SHORT DURATION WATERLOGGING EVENTS DURING GRAIN FILLING IN SUNFLOWER: EFFECTS ON YIELD AND ITS COMPONENTS

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Abstract

Temporary waterlogging events during grain filling can induce reductions of grain yield in sunflower. Putative causes include increased incidence of pests and radiation stress (due to cloudy conditions). Yield could also be reduced by impaired physiological processes directly linked to waterlogging stress. The aim of this work was to evaluate the existence and nature of a response of this type. Experiments were conducted during the 1998-99, 1999-00 and 2002-03 seasons (Experiments 1-3). Plants of Paraíso 20 were grown under nonlimiting conditions in large pots arrayed as a crop. Waterlogging events of 24 hours, 48 hours or 7 days were applied in three (Experiments 1 and 2) or one (Experiment 3) occasions during grain filling. In Experiment 3 two substrates of different apparent density were used. Grain yield and its components were measured and post-waterlogging leaf area dynamics were followed in all experiments. In Experiment 3 the rate of oxygen diffusion in the rooting substrate and leaf photosynthesis were measured during and after the stress period. Grain yield was reduced to an extent (range 10 to 60%) that was dependent mainly on the timing of waterlogging and the quality of the root substrate, and these effects were largely attributable to lower grain weight. Yield reductions were associated with reductions in leaf area duration and leaf photosynthesis. We conclude that there is a direct response of yield to waterlogging stress.

Introduction

Heavy rains during the grain filling phase of sunflower crops can impair grain yield (Magrín et al., 1998; Chapman and de la Vega, 2002). Frequently, this loss of yield is attributed to the increased incidence of pests and/or to radiation stress associated with cloudy weather. However, the existence of a direct physiological response to waterlogging cannot be discarded. Soil physical properties and the duration of the stress have been shown to be involved in plant responses to waterlogging (e.g., Kozlowski, 1984). The aim of this work was to evaluate the existence and nature of a direct physiological component in the response of sunflower yield to waterlogging, as a function of differences in the properties of root substrate, and of the opportunity and duration of the stress. To do this we applied waterlogging treatments of different durations and timing during grain filling to plants protected from the effects of diseases and pests grown in different substrates (high or low apparent density).

Materials and Methods

Three experiments were conducted during the 1998-99, 1999-00 and 2002-03 seasons (Experiments 1-3). Plants of Paraíso 20 were grown under drip irrigation in large (30 L) pots, arrayed as a crop of 4.2 plants per square meter. They were fertilized with 4 g N per plant as Ca (NO3)2 and 1.7 g of KH2PO4. Waterlogging events of 24, and 48 hours were applied in three different subphases (A,B, and C) of grain-filling in Experiments 1 and 2 (Figure 1) and during 7 days at mid-grain filling in Experiment 3.

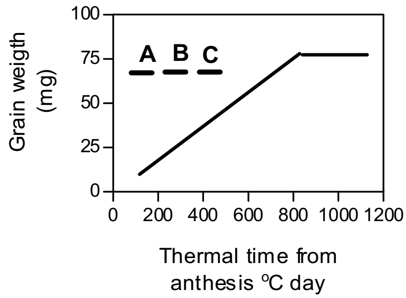

Figure 1. Diagram showing the normal dynamics of grain growth in sunflower as a function of thermal time from anthesis (C day, Tb = -1C). The bars indicate the notional timing of the different waterlogging treatments (A, B and C, Experiments 1 and 2). Waterlogging in Experiment 3 was centered around mid-grain fill.

In Experiment 3, two different substrates (S) were used: S1 contained equal parts of good black A-horizon soil, sand and peat; S2 had 55% horizon-B soil, 30% peat and 15% sand. The substrate used in Experiment 1 was similar to S2, and the one used in Experiment 2 was similar to S1. Leaf area per plant at anthesis was recorded, and dynamics of plant leaf area and individual grain weight were monitored during grain filling. At physiological maturity, grain yield and its components (grain number and grain weight) were determined (Experiments 1-3). Preventive applications of fungicides and insecticides were made throughout the crop cycle in the three experiments. In Experiment 3, the rate of oxygen diffusion (ROD) in the root substrate was measured during the waterlogging and recovery periods using a calomel electrode, as was the maximum (full sunlight) photosynthetic rate of leaves of the upper third of plants using a Li-Cor LI-6200 infrared photosynthesis meter.

