Plant Design Features that Improve Grain Yield of Cereals under Drought

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Abstract

A sound understanding of the crop physiological basis of drought adaptation in cereals can assist crop improvement programs to better target trait selection for variable stress environments, if such knowledge is incorporated into crop growth simulation models. Based on detailed experiments involving sorghum and maize, we identified physiological processes that explained observed differences in grain yield under drought stress for genotypes with similar transpiration efficiency. If water availability restricts crop growth, grain yield can be increased by restricting pre-anthesis water use and thus maximizing water availability post-anthesis. Sorghum can achieve this by restricting plant size through early anthesis or through reduced tillering in response to vigorous main shoot growth prior to tiller appearance. Albeit useful in genotype-by-environment combinations conducive to tillering, this mechanism has limited value in environments where tillers are absent, or for non-tillering crops. In the absence of tillers, maize can improve grain yield under drought by changes in dry matter partitioning that reduce competition for assimilates with the primary ear during the period when grain set is determined. Despite the different pathways, both mechanisms achieve a higher grain number under drought, presumably through a higher panicle (ear) growth rate around anthesis. These crop physiological processes will be incorporated into the APSIM-Cereal crop growth simulation model to identify adaptation mechanisms that are suited to specific drought patterns. This will allow breeders to match selection criteria to prevalent drought patterns in their target population of environments and thus improve the efficiency of crop improvement.

Media summary

Generic crop physiological processes have been identified that can increase grain yield of cereals under post-anthesis drought.

Key words

Drought adaptation, gene-phenotype modeling, leaf area, partitioning, physiological functionality, tillering

Introduction

With increasing world population, efficient use of available water resources becomes increasingly important. Although many papers have been published over the past decade on traits, QTL's, or genes associated with drought adaptation, many of these employ a black-box strategy, in which the underpinning physiological processes and consequences for whole plant function are not well understood (eg. Nelson et al., 2007). Knowledge of the dynamic crop physiological processes that determine drought adaptation will provide plant breeders with more targeted selection criteria and molecular biologists with more relevant genomic targets. Incorporation into dynamic crop growth simulation models allows the identification of genotypes with adaptation to specific environmental conditions (Hammer et al., 2006). Here we analyse experimental data within the context of developing a physiological framework for drought adaptation. The aim is to illustrate that crops with contrasting plant type can employ contrasting pathways to achieve a common endpoint for drought adaptation.

Methods

Plant material and experiments

Sorghum experiments included four hybrids, based on two female and two male inbred lines. The parents were either drought tolerant (A35, RQL12) or susceptible (AQL39, RQL36). Consequently, A35/RQL36, A35/RQL12, and AQL39/RQL12 were drought tolerant and AQL39/RQL36 was susceptible. Maize experiments included a drought tolerant and a susceptible hybrid. For both crops, differences in transpiration efficiency were absent.

Experiments were conducted in a shade house. Individual plants were grown in either lysimeters (LYS, 30 cm diameter, 75 cm high) or root chambers (RC, 240x120x10 cm^3). Plants in LYS were well-watered and well-fertilised and harvested around anthesis. Plants in RC were grown on stored soil moisture, harvested at maturity, and generally experienced severe terminal drought stress. Experiments were conducted during the summer at Warwick 2005 (RC, sorghum) and Gatton 2006 and 2007 (RC, LYS, both crops) and during the winter at Brisbane 2006 (LYS, both crops), all in SE Queensland, Australia. In addition, the sorghum hybrids were grown in a field experiment at two densities (5 and 10 plants m^{-2}) at Gatton 2006 under optimum conditions.

Observations and analyses
For all experiments in the shade house, the number of fully expanded main shoot leaves was counted twice a week. The size of each fully expanded leaf on each axis was obtained as length * width * correction factor. Root and shoot dry mass were obtained for each plant. For selected experiments, dry mass of the main shoot was obtained for each individual leaf blade, leaf sheath, and stem node.

For the field experiments, leaves were counted on five plants per plot. Dry matter samples (2 m^2 per plot) were taken at anthesis and maturity. The overlap in observations with the controlled environment data enabled us to verify that genotypic differences in the shade house were representative of field experiments.

Results

Restricting plant size in sorghum
A35 hybrids consistently had a higher leaf appearance rate (LAR) than their RQL39 counterparts, but this was offset by a higher leaf number (Table 1). As a consequence, A35 hybrids reached anthesis only marginally later than AQL39 hybrids (Table 1). The high LAR resulted in a high leaf area for the main shoot early in the season and hence a high biomass at stem elongation (Table 1). This was associated with low tiller formation for A35 hybrids (Table 1). As a consequence, under low plant density in the field, biomass at anthesis for drought tolerant A35 hybrids was low compared to that of drought susceptible RQL39 hybrids (Table 1).

