Differences in yield physiology in wheat cultivars grown under frost-prone field conditions in Southern Australia

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Abstract
Low temperatures during the flowering period of cereals can lead to floret sterility and subsequent yield reduction. In this study we aimed to understand the physiological bases of yield determination among wheat genotypes grown under frost conditions in southern Australia. One experiment was carried out at Mintaro in South Australia in 2016. Treatments consisted of five wheat cultivars and a synthetic-derived wheat line sown at two different times of sowing (TOS) under field conditions. Yield and yield components were analysed at maturity. To analyse in more detail changes in grain number m^{-2} in response to frost, we mapped the distribution of grains within the spike. The trial experienced early frosts that mostly affected TOS 1, as a result the grain yield of TOS 2 was 3-fold higher than TOS 1. Sterility varied depending on TOS, cultivars and their interactions. For example, the later maturing variety 'Yitpi', which in part avoided the early frost, had the lowest level of sterility in contrast to the earlier maturing varieties such as 'Scout', 'Wyalkatchem' and 'Mace' which showed up to 100% sterility in TOS 1. In addition, we showed a clear trend to increase the number of spikelets exhibiting a significant difference in fertility between TOS. Therefore, optimising flowering time to minimise frost exposure is amongst the most important strategies to minimise frost damage while managing heat and drought stress.

Keywords
Triticum aestivum L., sterility, grain mapping.

Introduction
Yield differences among wheat genotypes and its responsiveness to resource availability are usually related to grain number m^{-2} (Fischer 2007), which is commonly more responsive than grain weight not only to environmental but also to genetic factors (Slafer et al. 2014). Economic losses due to frost in Australian crops are reported to be in the order of $120M to $700M each year (Crimp et al. 2016; Zheng et al 2015; Frederiks et al. 2015). Wheat cultivars can be grouped into winter, facultative and spring types, depending on their requirement for vernalisation to achieve fertile florets at anthesis and set grains. Most winter wheats also respond strongly to long photoperiods only after their vernalisation requirement is met. In contrast, photoperiod is one of the primary factors controlling the initiation of flowering in spring types. Therefore, optimising flowering time to minimise frost exposure is amongst the most important strategies to minimise frost damage while managing heat and drought stress. The aim of this study was to determine and quantify spike fertility in relation to grain yield in wheat under frost-prone field conditions in Southern Australia.

Methods
Growing conditions
An experiment was carried out under field conditions at Mintaro (33°51'22.73"S, 138°45'50.94" E, Elev 410 m), South Australia. Five wheat cultivars ('Mace', 'Scout', 'Cosmick', 'Yitpi' and 'Wyalkatchem') and a synthetic derived line 'AUS30323', which contrast in their susceptibility to low temperature, were sown at two different time of sowings (TOS 1 was 12 May 2016 and TOS 2 was 7 June 2016) under rainfed conditions. Each genotype was replicated three times. Treatments were arranged within a randomised complete block design. Plant density was 180 plants m^{-2}. Nitrogen fertilisation was added following the farmer's management practices in the region. There were six rows per plot with a distance between rows of 0.23 m.

In-crop global radiation (MJ m^{-2}), in-crop average, minimum and maximum temperatures (°C), in-crop photo-thermal quotient (MJ m^{-2} day^{-1} °C^{-1}), and in-crop precipitation (mm) were recorded at daily intervals at standard meteorological stations located close to the experimental sites in Mintaro (SILO - Mintaro, station

id 21033; http://apsrunet.apsim. Info/cgi-bin/silo). Long-term data were recorded as well. Minimum canopy temperature was obtained using an infield weather station.
Weed, diseases and insects were managed by spraying recommended selective herbicides, fungicides and insecticides at the doses suggested by their manufacturers.

Measurements and analyses
At maturity, one linear meter was hand harvested from the inner row of each plot. Plants were pulled out of the soil and taken to the laboratory were the plants and tillers were counted and, after cutting the below ground parts, were divided into leaf laminae + stems (including leaf sheaths) and spikes, oven-dried at 65°C for 2 days and weighed. Then, aboveground biomass, grain yield and its main components were determined. In addition, we mapped the number of grains within the spikes at maturity in order to determine the distribution of grains across the spikes for all genotypes through the different TOS following the procedure described in Ferrante et al. (2017). Briefly, a sub-sample of five main-shoot spikes per experimental unit were randomly selected and in each of them we firstly separated each of the spikelets (maintaining their identity) and counted the number of grains in each of them, from the grain position most proximal (G1) to the most distal (Gn) to the rachis, "n" ranging from 1 to 4 depending on the spikelet positions and treatments. The percentage of sterility was determined by the ratio between the number of sterile florets (or aborted grains) in all position of each spikelet along the spike, and the total number of florets (or normal grains) along the spike. An analysis of variance was performed to study the relationships between traits of interest.