Results

Waterlogging during grain filling reduced grain yield significantly in Experiments 1 and 2. The magnitude of the reduction depended on the timing of the stress in Experiments 1 (Figure 2) but not in Experiment 2 (Figure 2). Yield reductions were less severe in Experiment 2 than in Experiment 1 in the two early waterlogging events, but this difference was not observed in the last event. These different results suggested that the effects of waterlogging could depend on the quality of the substrate, which could affect the speed with which waterlogging was relieved at the end of treatment. Under this hypothesis, two different substrates were used in Experiment 3. Consistent with this notion, in Experiment 3 yield reduction was significantly greater in plants grown on S2, the heavier substrate ($p<0.004$) (Figure 2).

The rate of oxygen diffusion (ROD) in the root substrate was used to evaluate the level of anoxia during and after the waterlogging treatment of Exp. 3. In the control treatment ROD mean values of 10 µA were registered during the treatment periods. Waterlogging reduced ROD drastically and rapidly to 10 % of the control values. Recovery of ROD to the control values after the waterlogging treatment took place in 75 hours in S1 and in 105 hours in S2, indicating a longer period of root stress for the plants in the heavier substrate.

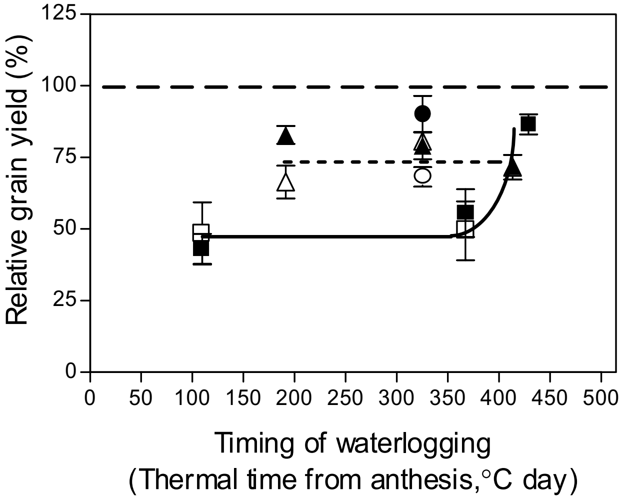

Figure 2. Reduction in relative (to control) grain yield caused by waterlogging events applied in different periods during grain filling, indicated as thermal time from anthesis (Tb = -1C). Symbols are plotted in relation to the x-axis at the mid point of the treatment period. Grain yield of control plants (g per plant) were 99.8±1.75 (Experiment 1, squares); 92.9±3.03 (Experiment 2, triangles); 76.8.5±5.4 (Experiment 3, S1, closed circles) and 72.5±4.62 (Experiment 3, S2, open circles). All yield reductions with respect to the control treatments were significant ($p<0.05$). Variations in the waterlogging events were of different durations: 24 h (closed symbols for Exp. 1 and 2); 48 h (open symbols for Experiments 1 and 2); 7 days (closed circle S1 and open circle S2 in Experiments 3. Bars indicate ± standard error of the mean (n= 7-9). Dashed line: Yield of control plants; full line: Experiment 1; dotted line: Experiments 2 and 3.

Grain number was significantly reduced only by the earliest waterlogging treatments (i.e., Treatment A in Experiments 1 and 2, data not shown). By contrast, grain weight was affected in many of the timings and/or durations of waterlogging (as exemplified in Figures 3 and 4). No clear pattern of responses of rate and duration of grain filling to waterlogging emerged, although both variables were quite often lower in waterlogged plants than in the controls (data not shown).

