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Yield enhancement of droughted wheat by film antitranspirant application: rationale and evidence

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ABSTRACT

Extensive research in the 20th century explored the potential for mitigation of drought by applying polymers (film antitranspirants) to leaves to reduce water loss. It was concluded that film antitranspirants are of limited usefulness, since the polymers reduced photosynthesis (in addition to transpiration) and this was assumed to be detrimental to growth and yield. We propose, however, that irrespective of reduced assimilate availability from photosynthesis, the most drought sensitive stage of yield formation in wheat may respond positively to antitranspirant application. Six field experiments involved applying the film antitranspirant di-1-*p*-menthene at five development stages and 10 soil moisture deficits (SMD) in total over three years. Yield was reduced when the film antitranspirant was applied at development stages less-sensitive to drought, from inflorescence emergence to anthesis, consistent with the conclusions from previous research. In contrast, yield was increased when the film antitranspirant was applied at flag leaf stage, just before the stage most sensitive to drought (boot stage). These results show that film antitranspirant has the potential to mitigate drought effects on yield of wheat.

Keywords: Di-1-p-Menthene; Triticum Aestivum; Water Deficit

1. INTRODUCTION

The majority of global food supply is from cereal crops in rainfed agriculture, and this is highly vulnerable to drought in many countries. An indication of grain yield lost from drought is given by comparing rainfed and irrigated yield: in developing countries rainfed cereal yield is less than half the yield of irrigated cereals [1]. The improvement of crop water productivity (yield per unit of water used) will be an important component of the response to future global pressures on food supply, such as population growth and climate change [2]. Recent reviews of methods of improving crop water productivity [1,3,4] have omitted one agronomic method: the use of film antitranspirants to reduce water loss from plants. This omission is understandable, since the three main reviews of antitranspirants [5-7] and subsequently textbooks on plant water relations and on drought management [8-10] have concluded that film antitranspirants have very limited usefulness.

Commercially-available film antitranspirants are generally polymers sprayed as emulsions in water and include hydrocarbons, terpenoids and latex. Research into film antitranspirants was conducted mainly from the 1950s to the 1970s, and the outcome of this work on a range of plant species was to establish clearly that although water loss from the leaf could be reduced, the films are also of low permeability to carbon dioxide entering the leaf and thus photosynthesis is restricted. A detailed review tabulates the published effects of 23 film antitranspirants in concurrently reducing transpiration and photosynthesis across 13 plant species [7]. Reviews and textbooks have therefore concluded that antitranspirants are only of value for situations where photosynthesis is not important but where reduction in water loss is beneficial [5-10]. Most of these uses are on ornamental species, e.g. on Christmas trees which have been detached from the roots and where growth is not needed, but it is desirable to reduce the needle drop resulting from desiccation (http://www.wiltpruf.com/Home/Story/tabid/392/Default.aspx). Film antitranspirants are not recommended on any large-scale crops. This is not surprising, taking account of the above conclusion, since photosynthesis is clearly important as the source of assimilate for crop yield.

The conclusion of limited usefulness is, however, based only on a consideration of the physiology of the processes of transpiration and photosynthesis. A more-holistic approach, embracing all aspects of crop physiology, recognises that growth and yield depend on the integration of these processes with the stage of development of the plant. It is well-known that the sensitivity of yield-forming processes to drought in most crops depends on the development stage at which drought occurs [11]. The most sensitive stage in wheat is just before emergence of the inflorescence [12]. This stage is externally visible as the swollen inflorescence inside the flag (final) leaf sheath, is referred to as the boot, booting, or boots swollen stage, and is designated growth stage (GS) 45 on the Zadoks scale [13]. We propose that the benefit to wheat yield of reduced loss of water from applying a film antitranspirant at this stage may outweigh the detriment of the concomitant reduction in photosynthesis leading to a net yield gain. Spraying too early or too late would, however, be expected to reduce yield. A yield reduction would also be expected if drought was insufficiently severe.

Six field experiments were conducted over three years to collect preliminary evidence in support of the above rationale for yield enhancement of droughted wheat from film antitranspirant application. The experiments were conducted on a low available water capacity soil with varying reproductive development stage and soil moisture status at application of a film antitranspirant. The combined data from these experiments was analysed by multiple regression to separately quantify the relationships of yield response to the antitranspirant with development stage at application and SMD at application. This enabled the hypothesis to be tested that film antitranspirant can increase yield of droughted wheat if applied at the boot stage.

