Change in biomass partitioning and transpiration efficiency in Australian wheat varieties over the last decades

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Abstract

Wheat productivity is commonly limited by a lack of water in rain-fed farming systems. Increasing transpiration efficiency, by increasing plant biomass produced per unit of available soil water, can lead to gains in crop yield. Although Australian wheat breeders have historically bred for increased yield, grain quality and disease resistance, other traits are expected to have been indirectly selected for. A set of 15 elite wheat varieties with wide adoption and narrow phenological range was chosen to study breeding progress achieved in Australia between 1973 and 2012. Performed in irrigated pots at normal field density, this study revealed changes in transpiration efficiency, biomass partitioning and senescence rate in varieties released over the last four decades. While plant biomass did not change significantly across cultivars, differences in partitioning were observed, with modern cultivars having greater biomass allocation to the stems and spikes, but reduced allocation to the leaves. Modern cultivars had a greater number of fertile tillers, less infertile tillers and less senesced leaves at flowering. Interestingly, a significant increase in whole-plant transpiration efficiency was observed with the year of cultivar release, giving promising results for future wheat improvement. Further study is needed to unravel the underlying physiological and genetic processes associated with increased transpiration efficiency and generate wheat lines that produce more 'crop per drop'.

Key words

Water-use, tillering, spike, stem, breeding.

Introduction

Bread wheat (*Triticum aestivum* L.) is one of the most significant staple crops. In Australia, wheat is mainly grown under rain-fed conditions and experiences major water stress that limits productivity (e.g. Chenu et al 2013). Although physiological responses to water deficit are complex, it is likely that traits associated with drought tolerance have been indirectly selected through conventional breeding programs in drought-prone areas. In a collection of Australian wheats released between 1958 and 2007, significant increase in yield over the year of release have been related to (i) a decrease in grain protein content and to (ii) an increase in pre-flowering radiation use efficiency, leaf greenness at flowering and nitrogen uptake, while (iii) no change in evapotranspiration, flag leaf stomata density, light-saturated photosynthesis and respiration was observed (Sadras et al., 2012; Sadras and Lawson, 2013). Looking at Australian cultivars released between 1973 and 2012, this project is investigating traits related to biomass partitioning and transpiration efficiency to determine other possible changes that may have resulted from the last few decades of breeding.

Material and methods

Trial description

Fifteen elite Australian wheat varieties with wide adoption and narrow phenological range were chosen to represent breeding progress achieved in Australia between 1973 and 2012 (Fig. 1). Plants were sown in pots at a density of 100 plant m^{-2} (i.e. two plants per pot) in a greenhouse at Gatton (-27.55°, 152.34°), in a row-column design with 5 repetitions (i.e. 10 plants) per variety. Plants were grown in the 'Pot in Bucket' (PIB) system adapted from Hunter et al. (2012), and had a continuous supply of water from independent water jugs, which allowed transpiration to be measured by the amount of water removed from each jug. A layer of white plastic beads was applied to cover the soil in each pot and avoid soil evaporation. A set of five pots with no plant was used to calculate remaining soil evaporation throughout the trial.

