Maximising water-limited yield in cereals by balancing pre- and post-anthesis growth

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Abstract
Pre- and post-anthesis growth and water-use must be balanced to create a sink demand at anthesis that can be filled using the remaining water after anthesis in order to maximize cereal yield in water-limited environments where crops rely on stored soil moisture. To better understand this balance, we expressed the relationship between post- and pre-anthesis biomass as a ratio, termed as the post- to pre-anthesis biomass ratio (PPABR). This ratio was assessed in three cereal species (sorghum, wheat and barley) in multiple seasons and environments to examine the extent to which it could be manipulated by genetics and management. Results suggest that post-anthesis water availability was closely linked to pre-anthesis green leaf area and biomass, and that at least in environments where crops relied on stored soil moisture, limiting canopy size is one strategy to enhance water availability for grain filling in the face of end-of-season drought.

Keywords
Biomass partitioning, crop water use, drought adaptation, stored soil moisture, stay-green

Introduction
End-of-season drought is a major constraint to cereal production in Australia. Better aligning crop development to the pattern of water supply is critical when water is limiting, ensuring that adequate water is available to fill grain after flowering. Crops facing end-of-season drought must conserve water during early growth to ensure that sufficient water is available for grain filling, particularly in drought-prone regions where crops rely heavily on stored soil moisture. Under these conditions at least, balancing pre- and post-anthesis biomass production appears to be a key factor determining grain yield.

Grain yield can be maximized if pre-anthesis growth and water use are such that sufficient post-anthesis soil water is retained to meet yield potential (Fischer, 1979; Hammer, 2006). Crop scientists have targeted canopy development traits and associated management strategies that optimize the ratio of post- and pre-anthesis water use in determinate grain crops to improve water-limited yield (Fischer, 1979; Hammer, 2006; Passioura and Angus, 2010).

The post:pre anthesis biomass ratio (PPABR) is proposed as an index to describe differences in partitioning of biomass before and after flowering. This paper examines the impact of pre- and post-flowering biomass production on grain yield in sorghum, wheat and barley grown in a region where end-of-season drought is common and where soils have a high water-holding capacity, thus retaining water. We hypothesize that canopy development in cereals is a key regulator of biomass allocation before and after flowering, affecting grain yield in water-limited environments.

Methods
Field experiments
Field experiments in rain-fed and irrigated conditions were conducted for sorghum (*Sorghum bicolor* L. Moench), barley (*Hordeum vulgare* L.) and wheat (*Triticum aestivum* L.) in the Australian north-eastern grain belt which is characterized by summer-dominant rainfall and mostly deep soils with relatively high soil water retention capacity. Two datasets were selected to evaluate the PPABR

concept in sorghum because they contained detailed data on crop growth from 16 hybrids under three managed water scenarios at Warwick, Queensland, Australia. In addition, wheat and barley datasets comprising a number of key genotypes grown in a broad range of water-limited scenarios (32 trials at 16 sites in 9 seasons) in the northern grain belt were selected to test the PPABR concept in winter cereals.

Genotypes

For sorghum, 16 hybrids (season 1) and 9 hybrids (season 2) varying in two sources of stay-green (KS19 and B35) were examined over two seasons. For barley, three common Australian cultivars were grown (Grout, Grimmett and Gairdner) over three seasons. For wheat, the genotype SeriM82 was chosen as a high-yielding drought-tolerant line and was contrasted with Hartog, a cultivar adapted to sub-tropical Australia. These lines were compared with up to three SeriM82 x Hartog derived doubled haploid lines chosen to contrast in yield performance under water-limited conditions.

Calculation of post:pre anthesis ratio

For each crop species, the PPABR was derived by dividing the post-anthesis biomass (biomass at maturity – biomass at anthesis) by the pre-anthesis biomass (biomass at anthesis) for each plot.

Environmental classification

The experimental environments were classified on the basis of the occurrence of water stress during the course of crop development with ET1 being the least stressed and ET5 most stressed for sorghum and ET3 for wheat and barley, respectively (Chapman et al., 2000; Chenu et al, 2013).