2. MATERIALS AND METHODS

Winter wheat seed (cultivar Claire) was sown on 5 November 2002, 17 November 2003, and 5 November 2004 on a loamy sand soil in Flat Nook Field on the Harper Adams University College farm (52° 46' N, 2° 25' W). The available water capacity of the soil is 180 mm/m with an average soil depth little more than 1 m. Agronomy followed typical practice for intensively-grown wheat in the UK with herbicide, insecticide, fungicide and growth regulator applications as required. Nitrogen fertilizer applications were adjusted to take account of soil nitrogen status in February. Two adjacent experiments were conducted in each of the three years with one experiment in each year exposed to rainfall and the other experiment covered by polythene tunnels to prevent rain reaching the root zone. Polythene tunnels were erected between GS 37 and GS 39 (21 May 2003; 26 May 2004; 19 May 2005). Three tunnels were used, each covering 20 × 9 m area and 3.2 m high, consisting of galvanized steel hoops mounted on rails as described by Beed *et al.* [14]. The tunnels were covered by polythene except at the ends and from ground level to about 0.5 m. The tunnels were maintained in position over the plots until harvest, and only moved for spraying the plots. The prevailing wind is from the West and the tunnels were orientated with the longer side East-West to maximise air flow through the tunnels and minimise temperature differences from the adjacent uncovered experiment. Plots were approximately 1.7 m by 10 m with the tunnels arranged perpendicular to the plots. Antitranspirant treatments were arranged in a randomised complete block design with two, six, and six blocks respectively in 2002-2003, 2003-2004 and 2004-2005 for covered plots. There were two, six and 15 blocks respectively in 2002-2003, 2003-2004 and 2004-2005 for uncovered plots. In 2002-2003 there were two replicate plots for each treatment randomised within each block. Weather and logistical constraints prevented antitranspirant application at the boots swollen stage in every year. Treatments were application of a film antitranspirant at one development stage in 2002-2003, and two development stages in 2003-2004 and in 2004-2005. Development differences of the uncovered plots and those under polythene tunnels were small and insufficient to allocate a separate growth stage. Di-1-*p*-menthene (96%, Emerald, Intracrop Limited, Lechlade UK) was sprayed on 24 June 2003 at anthesis complete (GS 69), on 24 May 2004 at flag leaf just visible (GS 37) and on 7 June 2004 at half inflorescence emerged (GS 55), on 27 May 2005 at flag leaf ligule just visible (GS 39) and on 3 June 2005 at GS 45. All sprays were in a volume of 200 litres applied through flat fan nozzles, at an application rate of 5 litres/ha in 2002-2003 and 2.5 litres/ha in 2003-2004 and 2004-2005. Control plots were unsprayed.

For the uncovered plots, SMD was calculated using irrigation scheduling software [15] which calculated potential evapotranspiration (PE) using a modified Penman equation and accumulated a daily SMD from 1st April by subtracting rainfall. Meteorological data for the calculations was collected at a weather station within 1 km of the experiments. For the plots under polythene tunnels the same PE calculation was used, but rainfall was not subtracted after the date on which the tunnels were erected. This model has performed well in estimating soil water measurements [15]. Plots were combine-harvested in late August and yield was adjusted to 85% dry matter.

Development stage at application and SMD would be expected to be confounded under the polythene tunnels, since the SMD accumulates progressively so that it is likely to be greater at later development stages at application. This might also be expected to apply to some extent for the uncovered plots since PE tends to increase over the spring treatment application period when air temperature and solar radiation are increasing. This inherent confounding means that statistical analysis of each separate experiment does not give clear information on the effect of antitranspirant application at the different development stages. Therefore the effects of development stage at application and SMD were separately quantified using multiple regression on the combined data from all experiments. The yield response to the antitranspirant was calculated as the difference between the means of antitranspirant and unsprayed plots for each of the ten SMD and GS combinations. The combined yield response data for all three years was then used as the response variate in multiple regression analysis with two explanatory variates: numerical values of the Zadoks code for the development stage of the crop on the date of spraying, and a variate calculated from the SMD in mm. Several SMD variates were used. The mean SMD was calculated over different periods before and after antitranspirant application, and also SMD on the date of application was used. In order to test whether there was a difference in response for uncovered or covered plots a factor with two levels, uncovered or covered, was included in the multiple regression analysis. GenStat software (11^{th} edition; VSN International Limited, Hemel Hempstead) was used for all analyses. Since significance tests in the multiple regression analysis were based on relatively few degrees of freedom, the robustness of the tests and of the estimation of the regression coefficients was evaluated by cross-validation. The multiple regression analysis was conducted 10 times omitting data for a different SMD and GS combination for each analysis.

