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Film antitranspirants increase yield in drought stressed wheat plants by maintaining high grain number

Araz S. Abdullah[a,b,c], Moyassar Mohammed Aziz[c], K.H.M. Siddique[a], K.C. Flower[a,b,*]

[a] The Institute of Agriculture, The University of Western Australia, Crawley, WA, Australia
[b] School of Plant Biology, The University of Western Australia, Crawley, WA, Australia
[c] Faculty of Agriculture and Forestry, Field Crop Department, The University of Mosul, Mosul-Nineveh, Iraq

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ABSTRACT

We investigated the use of film-forming antitranspirants (AT) to reduce transpiration and alleviate the adverse effects of late-season drought on wheat (*Triticum aestivum* L.) growth and yield. Two experiments were conducted in a controlled-temperature glasshouse from April to November 2014, to compare two watering regimes (well watered and water deficit) and three AT treatments (unsprayed control, sprayed before boot swollen and sprayed before anthesis complete). We measured plant water use, transpiration rate, stomatal conductance and photosynthesis. Relative leaf turgor was measured in real time using a non-destructive method of leaf patch clamp pressure. Drought stress reduced daily water use, transpiration rate, stomatal conductance and leaf turgor in wheat plants after about four days. In contrast, these measurements rapidly declined soon after AT application in both well-watered and water-deficit plants. Nevertheless, once soil moisture deficit increased markedly, AT-treated water-deficit plants maintained significantly higher levels of photosynthesis than untreated plants. Drought stress reduced grain yield in unsprayed control plants by more than 40%, compared to well-watered control plants, mainly due to fewer grains per spike. In contrast, drought stress with AT application prior to the most drought-sensitive boot stage reduced yield by only 14%. These results suggest that AT has the potential to improve wheat yields with late-season drought, as is common in semiarid regions; although, more research is required to test the wider applicability of these results in field conditions.

1. Introduction

Less than 5% of the water absorbed by roots is used for crop growth and development; the remaining 95% is transpired (Dawson et al., 1996; Prakash and Ramachandran, 2000). Reducing transpiration presents an opportunity to alleviate adverse effects of water deficit and improve crop productivity under semiarid conditions, where transpiration often exceeds water uptake (Poljakoff-Mayber and Gale, 2012). One agronomic approach to reducing transpiration is to use film-forming antitranspirants (AT) to increase leaf resistance to the diffusion of water vapour, thereby.

Commercially available film-type AT are generally emulsions of wax, latex or plastic that dry onto foliage and form a thin film that reduces stomatal conductance (Davenport et al., 1974). The potential for film-forming AT to reduce transpiration and crop water loss received considerable research attention between the 1950s and 1970s (e.g., Feddema, 1954; Hsiao, 1973). Early studies concluded that in addition to reducing transpiration and maintaining favourable plant water status, these films simultaneously reduced leaf permeability to carbon dioxide exchange consequently restricting photosynthesis (Davenport et al., 1974; Hsiao, 1973; Lipe and Skinner, 1979).

These observations were mainly based on physiological considerations of transpiration and photosynthesis. A broader approach has been suggested, since photosynthesis and yield not only depend on crop physiology but also on the interaction with crop developmental stages (Kettlewell, 2014; Kettlewell et al., 2010) and ambient CO_2 levels (del Amor et al., 2010). Wheat is most sensitive to drought during booting, which coincides with meiosis of pollen mother cells (Saini and Westgate, 1999; Sheoran and Saini, 1996). Water stress at this stage substantially impacts yield. Hence, the application of AT immediately prior to this stage may conserve water and improve grain set which could outweigh the photosynthetic limitations (Kettlewell et al., 2010).

Plant responses to drought stress are often expressed as changes in leaf hydration status. Therefore, the ability to monitor the

* Corresponding author at: The Institute of Agriculture, The University of Western Australia, Crawley, WA, Australia. Tel.: +61 8 6488 4576; fax: +61 8 6488 1108.
E-mail address: ken.flower@uwa.edu.au (K.C. Flower).

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hydration status of a plant leaf is vital when investigating possible strategies to improve drought tolerance in plants (Bramley et al., 2013). Leaf water potential measured using a pressure chamber (Scholander et al., 1965) is considered the most reliable technique for quantifying crop water stress (Siddique et al., 2001b). However, this technique is costly, time consuming and destructive, which limits the number of samples and results in temporal and spatial quantification errors (O'Toole et al., 1984). There is increasing evidence that the recently developed, non-invasive leaf patch clamp pressure (LPCP) has promise for precisely measuring plant leaf water status in real time (Bramley et al., 2013; Westhoff et al., 2009; Zimmermann et al., 2010). The LPCP probe consists of two pads equipped with magnets, one of which contains a pressure sensor chip (Ruger et al., 2010). The probe measures relative changes in leaf turgor pressure by applying a constant pressure generated by magnets to a small patch of an intact leaf. The turgor pressure in the leaf patch is inversely proportional to the magnetic patch pressure. This means that patch pressure is low at high turgor pressure and increases as turgor pressure drops. Therefore, clamping pressure increases when the leaf dehydrates during stomatal opening and in response to water deficit, and decreases when the leaf rehydrates.

In Mediterranean-type environments, such as those in the southwest of Western Australia, late-season terminal droughts occur relatively frequently (Siddique et al., 2001a). Under these conditions, grain yield is limited by the amount of water available for transpiration (Walter and Barley, 1974). Therefore, it is hypothesised that AT applied before the most drought-sensitive stage of booting will reduce water use, transpiration rate and stomatal conductance in wheat. This is expected to preserve soil moisture for grainfill, thereby increasing grain set and yield. The two main objectives of this research were: (i) to investigate the potential of film-type AT to reduce transpiration and alleviate adverse effects of late-season drought on wheat growth and yield, and (ii) to examine the hydration status of wheat plants subjected to film-forming AT and water deficit by providing real-time leaf turgor measurements.