Table 1. Analysis of variance of traits related to leaf area development and pre-anthesis biomass accumulation.

Female parent	A35		AQL39				
Male parent	RQL12	RQL36	RQL12	RQL36	Female	Male	F x M
Leaf appearance rate (leaf ºCd^{-1}) Data of 5 experiments	0.0308	0.0304	0.0283	0.0275	***	*	ns
Total leaf number GAT06-FLD-LD	20.1	21.1	17.6	18.5	***	*	ns
Time to anthesis (ºCd) GAT06-FLD-LD	694	738	677	723	*	***	ns
Dry mass at stem elongation (g pl^{-1}) GAT06-RC	12.53	13.88	9.5	6.67	**	ns	+
Fertile tiller number anthesis (m^{-2}) GAT06-FLD-LD	0.23	0.30	0.87	1.27	***	*	+
Dry mass at anthesis (g m^{-2}) GAT06-FLD-LD	487	533	522	599	**	**	ns
Dry mass at anthesis (g m^{-2}) GAT06-FLD-HD	635	691	636	660	ns	ns	ns

GAT06= Gatton 2006; FLD=field experiment; LD=low density (5 plants m^{-2}); HD=high density (10 plants m^{-2}); RC=root chamber experiment.
***,**,*: significant at P<0.001, P<0.01, and P<0,.05 respectively. ns: not significant at P<0.05.

RQL12 hybrids reached anthesis significantly earlier than their RQL36 counterparts and this earliness was associated with a low leaf number on the main shoot, rather than a high LAR (Table 1). In addition, RQL12 hybrids produced less tillers, although this was not associated with early vigour. The low leaf number and reduced tillering resulted in small plant size at anthesis under low density in the field (Table 1).

The importance of restricted plant size on water use pattern is illustrated in Fig. 1, which shows for two hybrids (A35/RQL12 vs AQL39/RQL12) the ratio in pre-anthesis daily water use. On average, A35/RQL12 produced one less productive tiller per plant than AQL39/RQL12. Until 40 days after emergence, when tillering started, A35/RQL12 consistently used more water than AQL39/RQL12, which was consistent with the better early vigour of the A35 parent (Table 1). Once tillering had started, however, A35/RQL12 consistently used less water, as a consequence of its lower tiller number. As daily water use increased throughout the experiment, A35/RQL12 had used less water (11.4 vs 12.3 liters/plant) when plants were harvested just after anthesis.
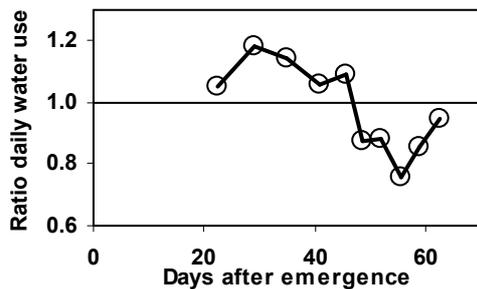

Fig.1 Ratio of daily water use between sorghum hybrids A35/RQL12 and AQL39/RQL12 in lysimeter experiment in Brisbane 2006. Data are means of four plants per hybrids.

Reduced pre-anthesis water use can increase post-anthesis water use under water-limited conditions, and this can increase grain yield (Hammer, 2006). The importance of restricted plant size on yield under water-limited conditions is illustrated in Fig. 2a, which shows for individual plants across two RC experiments a significant negative correlation between the panicle dry mass (including grain) and maximum leaf area of the main shoot. Low grain yield under drought in the RC was associated with a low grain number per unit non-grain mass panicle mass. In Warwick 2005, QL39/RQL36 (susceptible hybrid) had high leaf area and biomass at anthesis (consistent with low density field experiment in Table 1) and this resulted in a low grain number per unit panicle mass (Fig 2b) and hence a low grain yield. The poor grain set indicates a low growth rate around anthesis, due to excessive pre-anthesis water use as a result of the large plant size.