3. RESULTS

The SMD at the time of antitranspirant application varied from 118 mm to 41 mm (equivalent to 23% to 66% of available water). In 2002-2003 the SMD was already large at the antitranspirant application, but in 2003-2004 and 2004-2005 SMD was small at the time of the first application, although the SMD increased progressively for both uncovered and covered plots up to and beyond the time of the second spray (data not shown). Thus, as anticipated, the development stage at application and the SMD were confounded in 2003-2004 and 2004-2005, with greater SMD at later development stages. Therefore the unadjusted yield data cannot be used to draw clear conclusions on the effects of these two factors on the yield response to the film antitranspirant. Unadjusted yield was representative of UK intensively-grown winter wheat (range of control yield 6.39 t/ha to 8.92 t/ha).

The SMD variate, in combination with development stage at the time of application, that gave the largest percentage variance explained was the SMD at the time of application and results are presented for this analysis only. These two explanatory variates accounted for 60% of the variance in yield response to the antitranspirant ($P = 0.017$; 7 DF). The fitted model (yield response = 0.595 + 0.018 SMD − 0.040 GS) enabled the yield response to the antitranspirant to be calculated for each development stage as if the SMD had been the same. Cross-validation using nine GS and SMD combinations for each analysis showed that there were only small changes to the regression parameters from removal of any one of the 10 GS and SMD combinations, although the constant was only significant for three of the 10 regressions. The overall regression became marginally significant ($P = 0.060$) for one of the GS and SMD combinations, but since there were only small changes to the regression parameters it was concluded that the multiple regression analysis was relatively robust.

The results of the multiple regression analysis are presented as two graphs: yield response adjusted to the mean SMD at application against development stage, and yield response adjusted to the mean development stage at application against SMD. **Figure 1** shows that yield was linearly related to development stage at application and was reduced by application at GS 55 and GS 69 stages. In contrast, yield increased when antitranspirant was applied at the earliest two stages tested: GS 37 and GS 39. Application at GS 45 had little effect on yield. The inclusion of the factor testing the difference between uncovered and covered plots was not significant ($P = 0.832$), confirming that the allocation of a single GS for both covered and uncovered plots at the time of application was appropriate.

Multiple regression analysis also showed that, after adjusting for development stage, yield was linearly related to the SMD at the time of spraying, with substantial reductions in yield from the antitranspirant application at low SMD, but increases in yield at high SMD (**Figure 2**). Since the inclusion of a factor for uncovered or covered plots in the multiple regression was not significant, as described in the preceding paragraph, it was clearly a reasonable assumption that the same PE calculation was appropriate for both environments. The fitted model was used to calculate the threshold SMD needed to obtain a yield increase at the most responsive stage (GS 37). This threshold SMD is 48 mm for the cultivar Claire on this loamy sand soil (equivalent to 27% of the available water). The threshold SMD for an economic

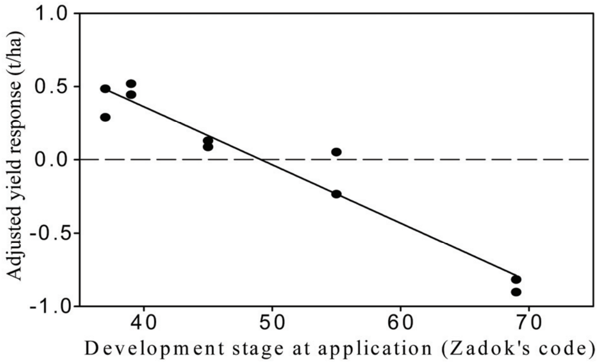

Figure 1. Relationship between yield response to film antitranspirant (adjusted for calculated SMD at application) and development stage at application in 2003, 2004 and 2005. Fitted regression model is described in the text.