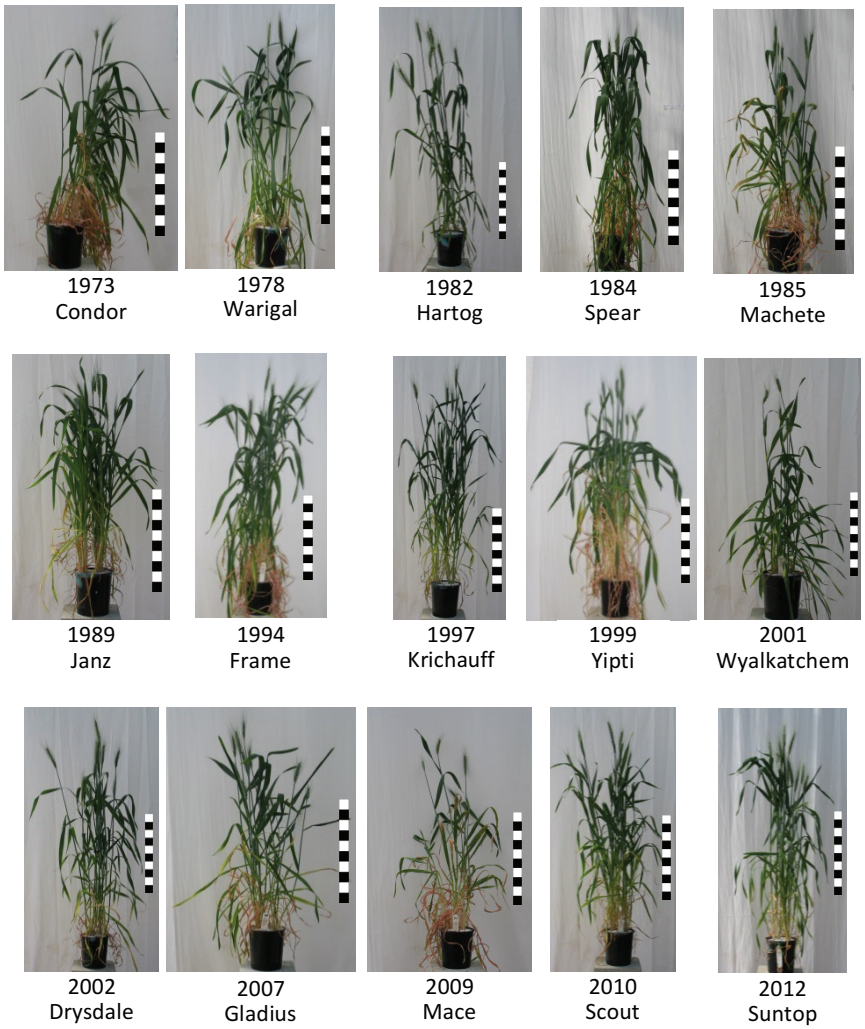

Figure 1 - Studied elite Australian wheat varieties with their year of release. The black and white scale corresponds to 45 cm.

Measurements and analysis

Transpiration was recorded weekly for each pot from 25 days after sowing until flowering. Zadoks scores (Zadoks et al., 1974) were recorded weekly for the main stem of one plant in each pot as a measure of phenological development. Each pot was harvested when at least 50% of the stems had reached flowering, i.e. at a Zadoks score of 65 or higher. Both plants in each pot had their total leaf area, number of fertile and infertile tillers, and dry biomass of roots, stems, dead and green leaves and heads measured at flowering. Transpiration efficiency was calculated as the ratio between either whole-plant dry biomass or shoot dry biomass at flowering over the amount of water transpired from 25 days after sowing till flowering. Cumulated transpiration was defined as the total water use minus the average cumulated soil evaporation measured in five pots with no plant. All data analysis was done using the R statistical language (R Core Team, 2014).

Results and Discussion

No trend in plant biomass, but biomass partitioning changed with the year of variety release

No significant trend in plant biomass was observed for varieties released between 1973 and 2012 (Fig. 2a) but differences were recorded in the partitioning of plant biomass (Fig. 2b-f). Significant differences were only observed in the partitioning among above-ground organs, as neither partitioning to the shoot, nor to root significantly changed with the year of release. Modern varieties had less biomass partitioned to the leaves, to the benefit of the stems and heads. Interestingly, changes observed for leaves arose from a decrease in dead leaves, while green-leaf biomass at flowering did not significantly change over the last decades. Hence, breeders seem to have indirectly selected for lines with reduced pre-flowering senescence, which invest an increasing amount of resources towards reserve and reproductive organs.