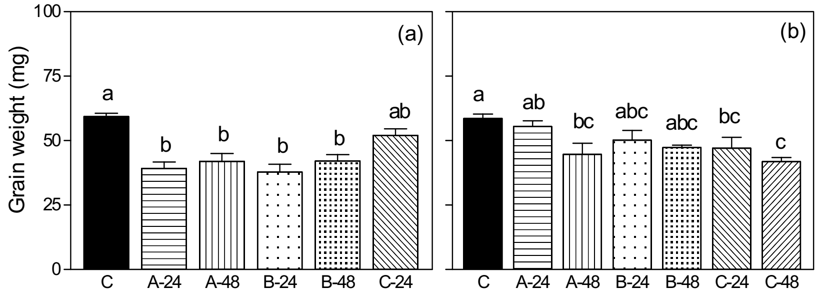

Figure 3. Unit grain weight for control plants (C) and for plants exposed to 24 or 48 h of waterlogging in treatment A, B and C (see Figure 1). Figure 3a: Exp1; Figure 3b: Exp 2. Bars indicate ± standard error of the mean (n= 3 plants, 15 grains per plant). Different letters above bars indicate significant differences (p<0.05) within each experiment.

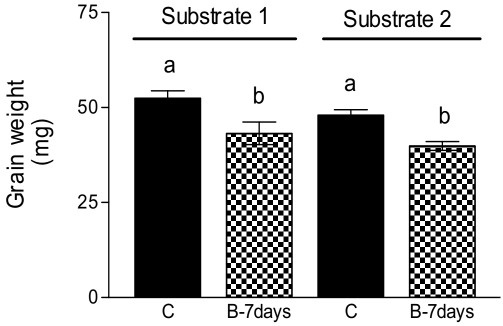

Figure 4. Unit grain weight for control plants (C) and for plants exposed to 7 days of waterlogging in treatment B in pots containing substrates S1 and S2 (Exp.3). Bars indicate ± standard error of the mean (n= 3 plants, 15 grains per plant). Different letters on bars indicate significant differences (p<0.05) within each experiment.

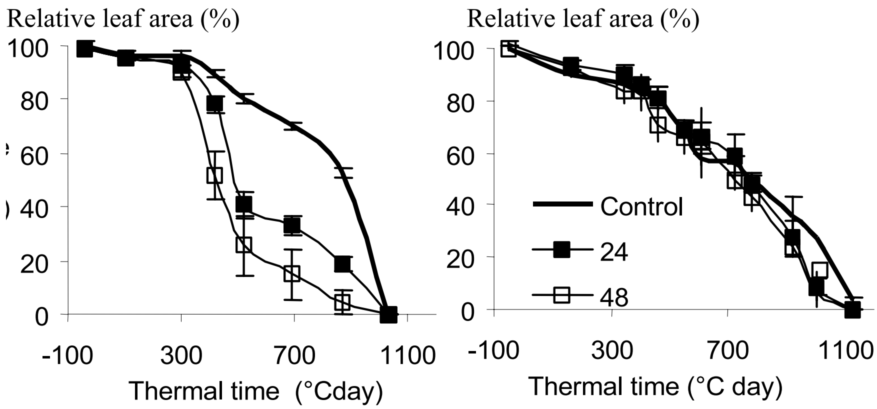

Figure 5. Dynamics of plant leaf area during post anthesis as a function of thermal time (Tb = -1C) from anthesis, relative to leaf area at anthesis. Mean plant leaf area at anthesis was 0.63 and 1.33 square meters/plant for Experiment 1 (left) and Experiment 2 (right), respectively. For clarity, only data from B treatments for each experiment are presented. Bars indicate ± standard error of the mean (n= 7-9).

In Experiment 1, plant leaf area duration (LAD) during grain filling was drastically reduced by waterlogging stress in all three subphases of grain filling (Figure 5). By contrast, in Experiment 2, only slight effects on LAD were registered. In Experiment 3 LAD was reduced from a control value of 970 m2 °C day to 87 and 79 % for treatments S1 and S2, respectively.

Grain yield was significantly related to LAD during grain filling when the data of the three experiments, expressed in relative terms, were pooled (Figure 6). However, most of the data points fell below the 1:1 line. This suggests that some other determinant of yield, different to leaf area, was impaired by the waterlogging stress. The measurements of maximum photosynthetic rate made in Experiment 3 indicated that leaf photosynthesis was reduced during the stress and continued to diverge from control values after relief of stress (Figure 7).

