et al. (2008) | 3 | 3 |
| Pleijel et al. (1991) | 2 | 2 |
| Pleijel et al. (1998) | 1 | 1 |
| Pleijel et al. (2000) | 1 | 1 |
| Pleijel et al. (2006) | | 1 |
| Rai et al. (2007) | 1 | |
| Slaughter et al. (1989) | 2 | |

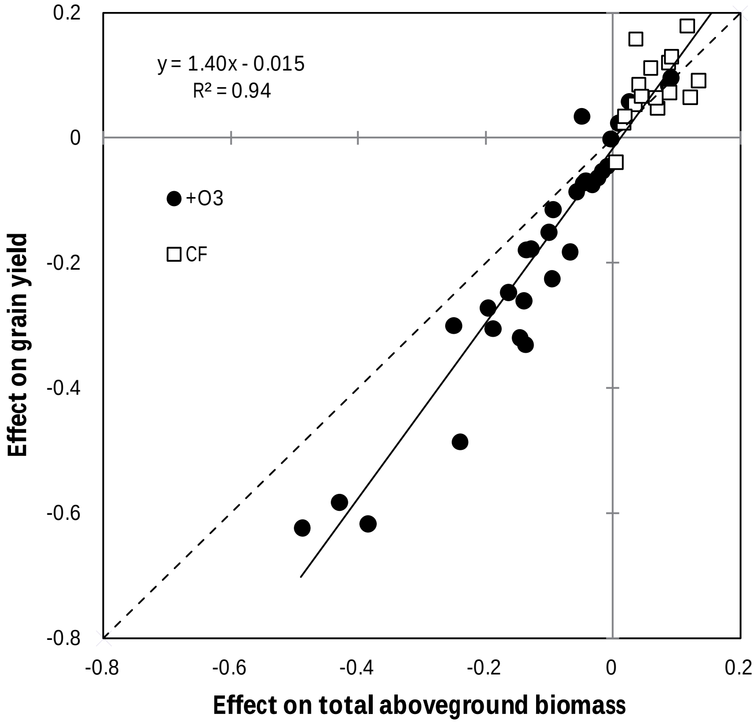

**Fig. 1.** Relative effects of ozone on grain yield vs. above-ground biomass based on 21 experiments with field-grown wheat from eight countries. Effects are relative to the treatment with near ambient concentration (non-filtered chamber air). Charcoal filtered air treatments (CF) with reduced ozone are shown as open squares (☐) and elevated ozone treatments (+$O_3$) as filled circles (•). The broken line represents a hypothetical 1 : 1 relationship.

