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Effects of Ozone on Leaf Senescence in Spring Wheat - Possible Consequences for Grain Yield

By

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Key words: Leaf duration, ozone, senescence, spring wheat, yield.

Summary

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Results from three open-top chamber experiments, in which field grown spring wheat was exposed to different concentrations of ozone, were used in order to study the negative effect by ozone on leaf duration. In 1987 a clear pattern of fast yellowing with increasing ozone concentration was observed. In 1988, the flag leaf development was characterised by studying the ultrastructure of cells and the senescence was quantified by the average chloroplast area. A consistent pattern of enhanced senescence, expressed as a decrease in the chloroplast area, together with an increased ozone concentration was observed, as well as a linear relationship between grain yield and flag leaf duration. In 1995, an experiment was performed in which ozone fumigation of the plants took place either before or during and after anthesis. Ozone gave rise to a decrease in the green leaf area of plants only with exposure during and after anthesis. It is concluded that a limited shortening of leaf duration is likely to affect only the accumulation of total biomass (accelerated senescence), while higher rates of senescence stop the whole life cycle of the plant prematurely, thus influencing also the carbon allocation in plants (premature senescence).

Introduction

Tropospheric ozone pollution in the industrialised parts of the world is considered to cause important crop yield loss. Wheat (*Triticum aestivum* L.) is a

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well studied and ozone sensitive crop (FUHRER & ACHERMANN 1994). The negative effects by ozone on wheat yield have been reported to be accompanied by enhanced senescence of the leaves. The pattern of change has been similar to that of normal senescence. It includes early yellowing (AMUNDSON & al. 1987), loss of chlorophyll and leaf protein decomposition (GRANDJEAN & FUHRER 1989), reduced content of acyl membrane lipids (SANDELIUS & al. 1995) and reduced chloroplast area (OJANPERÄ & al. 1992) of the leaves.

The duration of the green leaf area after anthesis is a predominant factor in the determination of the grain yield of wheat (see e. g. EVANS 1993). The very strong link between the time period of assimilation and production is considered as a general phenomenon in plant ecophysiology (LARCHER 1995). Based on this observation it seems likely that the reduction of leaf duration caused by ozone explains a major part of the negative effect by ozone on grain yield. The aim of the present paper is: 1) to present evidence of the negative ozone effect on leaf duration, 2) to show how the ozone-induced reduction in wheat grain yield can be related to enhanced senescence.

Materials and Methods

The experiments were made with field grown spring wheat at Östad, 40 km north-east of Göteborg, south-west Sweden (N57°54',E12°24'). Details concerning agricultural practices, ozone exposure and chamber design were presented in PLEIJEL & al. 1991,1996. Open-top chambers with a diameter of 1.25 m were used. In 1987, the number of non-wilted leaves (leaves with visible green colour) was counted on 10 randomly chosen plants in each of the four replicate chambers of the three ozone treatments CF (charcoal-filtered air), NF (non-filtered air) and NF+ (non-filtered air with extra ozone) two weeks before the final harvest. In 1988, a treatment with a higher ozone exposure (NF++) than that used in 1987 was carried out and the dry weight of the straw and grain was determined at plant maturity. Five flag leaf samples were collected weekly in all five replicate chambers of each ozone treatment from two days before anthesis until harvest and the average chloroplast area was determined using light microscopy. The method was described in detail by OJANPERÄ & al. 1992. In 1995, ozone exposure was made one month before (NF+pre) or one moth during and after anthesis (NF+post). Non-filtered air (NF) was used as control and five replicate chambers per treatment were used. Total green leaf area was determined by photocopying leaves, stems and ears of 10 randomly harvested plants per replicate for each sampling time. The green area was measured using an image analyser. Yellow parts of the leaves were not measured. Further details of the 1995 experiment are presented in PLEIJEL & al 1996. The significance of differences among treatments was determined using ANOVA and LSD tests.

Results and Discussion

Fig. 1a shows the percentage of non-wilted leaves of 10 shoots per plot in the different ozone treatments in 1987, two weeks before harvest. The effect of ozone was statistically significant and visibly discernible. It was similar to and consistent with the effect found by AMUNDSON & al. 1987. The symptoms caused by ozone were very similar to those caused by normal senescence in wheat. Leaf senescence in wheat is characterised by a general yellowing. From the beginning it is most pronounced at the leaf tip and then spreads downwards along the leaf.