Under high plant density in the field, where tillering was virtually suppressed, differences in plant size due to tillering disappeared (Table 1). The mechanism of adaptation to drought through restricting plant size thus has limited value in situations were genotypic differences in tillering are absent.
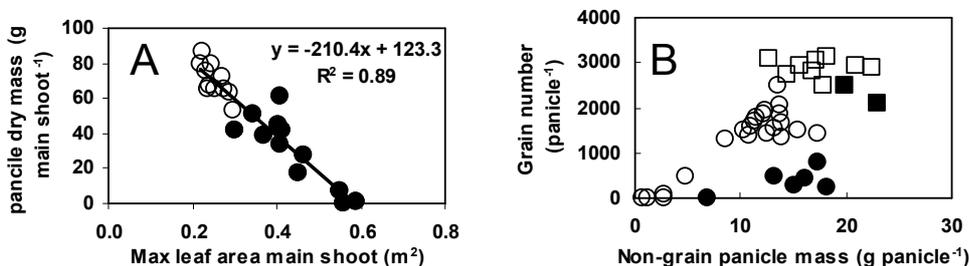

Fig. 2a. Main shoot panicle dry mass (incl. grain) at plant death as a function of main shoot leaf area for individual plants, grown on stored soil water in root chambers at Warwick 2005 (○) and Gatton 2007 (●)
Fig. 2b. Grain number per panicle as a function of non-grain panicle mass for main shoot (□,■) and tiller (○,●) for individual axis of plants of 3 drought tolerant (□,○) and 1 susceptible (■,●) hybrid, grown at Warwick 2005.

Partitioning in maize

In the absence of tillering, maize plants need to employ a different mechanism of adaptation to drought. For the two hybrids we used, total (root+shoot) biomass and phenology across three experiments was not significantly different, even though the tolerant hybrid did produce some kernels in the one experiment that was carried on till maturity, whereas the susceptible hybrid did not. This indicated a difference in biomass partitioning.

Total dry mass (blade+sheath+stem) of individual phytomers was very similar for the two hybrids (Fig. 3a). However the tolerant hybrid had one extra phytomer, but the same number of leaves above the primary ear. Therefore, if the dry mass per phytomer was plotted relative to the ear phytomer, the tolerant hybrid had smaller phytomers above the ear than the susceptible hybrid (Fig. 3). For the LYS experiment at Gatton 2006, this difference in dry mass per phytomer became progressively larger from the leaf blade (0.04 g), to the leaf sheath (0.51 g) to the stem (1.11 g). In the tolerant hybrid, the growing ear thus experienced less competition from the growing stems than in the susceptible hybrid. This could affect grain number, as grain set is highly related to the ear growth rate around silking (Zinselmeier et al., 1999). It should be noted that differences in dry matter partitioning also occurred in sorghum, but the importance seemed to be less than in maize.
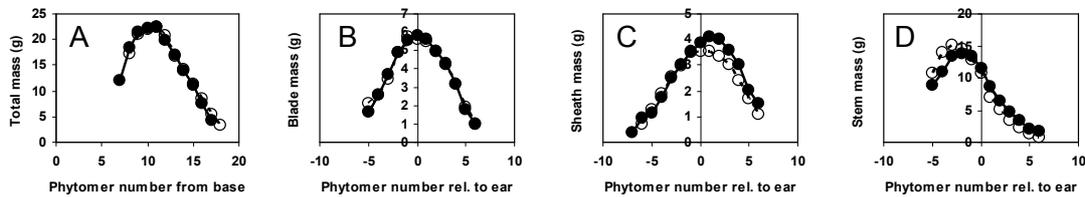

Figure 3. A. Total dry mass per phytomer from base up and dry mass per (B) leaf blade, (C) leaf sheath, and (D) stem for individual phytomers, relative to the phytomer carrying the primary ear for a drought tolerant (○) and susceptible (●) maize hybrid. Data are means of four individual plants, grown in lysimeter pots at Gatton, 2006.

Conclusion

Drought-adapted sorghum restricted pre-anthesis water use by restricting canopy size, whereas drought-adapted maize altered its dry matter partitioning. The contrasting mechanisms, which were a consequence of contrasting tillering behaviour, both had a positive effect on grain number, presumably through an effect on panicle (ear) growth rate around anthesis. Our results support the hypothesis that restriction of plant size is a useful drought adaptation mechanism, but that in genotype * environments combinations with restricted tillering, changes in dry matter partitioning are the preferred adaptation mechanism. We are incorporating these crop physiological determinants into the APSIM-Cereal crop growth model to simulate adaptation for a range of sorghum and maize genotypes, grown across locations and years that encompass a range of drought stress patterns. Such analyses allow breeders to match selection criteria to prevalent drought patterns in their target population of environments and, hence, improve the efficiency of crop improvement.

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