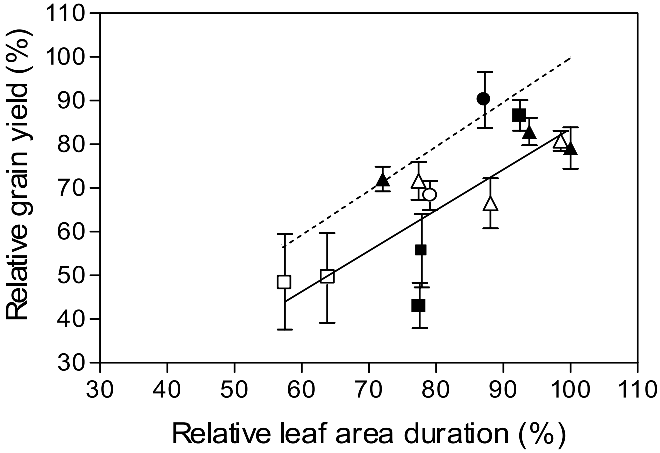

Figure 6. Relative grain yield of waterlogged plants as a function of postanthesis leaf area duration. Both variables are expressed in relation to their respective control values. Symbols as in Figure 2. Bars indicate ± standard error of the mean (n= 7-9). R2 of regression = 0.68 (p<0.001). The dotted line indicates the 1:1 relationship.

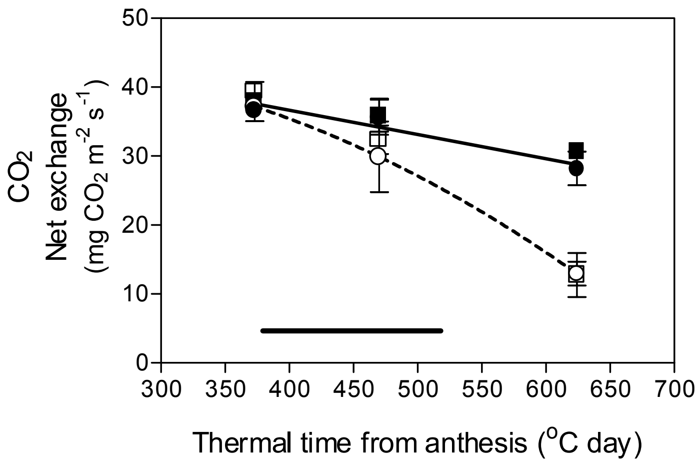

Figure 7. Photosynthesis rate measured at noon in the upper leaves of plants during grain filling growing on substrates S1(circles) and S2 (squares) in Exp. 3 (see Materials and Methods). Control plants: closed symbols; waterlogged plants: open symbols. Vertical bars indicate ± standard error of the mean (n=3); the horizontal bar indicates the period of waterlogging.

Conclusions

Our results indicate that episodes of waterlogging, even short duration ones, during grain filling in plants protected from disease and subjected to the same radiation regime, provoked physiological responses that impaired grain yield. The extent of the detrimental effect on yield depended more on the timing (subphase of grain filling) of the stress and the substrate situation during and after the waterlogging events than the duration of the imposed stress. The recovery of the oxygen status of the substrates, as evaluated through ROD, was slower in the case of the heavier substrate and consequently, the effects of waterlogging stress tended to be more severe in heavier than in lighter substrates.

Plant leaf area duration during grain filling was reduced by waterlogging stress explaining, at least in part, the reduction in grain yield. The photosynthetic capacity of the remaining leaves was also impaired by waterlogging, with expected additional consequences on grain filling, as reflected in the observed changes in unit grain weight. Our work does not allow us to rule out further additional effects, such as the increased transport of ethylene precursors from anoxic roots to leaves and fruit and/or negative feedback on photosynthesis imposed by slower-growing grain. It appears that waterlogging evokes a range of responses, whose links, timing and interactions merit further study.

Acknowledgments

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