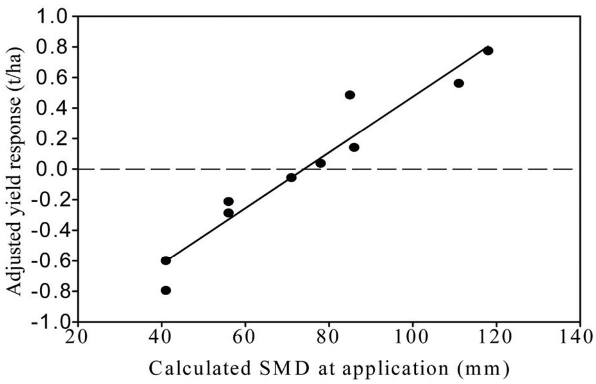

Figure 2. Relationship between yield response to film antitranspirant (adjusted for development stage at application) and calculated SMD at application in 2003, 2004 and 2005. Fitted regression model is described in the text.

response will depend on the relative prices of antitranspirant and grain.

4. DISCUSSION

The reduction in yield from application of the film antitranspirant after the most drought-sensitive boot stage was expected from the conclusions of the reviews and textbooks on this topic, *i.e.*, from the prevailing paradigm. The film restricts photosynthesis and therefore reduces the supply of assimilate available for the growth of the developing florets/caryopses. In contrast, the increase in yield from application of the film antitranspirant just before boot stage is counter-intuitive in relation to the prevailing paradigm, but supports our hypothesis. The benefit of reducing water loss just before boot stage must have exceeded the detriment of reducing photosynthesis. An application before the boot stage is presumably needed so that water stress is ameliorated in advance of the most sensitive stage. It is possible that application to droughted plants at an earlier stage than flag leaf visible may prove to be even more effective.

Support for the concept that reducing water loss from leaves with a film antitranspirant may lead to increased yield in certain circumstances is shown by the work of Davenport *et al.* [16]. They articulated a similar counter-intuitive principle to that outlined here based on experiments with oleanders. Despite a reduction in photosynthesis, increased growth in size of stem internodes through cell expansion was found following antitranspirant application. Further support is found in reports of yield enhancement from film antitranspirants applied at or near the time of sensitive stages in other seed crops from the early years of antitranspirant research, including sorghum [17], rapeseed [18] and corn (maize) [19]. More-recently, such reports have been cited to cast doubt on the conclusion in reviews and textbooks of limited usefulness of film antitranspirants [20]. Our study has, however, provided a further advance in knowledge by demonstrating quantitatively that film antitranspirant applied to a seed crop can both increase and decrease yield depending on development stage at application and soil moisture status, and therefore allows a simple SMD threshold for application to be calculated. This is a particular advantage in the UK where pre-anthesis droughts occur relatively infrequently [21]. A threshold SMD may help agronomists and growers decide whether a spray will be justified in a given year, analogous to current practice with pest or disease thresholds for decision support on insecticide or fungicide applications.

Saini and Westgate [22] reviewed the effects of drought on reproductive development of cereals and concluded that meiosis in the pollen mother cells during inflorescence development is the process affected during the sensitive boot stage. Drought at this stage leads to pollen sterility and lower yield through reduced seed set. Drought-induced pollen sterility has been linked to reduced invertase activity, which in turn appears to result from water stress effects on transcription of genes coding for invertase [23]. No data on the mechanism by which film antitranspirant increases yield has been collected in our study, but it can be speculated that this may have occurred through a reduction in drought-induced pollen sterility. Further research is needed to study the physiological effects of film antitranspirant on wheat, especially effects on plant water status, gas exchange, pollen development and yield components.

The frequency and severity of pre-anthesis drought is greater in many other wheat-growing countries, e.g. much of the USA and Australia [24], than in the UK. The benefits from using film antitranspirant may therefore be greater in these countries, which produce a large proportion of the world's wheat supply. Furthermore, since the sensitivity of yield to meiotic-stage water stress is common to other small-grain cereal species [22], the findings reported here may be applicable to a large proportion of rainfed cereal production and hence global food supply. Indeed the findings may be applicable to any crop relying on reproductive development for the formation of yield. Further research is needed with a range of species and environments to test the wider applicability of these results.

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