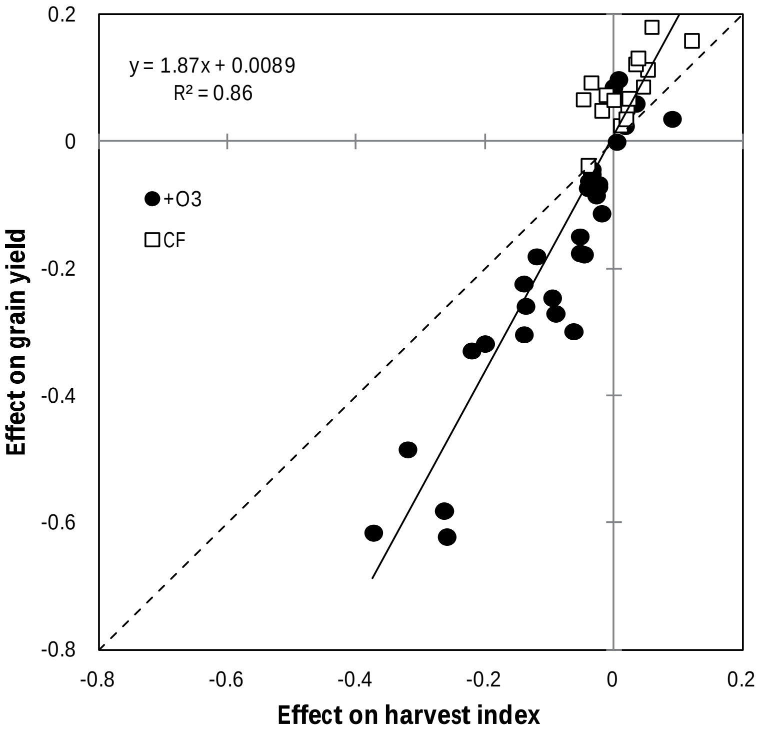

**Fig. 2.** Relative effects of ozone on grain yield vs. harvest index based on 21 experiments with field-grown wheat from eight countries. Effects are relative to the treatment with near ambient concentration (mostly non-filtered chamber air). Charcoal filtered air treatments (CF) with reduced ozone are shown as open squares (☐) and elevated ozone treatments (+$O_3$) as filled circles (•). The broken line represents a hypothetical 1 : 1 relationship.

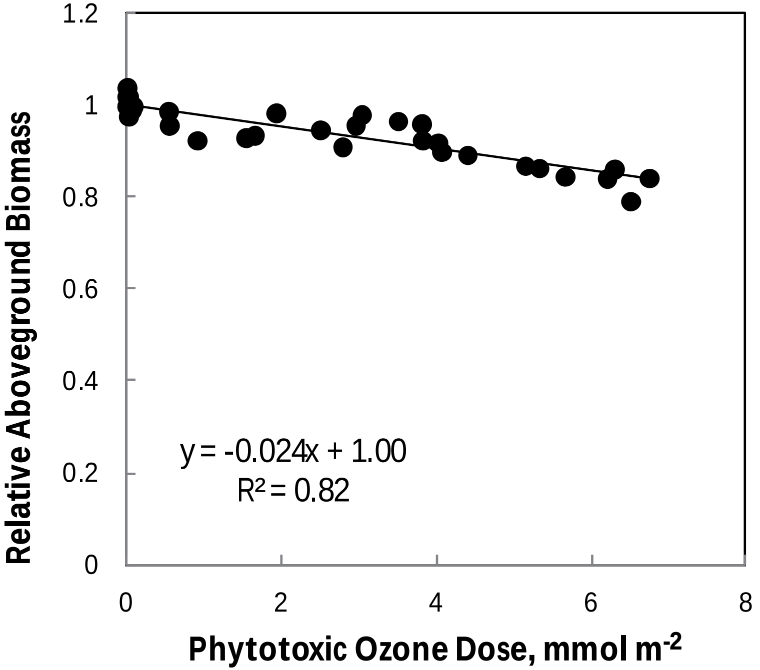

**Fig. 3.** Relative above-ground biomass vs. Phytotoxic Ozone Dose above a threshold of 6 nmol m$^{-2}$ s$^{-1}$ (POD$_6$) based on 12 experiments from three countries (Belgium, Finland, Sweden). The relative scale is based on the assumption that there is no ozone effect on above-ground biomass at zero POD$_6$ in each experiment.

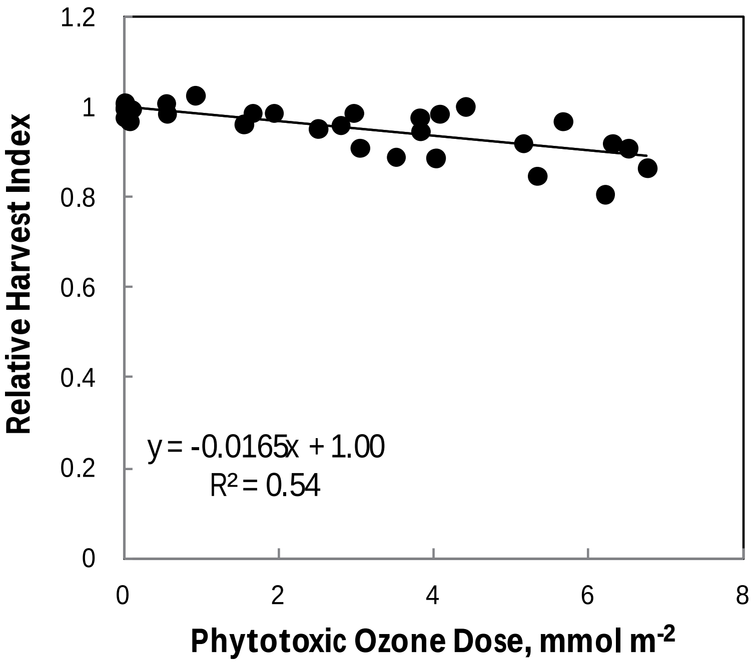

**Fig. 4.** Relative harvest index vs. Phytotoxic Ozone Dose above a threshold of 6 nmol m$^{-2}$ s$^{-1}$ (POD$_6$) based on 12 experiments from three countries. The relative scale is based on the assumption that there is no effect of ozone on harvest index at zero POD$_6$ in each experiment.