Results and Discussion

Pre- and post-anthesis biomass accumulation were generally negatively correlated

Under water-limited conditions where crops relied on stored soil moisture, genotypes that produced more biomass (and leaf area) before flowering, likely using more water, produced less biomass after flowering, suggesting that they had depleted water reserves remaining during grain filling (not shown). On the other hand, those genotypes that produced less biomass before flowering, conserving water, produced more biomass after flowering, presumably utilising pre-anthesis water savings. Hence pre- and post-anthesis biomasses were negatively correlated in all tested drought environments (ET2-3-5) for all crop species at all studied sites and years (the only exception was the neutral response in the second sorghum experiment). However, when water was not limiting growth (ET1), the relationship was not consistent, with crops exhibiting neutral and negative relationships, depending on the experiment (site and/or year) for all crops. This inconsistency is likely a consequence of the fact that there was little or no water restriction post-anthesis, meaning that plants exhibiting high early vigour were not disadvantaged during the post-anthesis period.

While our results suggest that the negative correlation between pre- and post-anthesis biomass accumulation under water deficit is a key principle across cereals, at least in environments where the crops depend on stored soil moisture, there will be exceptions. For example, recent studies in sorghum found that pre-flowering canopy size was uncorrelated or very weakly correlated with the stay-green trait at two locations where water stress was severe enough that senescence due to water limitation occurred across all genotypes (Liedtke et al., 2020). These different findings likely result from the broader range of germplasm used in that study and suggest that traits influencing water capture or water use efficiency may play a greater role in the expression of the stay-green phenotype in this material than maximum canopy size. While not tested here, in cropping systems depending mostly on in-season rainfall (e.g. southern and western Australia), this relationship may vary with the magnitude and timing of post-flowering rainfall. In these environments, less vigorous crops would have a lesser water demand and thus be less prone to drought stress, but at the same time they would also have a lesser potential to accumulate high post-flowering biomass and yield.

Ratio of post- and pre-anthesis biomass is positively correlated with grain yield under drought

The relationship between post- and pre-anthesis accumulated biomass can be expressed as a ratio, designated as the post:pre-anthesis biomass ratio (as described above). A value of 1 indicates that post- and pre-anthesis biomasses were equal. A value of <1 indicates that the pre-anthesis biomass exceeded post-anthesis biomass. A value of >1 indicates that post-anthesis biomass exceeded pre-anthesis biomass.

The PPABR/yield regression was positive for all crop species, seasons and sites in water-limited environments (Fig. 1). Our hypothesis that the slope of the PPABR/yield regression should increase with increasing water deficit was generally supported, particularly in sorghum and wheat. This suggests that post-anthesis water availability was closely linked to pre-anthesis green leaf area and biomass, and that limiting canopy size should help to ensure adequate water availability for grain filling in the face of end-of-season water-stress.