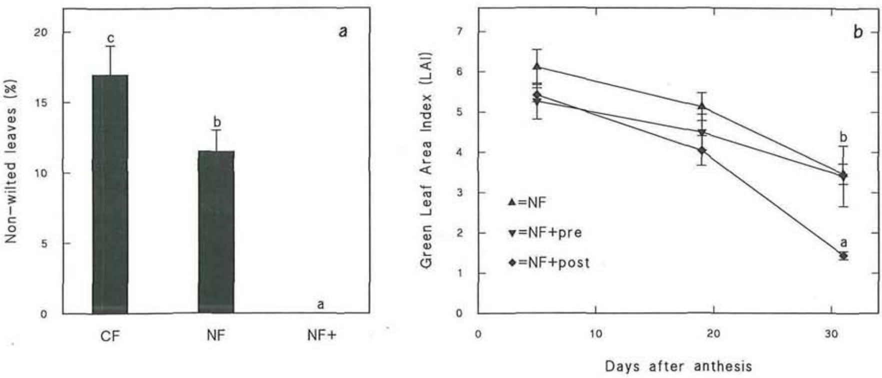

Fig. 1. Early senescence effects of ozone in spring wheat. a) Percentage non-wilted leaves two weeks before harvest of spring wheat grown in charcoal filtered air (CF), non-filtered air (NF) and extra ozone (NF+). b) Green leaf area index of spring wheat treated with (NF), or ozone (2 500 ppb hours AOT40, the Accumulated exposure Over Threshold 40 ppb in ppb hours) for one month before anthesis (NF+pre) or for one month after anthesis (NF+post). Error bars show standard error.

The plants in the 1988 data set used in the present paper were also studied regarding the acyl membrane lipid composition and chlorophyll content (SANDELIUS & al. 1995). It was concluded that the series of changes caused by ozone in flag leaves resembled the that of normal senescence. The loss of chlorophyll and the pattern of lipid decomposition with time was similar in all four ozone treatment, but proceeded faster at higher ozone concentrations.

In Fig. 1b, the development of the green leaf area index after anthesis in the 1995 experiment is presented: It can be inferred that only the NF+post treatment had a significant negative effect on the green leaf area duration. This effect was accompanied by a significant negative effect of about 11% on the grain yield in the NF+post treatment, compared to NF (results not shown). A similar pattern of ozone sensitivity in relation to the developmental stage was found by SOJA 1996. Exposure around and after ear emergence caused larger yield loss than earlier exposure in that study. Thus, the ozone effect on leaf duration in wheat seems to be related mainly to exposure after the onset of anthesis. This is consistent with the results by NIE & al. 1993, who showed that the ozone sensitivity in wheat leaves increased with leaf age.

Based on these observations it seems justified to consider the effect of ozone on wheat leaves as an enhanced senescence, which is caused mainly by post-anthesis exposure. Consequently, it seems reasonable to consider the negative ozone effect on grain yield as an example of the relationship between yield and leaf duration (EVANS 1993).

In Fig. 2a the average chloroplast area of cross sections of wheat flag leaves (1988) from two days before anthesis until senescence is presented. The flag leaf was studied because it is considered the most important source for grain filling in wheat. The senescence-promoting effect of ozone in terms of loss of chloroplast area was clear and significant.

There is evidence that the effect of ozone on grain yield in wheat is composed by two different parts. PLEIJEL & al. 1995 have shown that in a number of ozone studies of field-grown wheat, low ozone exposure mainly affects yield by reducing the total above-ground biomass with equal influence on grain and straw yield. Higher exposure also influences negatively the harvest index (the proportion of the above-ground biomass which is partitioned into the grain).

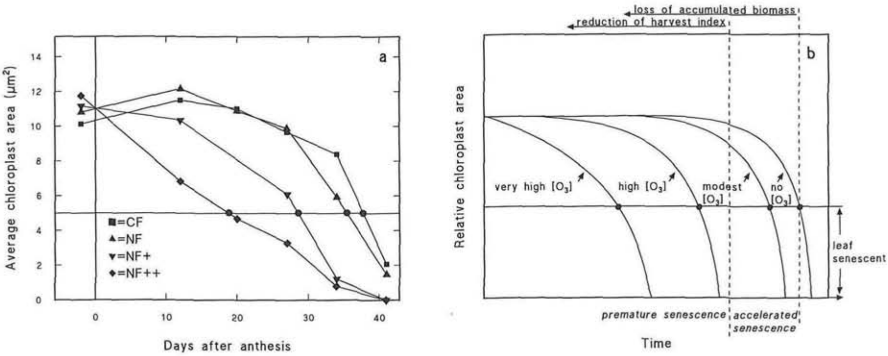

Fig. 2. Flag leaf duration in spring wheat in relation to ozone exposure. a) Average chloroplast area of the flag leaves during the grain filling period. Day 0 represents onset of anthesis and start of ozone treatment (recalculated from OJANPERÄ & al. 1992). CF = charcoal filtered air, NF = non-filtered air, NF+ and NF ++ non-filtered air with two different levels of extra ozone. b) A model of how the shortening of the flag leaf life span can be divided in "accelerated senescence", which influences mainly the accumulation of biomass of the plant, and "premature senescence", where the leaf senescence is so early that the life cycle of the plant is not completed and carbon partitioning is also influenced.

