Exploiting the variability and heritability of leaf angle in sorghum to design optimal canopies for different target environments

Barbara George-Jaeggli[1,2*], Alex Wu[3], Greg McLean[3], Xiaoyu Zhi[2], Sean Reynolds Massey-Reed[2], David Jordan[2] and Graeme Hammer[3]

[1] Agri-Science Queensland, Queensland Department of Agriculture and Fisheries, Hermitage Research Facility, Warwick, QLD 4370
[2*] Queensland Alliance for Food and Fibre Innovation, The University of Queensland, Hermitage Research Facility, Warwick, QLD 4370 b.georgejaeggli@uq.edu.au
[3] Queensland Alliance for Food and Fibre Innovation, The University of Queensland, St Lucia, QLD 4072

Abstract
In cereal crops, average leaf angle of the canopy affects the total amount of radiation that is intercepted and how effectively light is distributed through the canopy. Selecting for more erect leaves in maize and rice has allowed higher density plantings and has been associated with significant productivity gains in those crops. The effects of leaf angle on crop productivity depend on how it influences within-canopy light distribution and the plants' efficiency in using that light to produce biomass. Canopy light distribution is influenced by agronomic interventions such as growing at different locations, sowing on different dates, using different plant densities (leaf area index). For sorghum, which may be grown across a large range of latitudes and plant population densities, the effects of leaf angle manipulations have not previously been studied. We used the APSIM-DCaPST sorghum model to simulate the effects of more erectophile canopies on yield for two locations with different latitudes and planting dates, assuming low-and high- intensity agronomies. The simulations showed that more erect leaves would result in yield benefits in most years at both of those locations. Contrary to the situation in maize, the simulated yield gains were greatest in the low-yielding rather than the high-yielding years. Interestingly also, the simulated productivity gains in erectophile sorghum canopies were not due to enhanced light penetration as suggested in maize, but rather through effects on extent of radiation interception and its implications for early crop growth and crop water balance through the crop life cycle.

Keywords
Population density, light interception, productivity, crop simulation modelling, cereal breeding.

Introduction
In dense cereal crops, the angle of leaves affects light distribution through the canopy. It is thought that more erect leaves have significantly contributed to yield gains in crops such as maize and rice (Sinclair and Sheehy 1999; Sakamoto et al. 2006; Hammer et al. 2009). However, the effects of leaf angle on daily light capture and distribution of light through the canopy is affected by plant population densities, as well as sun angle and therefore depends on latitude and time of year (Duncan et al. 1967; Duncan 1971). A simulation study for maize grown across the US Corn Belt showed that yield gains from more erect upper leaves were likely limited to the highest yielding environments, where they enabled better distribution of light through the canopy resulting in improved light use efficiency and increased productivity of crops grown at high planting densities (Hammer et al. 2009). Leaf angle in sorghum has not previously received much attention and to our knowledge has not been a direct selection target in breeding programs nor has it been considered in relation to agronomic interventions.

In a recent detailed Genome-Wide Association Mapping study (Zhi et al. 2021) into the genetics of leaf angle in sorghum, we found that the relatively small, but additive effects of a number of QTL distributed throughout the genome, contributed to large variation in leaf angle. Leaf angle showed little genotype x environment interaction across multi-environmental trials and the trait had moderate heritability. Also, we found consistent differences in leaf angle among the five sorghum races indicating environmental adaptation. Sorghum in Australia is grown across a range of latitudes and edaphic environments and as a dry-land summer crop its yield is affected by large inter-year climate variability (Muchow et al. 1994), so that the effects of leaf angle cannot be readily evaluated in single experiments.

To examine the potential effects of leaf angle on sorghum productivity, we used the APSIM sorghum crop growth model with a diurnal canopy photosynthesis-transpiration module to simulate 50 seasons of yields of both planophile and erectophile sorghum canopies grown at a low- and a high-latitude location within the Australian sorghum growing area with either high or low intensity agronomy.

Methods

We used the APSIM sorghum crop model (version 7.10, revision 4210) (Hammer et al. 2010) with the DCaPST module (Wu et al. 2019; Holzworth et al. 2014) parameterised for commonly used genotypes in Australia to simulate the effects of different leaf angles. Planophile (35° measured from the horizontal) and erectophile (70° measured from the horizontal) average canopy leaf angles were applied in the simulations. Simulations were conducted for the genotype Buster at Emerald (QLD; 23°31'S, 148° 9' E) and Gunnedah (NSW; 30° 58' S, 150° 15' E). Standard (1-m rows at 50,000 plants per ha; 90 mm plant available SW at sowing) and high intensity (0.5-m rows at 100,000 plants per ha; 150 mm plant available SW at sowing) agronomy were assumed. Typical planting dates for the locations were chosen, i.e., mid-December for Emerald (which also results in high sun angle (around solstice on Tropic of Capricorn)) and mid-October for Gunnedah (which results in lower sun angle higher latitude, spring). Deep soils (120 cm with 150 mm PAWC at Emerald and 150 cm with 260 mm PAWC at Gunnedah) and unlimited nitrogen supply were used for both locations. The simulations were run using 50 years of historical climate data to sample seasonal variabilities