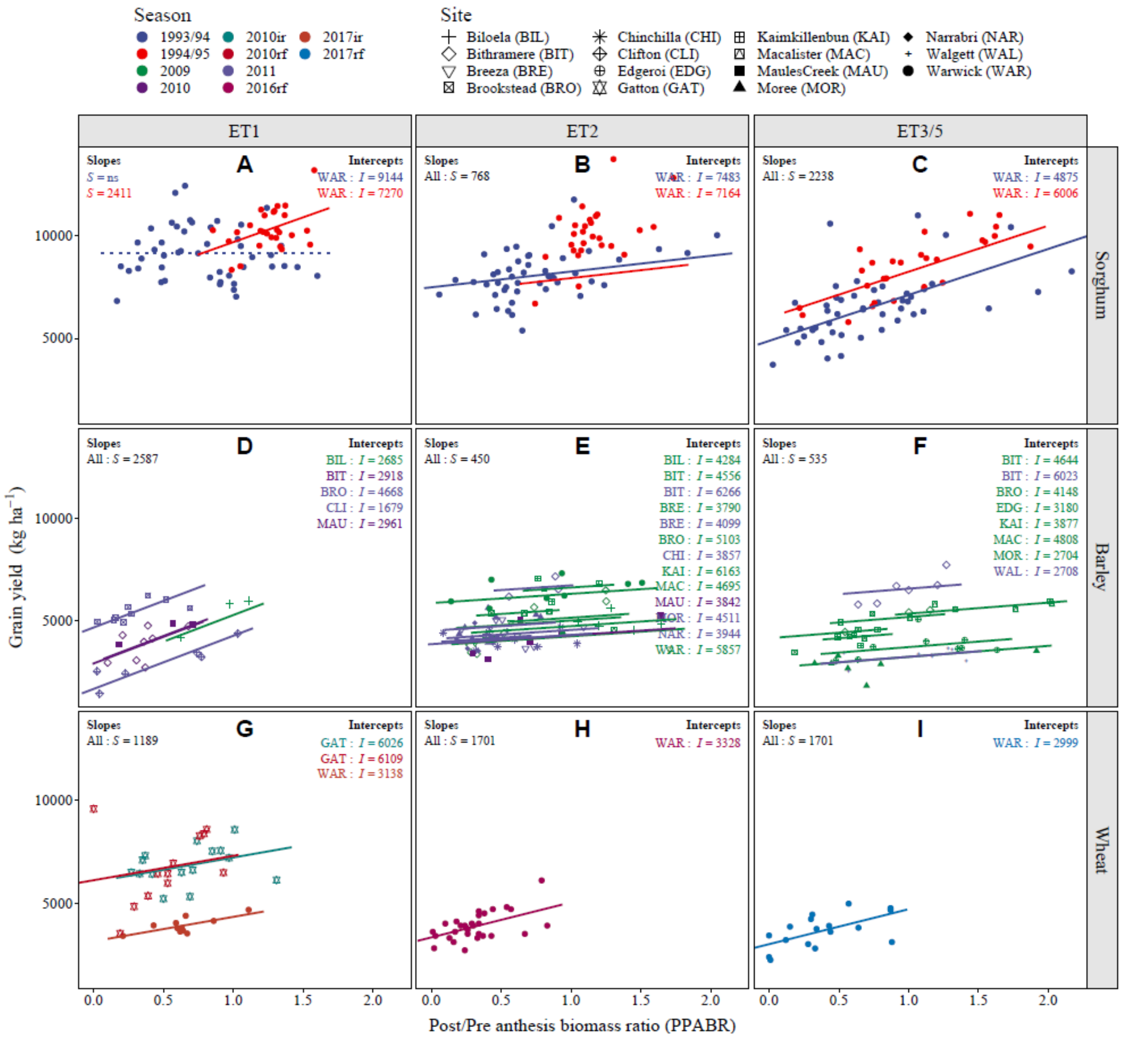

Figure 1. Post/Pre anthesis biomass ratio (PPABR) versus grain yield for sorghum ET1 (A), ET2 (B) and ET5 (C); barley ET1 (D), ET2 (E) and ET3 (F); and wheat ET1 (G), ET2 (H) and ET3 (I). Individual plot data are presented. ET1 = absence of drought before and after anthesis; ET2 = mild post-anthesis drought which could be or not be relieved; ET3 = pre-anthesis drought which was relieved post-anthesis to varying degrees; ET5 = post-anthesis drought that commenced prior to anthesis and was not relieved.

However, when water was not limiting (ET1), the slope of the PPABR/yield regression was variable, with a neutral response for sorghum (season 1 only, Fig. 1A), and positive slopes for wheat (all sites and seasons), barley (all sites and seasons) and sorghum (season 2 only). This indicates that when water is not limiting, grain yield is either not affected by PPABR (i.e. grain yield is largely independent of biomass production before anthesis) or, in some cases, positively correlated (likely due to the capacity to develop and fill a large grain sink when water is not limiting).

Genetic and management strategies for optimising the PPABR in cereals

Different traits and genes can impact PPABR. For instance, major genes responsible for phenology can be manipulated, enabling temperate cereals to be grown across a wide range of durations (Richards, 2000; Zheng et al., 2016). Manipulation of genes that shift water use from pre- to post-anthesis, regardless of phenology, may also significantly impact the PPABR by i) utilizing water conserved before flowering (e.g. reduced leaf area, increased transpiration efficiency), and/or ii) increasing water uptake during grain filling (e.g adapted root system).

A range of management strategies can be used to manipulate the PPABR in cereals, including pre-crop factors, plant density, nitrogen fertilization, weed control, crop rotations and soil type. Interactions are inevitable among the genetic and management factors listed here. To some extent, GxMxE interactions may be overlooked, since breeders traditionally deal with GxE rather than management (M), while agronomists often investigate impacts of management on new varieties (Messina et al, 2009). However, GxMxE interactions are important. For instance, yield improvements in US maize have resulted from taking advantage of the interactions between new hybrids and plant density (Duvick et al., 2004). A modelling approach to assess the extent to which various genetic and management strategies impact PPABR should be considered.

Conclusion

The post:pre anthesis biomass ratio (PPABR) is an index that integrates crop growth before and after flowering, highlighting how the partitioning of water use between these two periods is critical to grain yield in rain-fed environments. The consistent negative correlation between PPABR and canopy size at anthesis indicates that canopy development is one of the key factors (but not the only one) determining crop water use before and after anthesis, at least in the tested environments where crops rely partly on stored soil moisture. Therefore, manipulating canopy development in cereals via genetic and management mechanisms should enable the balance between pre- and post-anthesis water use to be optimised.

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