In Fig. 2b an explanation of this pattern is presented that suggests that both the loss of total biomass and the reduction in harvest index can be explained in terms of enhanced senescence. When senescence starts very early in relation to the normal life cycle, all photosynthate stored in leaves and stems is not transported to the growing kernels. This is supported by the fact that in some experiments the absolute straw yield in high ozone treatments was higher than in the next lower ozone treatment, although the grain yield, as well as the total above-ground biomass, was significantly lower in the higher ozone treatment (PLEIJEL & al. 1995). Harvest index is only affected if the reduction of leaf duration is of a certain magnitude. Thus, the enhanced senescence caused by ozone can be divided into two types: 1) accelerated senescence, where the life of the plant is shortened, but all parts of the life cycle are complete, and 2) premature senescence, where the life processes are stopped prematurely, and all parts of the life cycle are not complete. In the 1988 experiment the harvest index was 0.50 in CF and NF, and 0.48 and 0.43 in the NF+ and NF++ treatments, respectively (PLEIJEL & al. 1991). Linear extrapolation of the harvest index data for the two higher ozone treatments indicated that when the flag leaf duration was shortened by five days or more compared to the charcoal filtered treatment, a negative effect on the harvest index was obtained. Studying yield components, the most important criterion of premature senescence in wheat is a reduction in the harvest index. According to the suggestions made above, all carbohydrates are not distributed to the grain, while more or less all carbohydrates are distributed to the grain if the life cycle is not prematurely interrupted. To our knowledge this has not yet been tested experimentally.

Assuming that chloroplast size (area) reflects chloroplast function, the grain yield of spring wheat was plotted against the duration of the flag leaves from anthesis, defined as the number of days with chloroplast area of the flag leaves exceeding 5 μm^2 (Fig. 3). A linear relationship was obtained. Our suggestion of this definition of the flag leaf duration (FLD) was based on data presented by ARAUS & LABRAÑA 1991 who showed that the end of grain filling (the time when there is no further dry weight increase of the kernels) was reached when some parameters, such as chlorophyll content and photosynthesis capacity of the flag leaf, had decreased to approximately 50% of their maximum values. High linear correlations were obtained for chloroplast areas in the range of 4 to 8 μm^2, but the highest value was obtained with 5 μm^2 and the second with 6 μm^2.

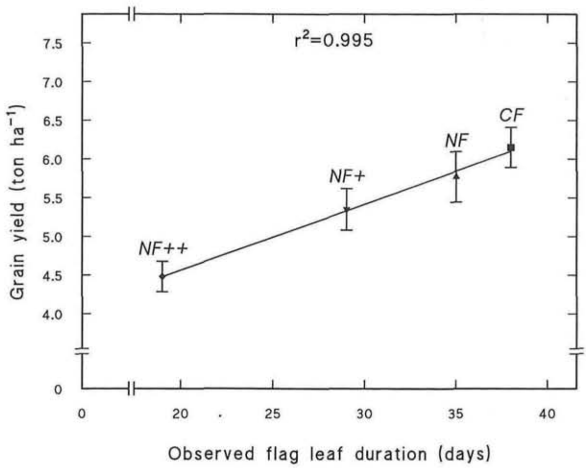

Fig. 3. Grain yield of spring wheat in relation to flag leaf duration. The flag leaf duration was defined as the number of days with chloroplast area of the flag leaves exceeding < 5 μm^2. CF = charcoal filtered air, NF = non-filtered air, NF+ and NF ++ non-filtered air with two different levels of extra ozone.

The relationship between grain yield an leaf duration obtained in Fig. 3a is strong. Evidence from crop physiology has established that there exists a linear relationship between grain yield and leaf duration after anthesis in wheat (EVANS 1993). Our results are consistent with the view that grain yield loss in wheat can be linked to an ozone-induced shortening of leaf duration. Rather few investigations have been undertaken where yield effects and physiological changes in different compartments of the plants have been studied in parallel on the same plant material. In order to improve the understanding and predictions of ozone-induced grain yield loss in cereals further study should be undertaken of 1) the relationship between ozone exposure and wheat leaf senescence, 2) the relationship between leaf duration and grain filling and 3) the characteristics of premature senescence in terms of carbon partitioning of the plant.

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