Results

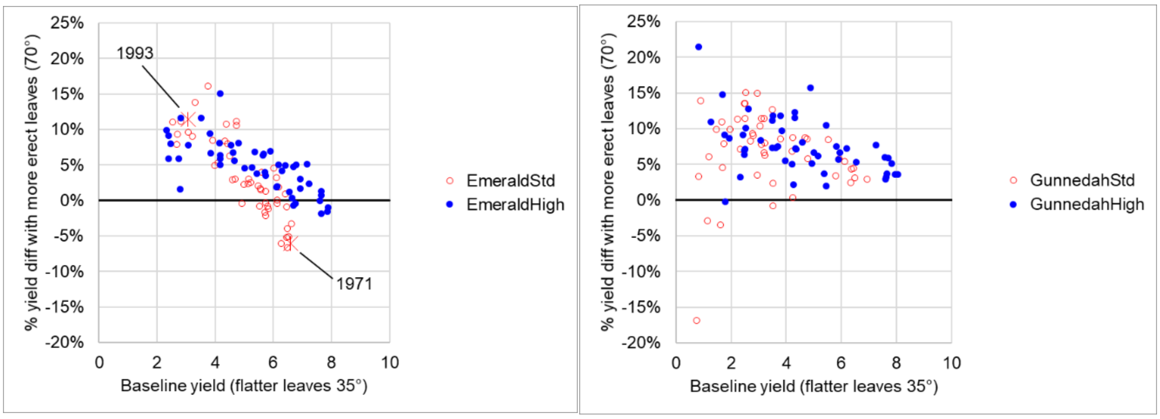

Figure 1. Simulated yield gains (or penalties) conferred by more erectophile canopies at Emerald and Gunnedah with standard (Std) or high (High) intensity agronomy for 50 years of historical climate data. A low- (1993) and high- (1971) yielding year with standard agronomy at Emerald were selected to explain the yield response in more detail (see text).

Leaf angle manipulation generated the largest yield percentage change of ca. 5-15% increase in the low-yielding seasons and this effect generally reduced to <5% for the high-yielding seasons at both sites (Fig. 1). The overall response to seasonal conditions was affected by the site and agronomic practice. Manipulating leaf angle can lead to yield gains under most conditions, but it can have trade-offs in others. At Emerald, yield decline with erect leaves was predicted for the high-yielding seasons when using the standard agronomy. At Gunnedah, yield gain was predicted with a more erectophile canopy except for a small number of the lowest-yielding seasons with standard agronomy.

A detailed analysis comparing a high- and low-yielding season with the standard agronomy at Emerald was conducted to help explain the yield response to leaf angle manipulation (data not shown). It is generally thought increasing leaf angle favours high-yielding conditions as erect canopies can allow more light penetration thus enhancing radiation use efficiency (RUE) in canopies with a high leaf area index. A low- (1993) and a high-yielding season (1971) were examined. In the low-yielding season, increased canopy erectness reduced the amount of radiation interception across the crop cycle, because at low plant populations, erect leaves are less efficient at intercepting radiation compared to more horizontal leaves. Reduced radiation interception in turn reduced early season biomass and leaf area growth which also generated a reduction in crop water demand. This led to a 'water-saving' situation with increased preservation of water content in the subsoil which sustained crop growth rate later in the season during grain-filling, giving improved grain yield via larger grain size. The interaction with water supply and demand was mostly absent in the high-yielding season as soil water was replenished by rain events. Hence, with more erect canopies, crop biomass growth with standard agronomy was reduced due to less light interception and reduction on biomass growth. This resulted in a decline in grain number and yield. The yield penalty with having a more erect canopy did not occur when using the high-intensity agronomy at Emerald as the higher leaf area index would increase canopy light interception. In fact, the small advantage from erect leaves in this situation related to the anticipated effect on enhanced light penetration and higher RUE.

For the Gunnedah site, there was generally no yield penalty with having a more erect canopy for high-yielding seasons for either standard or high-intensity agronomy scenarios. A likely explanation is the angle of incoming radiation. Being at the southern part of the sorghum belt, the site would have lower sun angles such that a greater amount of incoming radiation would be intercepted by crop canopies than at Emerald. In general, the greater yield advantage associated with more erect leaves was evident under lower-yielding conditions due to the same 'water-saving' mechanism noted above. The instances of yield penalties occurring in very low-yielding seasons with standard agronomy likely relate to changes in timing of critical stress events. Unravelling this would require further detailed analysis.