Results

Weather conditions
In-crop rainfall, averaged across the TOS, was 39% higher (721.9 mm) than the long term mean in-crop rainfall (440.7 mm; decile 9.8, Table 1). In-crop minimum air temperature was the same compared to the long term in-crop. Minimum canopy temperature during the critical period around anthesis ranged from -2.7°C to -3.7°C. The two most important frost events occurred on 26 September and 23 October resulting in significant yield losses during the first sowing time (Figure 1).

Table 1. Mean and standard error of the means for temperature minimum (Tmin), maximum (Tmax) and average (Taverage), global radiation (MJ m^{-2} day^{-1}), photo-thermal quotient (PTQ (MJ $m2^{-2}$ day^{-1} $°C^{-1}$)), accumulated rainfall and rainfall decile for each time of sowing (TOS) in Mintaro.

Time of sowing	Growing season	Tmax. (°C)	Tmin. (°C)	Taverage (°C)	Glob. Radiation	PTQ	Rainfall (mm)	Rainfall Decile
TOS 1	In-crop 2016	18.1±0.46	7.0±0.27	12.5±0.33	15.9±0.56	0.79	757.0	
(12/05/2016)	**Long term (1889-2015)**	**18.8±0.07**	**6.8±0.04**	**12.8±0.05**	**16.1±0.05**	**0.80**	**471.3±11.4**	**9.8**
TOS 2	In-crop 2016	18.3±0.48	6.9±0.29	12.6±0.35	16.8±0.59	0.75	686.8	
(07/06/2016)	**Long term (1889-2015)**	**19.2±0.07**	**6.9±0.05**	**13.6±0.04**	**17.0±0.05**	**0.80**	**410.1±9.75**	**9.8**

Aboveground biomass, yield and yield components
The different cultivars and treatments resulted in a wide range of yields, which ranged from 0.4 to 575 g m^{-2} (oven dry). The largest effect in yield was the time of sowing, in which TOS 2 was on average 3-fold higher than TOS 1(data not shown). The synthetic line 'AUS30323' on average achieve the highest yield across both sowing times (data not shown). The above ground biomass was lower in TOS 1 compared to TOS 2; however, this was above the significance threshold (P = 0.053). There was a positive linear correlation between grain number m^{-2} and grain number $spike^{-1}$.

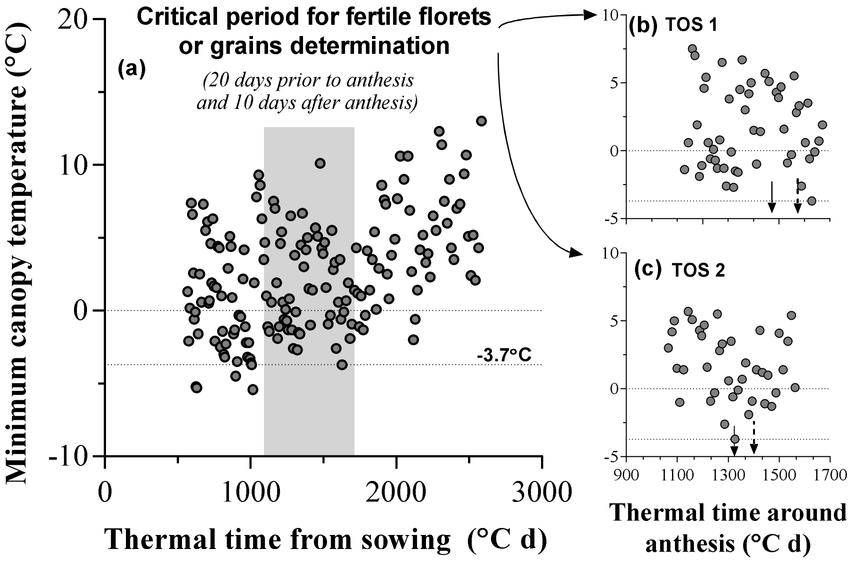

Figure 1. (a) Relationship between minimum canopy temperature and thermal time (GDD, base = 0°C) from sowing. Inset figures show the same relationship around anthesis for (b) TOS 1 and (c) TOS 2. Plain arrow correspond to the thermal time at anthesis for 'Mace', 'Scout', 'Cosmick', 'AUS30323' and 'Wyalkatchem'. Dotted arrow is the thermal time at anthesis for 'Yitpi' cultivar.