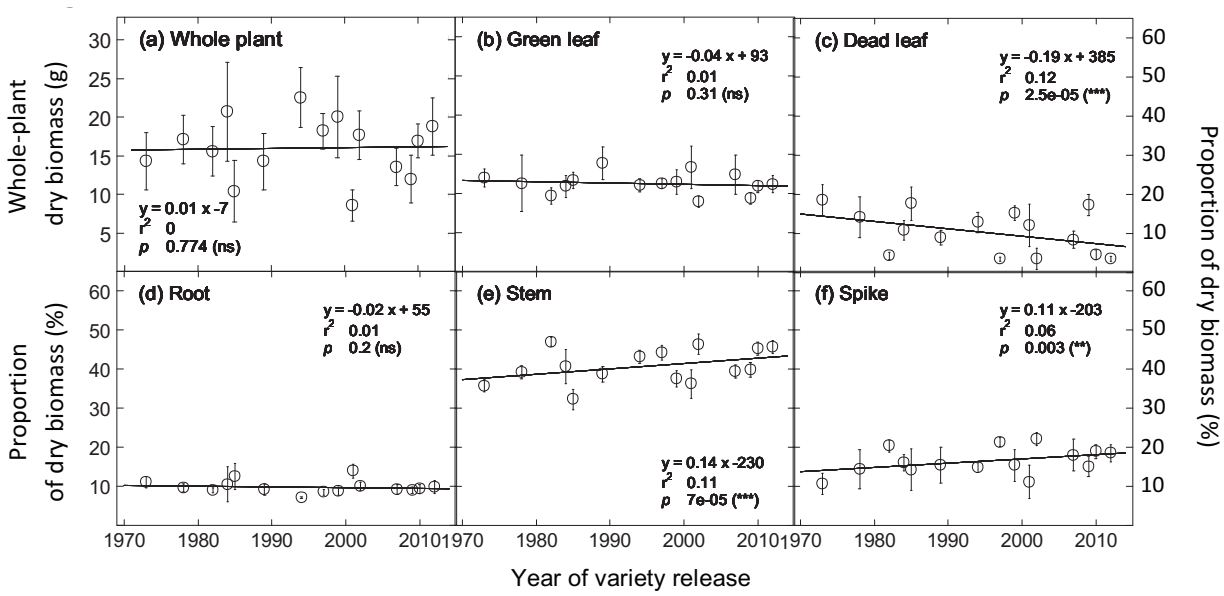

Figure 2 - Change in biomass over year of variety release for (a) whole-plant dry biomass, and the portion of dry biomass allocated to (b) green leaves, (c) dead leaves, (d) roots, (e) stems, and (f) spikes. Error bars correspond to 95% confidence interval (n = 5-10). Linear regressions were calculated on row data (individual pots for root biomass or individual plants for all other traits). Abbreviations: ns, not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Since the 1970's, for the genotypes studied, the proportion of biomass allocated to the stems and the spikes has increased by +0.14% and +0.11% per year, respectively, meaning an average increase of +10% for stems plus spikes in four decades. Interestingly, the most noticeable effect was for the spikes, which increased from 13 to 18% of the plant biomass, over the last four decades (Fig. 2f). For comparison, the stem portion increased from 37% to 42% during the same period (Fig 2e).

Such change in partitioning can be at least partly explained by the change observed in tiller number (Fig. 3a). While the number of total tillers has slightly but significantly decreased since 1970's (from 10.3 to 8.8 between 1970 and 2010), the number of fertile tillers (Fig. 3b) has substantially increased (from 5.5 to 7.0). Accordingly, the number of infertile tillers has drastically decreased, with the most modern varieties having almost no infertile tiller (Fig. 3c).

Overall, the changes observed in tillering, senescence and biomass partitioning reflect that modern varieties (i) invest less resources in plant structure that die relatively early during the crop cycle, (ii) accumulate more biomass in reproductive organs (spike) and in reserve organs (stems), which can benefit yield under late drought conditions (Dreccer et al., 2009) that are frequently occurring in Australia (Chenu et al., 2011 and 2013).