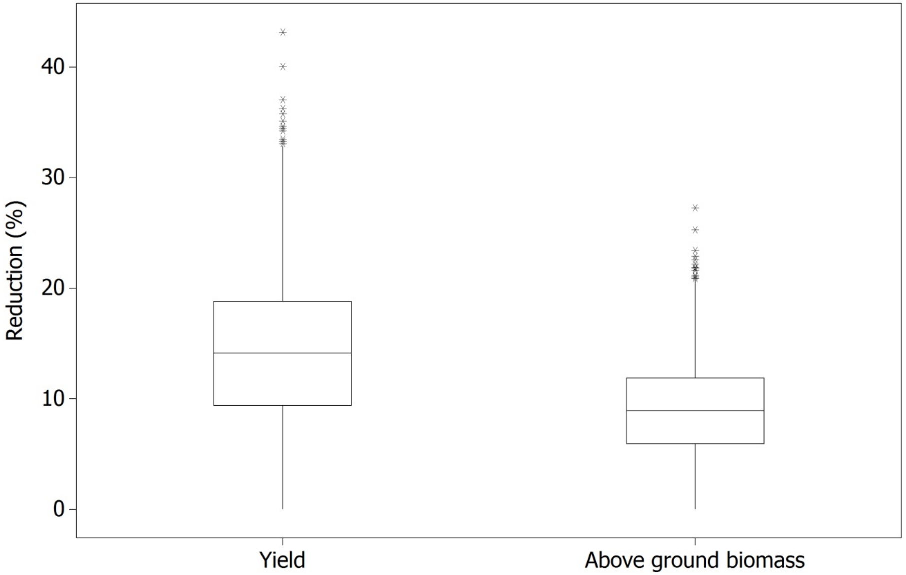

**Fig. 5.** Estimated relative grain yield and above-ground biomass loss of wheat in Europe. The box-whisker plots are based on calculations of $POD_6$ for all (ca. 50 km × 50 km) grid squares from the EMEP MSC-W model in which wheat is grown. The box represents the 25–75 % range of the data, whiskers show the full range of the data and * indicates outliers.

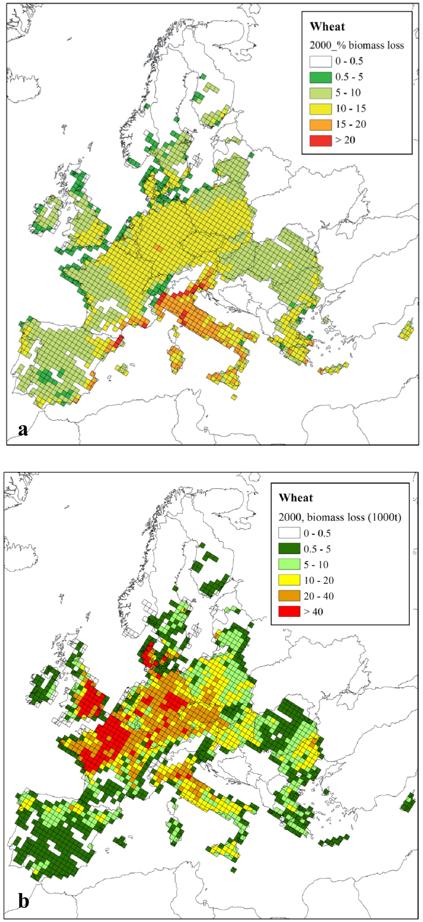

**Fig. 6.** Geographical distribution of ozone effects on wheat biomass over Europe based on results from the EMEP MSC-W model for the year 2000: **(a)** percentage losses in biomass and **(b)** effects on total above ground biomass per 50 km × 50 km grid square.

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