Grain number mapping

To understand the physiological differences in yield among wheat genotypes in response to frost, we analysed in detail the components that contribute to grain number m^{-2}. This showed that the number of grains m^{-2} contributed exclusively from the main shoot spikes was largely correlated to the number of grains m^{-2} of the whole crop. Differences in yield between the TOS among genotypes were largely due to differences in spike fertility. Variation in fertility was observed both along the whole spike and within the individual spikelets (Figure 2). It was not consistent which spikelets showed differences in grain number between the two TOS, in some cases central spikelets showed more clear differences (e.g. 'AUS30323') whilst in others the basal spikelets seemed to have been more responsible for the differences (e.g. 'Cosmick') or the variation was observed across all spikelets (e.g. 'Wyalkatchem', Figure 2).

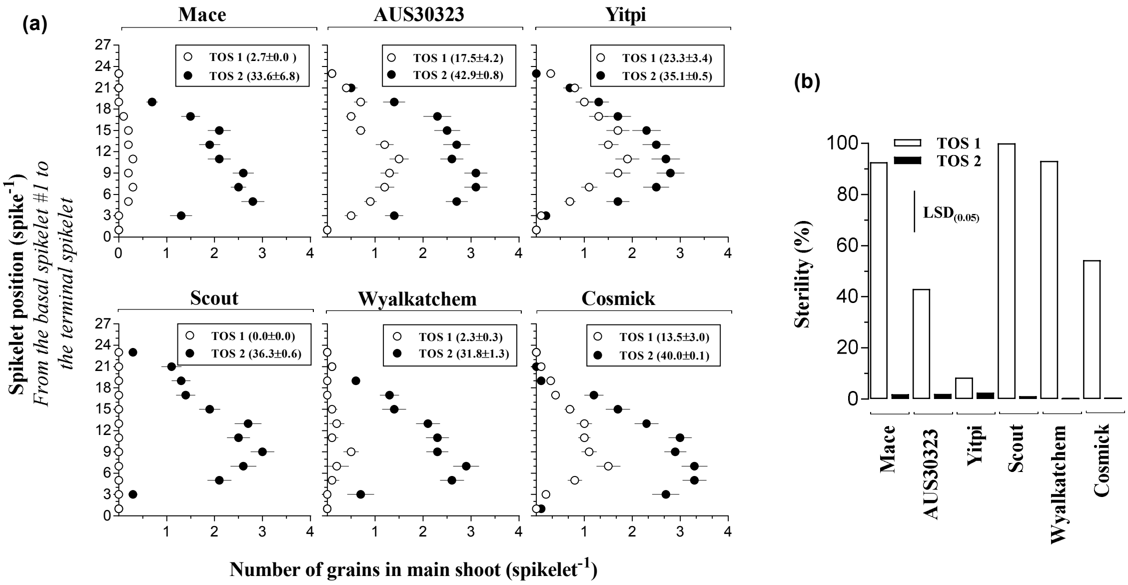

Figure 2. (a) Number of grains per spikelet along the spike for TOS 1, (open symbols) and TOS 2 (closed symbols) for each of the six genotypes. The error bars represent the ±SE (not visible in some cases as it was smaller than the diameter of the symbol). (b) Sterility for each particular genotype in TOS 1, (open bars) and TOS 2 (closed bars).

There was a wide range of sterility among genotypes in TOS 1. For example, 'Scout' was most affected by the early frost events (100% of damage), whilst 'Yitpi', by flowering later to avoid the early frosts, showed the lowest level of sterility. In contrast, TOS 2 was practically unaffected by frost damage (Figure 2, right panel).

Conclusion

Significant differences were observed when we compared grain number m^{-2} for each cultivar across TOS. The main differences among wheat genotypes were related to grain number $spike^{-1}$, as well as in the case of main shoot grain number $spike^{-1}$, with no significant differences related to spikes m^{-2}. Within TOS 1, 'Yitpi' had the higher grain yield with minimal frost damage as a consequence of a longer time to maturity compared to the other genotypes (i.e. frost avoidance). However, there was no direct evidence that sterility was frost induced. Optimisation of flowering needs to account for trade-off with heat and drought stress. In addition, differences may be related to other physiological characteristics of this cultivar that should be tested with more detail. Finally, understanding yield physiology, in particular the spike fertility and the fate of the fertile florets becoming grains, should be used to provide more accurate results related to frost damage in wheat.

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