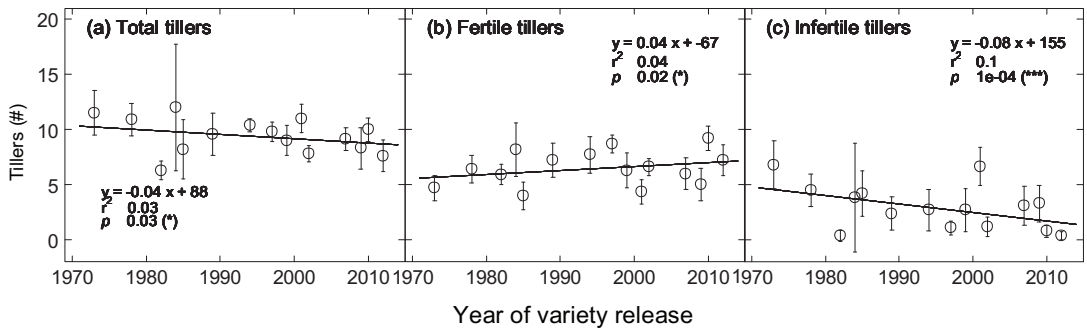

Figure 3 - Change in (a) tiller number, (b) fertile tillers, and (c) infertile tillers over year of release. Error bars correspond to 95% confidence interval (n = 10). Linear regressions were calculated on row data (individual plants). Abbreviations: ns, not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Transpiration efficiency increased over the last decades

While modern cultivars seem more efficient in partitioning their resources towards reproductive organs, they were also found to be more efficient in converting transpired water into biomass (Fig. 4). Plant transpiration

efficiency, whether it was calculated for above-ground biomass (Fig. 4a) or for the whole plant (Fig. 4b), has increased significantly with the year of release. Such increase resulted from a slight increase (not significant) in biomass (Fig. 2a) and a slight decrease (not significant) in cumulated transpiration (data not shown).

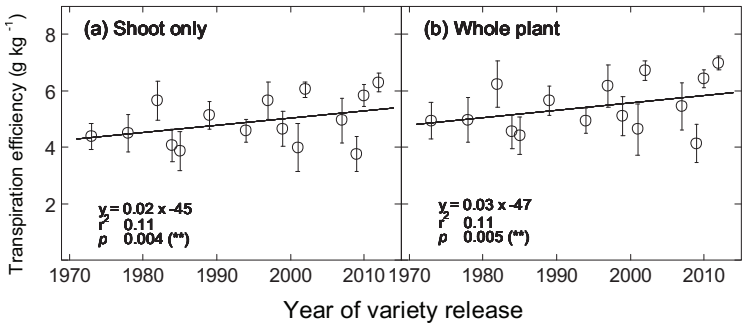

Figure 4 - Change in transpiration efficiency for (a) above-ground dry biomass and (b) whole-plant dry biomass for varieties released between 1973 and 2012. Error bars correspond to 95% confidence interval (n = 10). Linear regressions were calculated on row data (individual plants). Abbreviations: ns, not significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Conclusion

This study focused on Australian wheat lines that breeders have selected under rain-fed conditions. While conducted in well-watered conditions, substantial changes were identified in traits likely to be beneficial under drought. A significant trend in increasing number of fertile tillers was observed with the year of release, while the number of total tillers significantly decreased. Modern cultivars had less infertile tillers, less early senescence, but maintained a similar plant leaf area and green-leaf biomass as old varieties at flowering. In this small-pot experiment, no trend in root biomass or in shoot:root ratio was observed over the year of variety release. Interestingly, a significant increase in transpiration efficiency was observed for modern varieties. Further study is needed to confirm those results, to assess existing variability in promising traits that could further be improved such as transpiration efficiency, and to unravel associated physiological and genetic processes to assist breeding for lines that produce more 'crop per drop'.

Acknowledgments

The authors thank Drs Jack Christopher and Victor Sadras for constructive comments and providing the seeds of the studied genotypes. This study was partly funded by the ARC Centre of Excellence for Translational Photosynthesis.

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Year of variety release