Conclusion

The yield gains due to more erectophile plant canopies seen in other cereals, particularly maize, are limited to high-yielding environments where they confer better light use in high-density plantings. Our study showed that in sorghum, which is typically grown across a large range of dry-land environments at low population densities, more erect leaves are predicted to result in yield gains in most cropping situations, with the largest yield gains expected in low-yielding years. The simulations suggest that this is likely due to interactions between water use and radiation use efficiency. Steeper leaf angles reduce intercepted radiation early in crop growth which has a depressing effect on crop water use. In low-rainfall years, preserved subsoil moisture has a beneficial effect on water supply during the critical grain fill phase resulting in yield benefits via larger grains in the more erectophile crops.

On the other hand, if water is not limited, reduced early growth via steeper leaf angles may in fact reduce yield potential. This may occur in situations with predominantly high sun angles (such as the near-solstice planting time and low latitude at Emerald) and may be compensated by increased plant population densities.

There is ample natural variation for leaf angle in sorghum and the genetic architecture of the trait make it amenable to manipulation through breeding to design optimal canopies. This preliminary study using the modelling tool highlights the potential to better integrate genetics with agronomic management for different target environments.

References

Duncan WG (1971). Leaf Angles, Leaf Area, and Canopy Photosynthesis. Crop Science 11 (4):cropsci1971.0011183X001100040006x. doi:10.2135/cropsci1971.0011183X001100040006x

Duncan WG, Loomis RS, WillIams WA, Hanau R (1967). A model for simulating photosynthesis in plant comunities. Hilgardia 38:181-205

Hammer GL, Dong Z, McLean G, Doherty A, Messina C, Schussler J, Zinselmeier C, Paszkiewicz S, Cooper M (2009). Can changes in canopy and/or root system architecture explain historical maize yield trends in the U.S. corn belt? Crop Science 49 (January-February 2009):299-312

Hammer GL, van Oosterom E, McLean G, Chapman SC, Broad I, Harland P, Muchow RC (2010). Adapting APSIM to model the physiology and genetics of complex adaptive traits in field crops. Journal of Experimental Botany 61 (8):2185-2202. doi:10.1093/jxb/erq095

Holzworth DP, Huth NI, deVoil PG, Zurcher EJ, Herrmann NI, McLean G, Chenu K, van Oosterom EJ, Snow V, Murphy C, Moore AD, Brown H, Whish JPM, Verrall S, Fainges J, Bell LW, Peake AS, Poulton PL, Hochman Z, Thorburn PJ, Gaydon DS, Dalgliesh NP, Rodriguez D, Cox H, Chapman S, Doherty A, Teixeira E, Sharp J, Cichota R, Vogeler I, Li FY, Wang E, Hammer GL, Robertson MJ, Dimes JP, Whitbread AM, Hunt J, van Rees H, McClelland T, Carberry PS, Hargreaves JNG, MacLeod N, McDonald C, Harsdorf J, Wedgwood S, Keating BA (2014). APSIM – Evolution towards a new generation of agricultural systems simulation. Environmental Modelling & Software 62 (0):327-350. doi:http://dx.doi.org/10.1016/j.envsoft.2014.07.009

Muchow RC, Hammer GL, Vanderlip RL (1994). Assessing climatic risk to sorghum production in water-limited subtropical environments II. Effects of planting date, soil water at planting, and cultivar phenology. Field Crops Research 36 (3):235-246. doi:http://dx.doi.org/10.1016/0378-4290(94)90115-5

Sakamoto T, Morinaka Y, Ohnishi T, Sunohara H, Fujioka S, Ueguchi-Tanaka M, Mizutani M, Sakata K, Takatsuto S, Yoshida S, Tanaka H, Kitano H, Matsuoka M (2006). Erect leaves caused by brassinosteroid deficiency increase biomass production and grain yield in rice. Nature Biotechnology 24 (1):105-109. doi:10.1038/nbt1173

Sinclair T, Sheehy J (1999). Erect leaves and photosynthesis in rice. Science 283 (5407):1456

Wu A, Hammer GL, Doherty A, von Caemmerer S, Farquhar GD (2019) Quantifying impacts of enhancing photosynthesis on crop yield. Nature Plants 5 (4):380-388. doi:10.1038/s41477-019-0398-8

Zhi X, Tao Y, Jordan DR, Borrell A, Hunt C, Cruickshank A, Potgieter AB, Wu A, Hammer GL, George-Jaeggli B, Mace E (2021). Genetic control of leaf angle in sorghum and its effect on light interception. Journal of Experimental Botany, in press.