2. Materials and methods

Two similar experiments were conducted in a controlled-temperature glasshouse, set at 22 °C/15 °C day/night temperature, at The University of Western Australia, Perth, Western Australia (31°98'S, 115°81'E) from April to November 2014.

2.1. Experiment 1

2.1.1. Management

Plants were grown in round polyvinyl chloride pots (20 cm diameter, 30 cm deep) which were sealed at the bottom to prevent soil and water losses. Pots were filled with 5 kg of a 4:1 (v/v) mixture of sieved, air-dried yellow sand and reddish-brown clay loam soil (pH 7.4; 1:5 soil: 0.01 M $CaCl_2$ extract) collected from a farm site at Bindi Bindi, Piawaning, Western Australia. The 5 kg soil mixture had a water holding capacity of 1.2 L pot^{-1} (~33% volumetric water content) at field capacity (FC) and 0.54 L pot^{-1} (~15%) at wilting point, which were determined using a pressure plate apparatus before the experiment commenced (Givi et al., 2004). Pots were fertilised with 4 g (w/w) of slow release granular fertiliser (Amgrow Ferticote All Purpose Plant Food, N:P:K:Mg 27:5.5:9:1 plus trace elements) incorporated into the top 3–4 cm of the soil prior to sowing.

Wheat seeds (*Triticum aestivum* L. cv. Mace) were surface sterilised with commercial bleach (active constituent 2.1% sodium hypochlorite) and germinated in Petri dishes lined with wet filter paper on 14 April 2014. Four uniform seedlings were transplanted into each pot when the coleoptiles were approximately 2 cm long. Pots were pre-watered with 1.2 kg water to bring the soil to FC. Ten days after sowing, seedlings were thinned to one plant per pot. The soil was then covered with plastic beads (150 g pot^{-1}) to minimise soil evaporation. Pots were weighed every 2–3 days to determine their watering requirement and kept above 80% FC until the imposition of water-deficit treatments.

2.1.2. Experimental design and treatments

The pots were arranged on benches in a randomised complete block design with six replicates. The factorial experiment consisted of two watering regimes and three AT treatments. The six treatment combinations were: well-watered with no AT (WW/AT_0), well-watered sprayed with AT two days before booting (WW/AT_B), well-watered sprayed with AT two days before anthesis was complete (WW/AT_A), water-deficit with no AT (WD/AT_0), water-deficit sprayed with AT two days before booting (WD/AT_B) and water-deficit sprayed with AT two days before anthesis was complete (WD/AT_A). Pots were rearranged weekly within and between benches to minimise possible variation caused by their position in the glasshouse.

2.1.3. Crop phenology, and water and antitranspirant treatments

Crop phenology was monitored using Zadoks decimal code (Zadoks et al., 1974). Booting was recorded when the flag leaf collar of the main stem was just visible and the swollen inflorescence visible inside the flag leaf sheath (Z39 Zadoks decimal code). Anthesis complete (Z69) was recorded when anthers had emerged from the main stem in more than 70% of the plants.

Water-deficit (WD) treatments began (i) two days before the swollen boot stage (Z39) on 21 June and (ii) two days before anthesis complete (Z69) on 14 July. Well-watered (WW) control pots were watered every 2–3 days to maintain the soil above 80% FC. WD treatments were imposed by withholding irrigation for ten days, after which normal watering to above 80% FC resumed. Total crop transpiration was estimated by pot weight as the difference between evapotranspiration (ET) and evaporation (E) measured from unplanted pots (Gusmao et al., 2012). Total ET was determined by summing daily ET during the ten-day drying cycle from planted pots. Total water consumption was measured from the water applied to the pots. Pot weight was monitored at 10:00 every morning (Australian Western Standard Time).

The commercially available film-type antitranspirant Vapour Gard® (96% Pinolene in 4% inert ingredients, Miller Chemical and Fertilizer, Agspec, Australia Pty Ltd) was mixed with water and sprayed on the plants on the day each drought treatment was imposed (AT_B and AT_A). A preliminary test with Vapour Gard® showed that a rate of 2.5 L ha^{-1} was optimal to reduce transpiration in wheat plants, as higher concentrations (up to 5 L ha^{-1}) did not enhance the effect. Therefore, the AT was applied at a rate of 2.5 L of commercial product using a hand-held sprayer that delivered 90 L ha^{-1} of mix at 200 kPa. Untreated control plants (AT_0) were sprayed with an equivalent volume of water with 4% (v/v) inert spray oil (Synertrol Horti Oil, Organic Crop Protectants Pty Ltd., NSW, Australia) to promote surface wetting. Both solutions were sprayed onto the whole plant canopy until the canopy was evenly covered but not dripping. Full canopy coverage was confirmed in a preliminary test using water-sensitive paper.

2.1.4. Gas exchange measurements

Net photosynthesis, stomatal conductance and transpiration rate were measured between 10:00 and 15:00 with a portable, open gas exchange system (LI-6400; Li-Cor, Inc., Lincoln, NE, USA). Reference CO_2 concentration was set to 380 μmol mol^{-1} and light intensity PAR 1000 μmol m^{-2} s^{-1}, which is the average saturation intensity for photosynthesis in wheat (Saradadevi et al., 2014). A leaf chamber equipped with a red/blue LED light source was used. All measurements were conducted on the middle section of the