

Evidence for excess photosynthetic capacity and sink-limitation to yield and biomass in elite spring wheat

Matthew Reynolds¹, Anthony G. Condon², Gregory J. Rebetzke² and Richard A. Richards²

¹CIMMYT, Int. AP 6-641, 06600 Mexico, DF, Mexico www.cimmyt.cgiar.org Email m.reynolds@cgiar.org

²CSIRO, Plant Industry, Canberra, Australia www.csiro.au Email tony.condon@pi.csiro.au; greg.rebetzke@csiro.au; r.richards@pi.csiro.au

Abstract

Yield improvement in spring wheat has largely resulted from increased harvest index (HI), and since HI has remained static since the mid 1980s, increasing radiation use efficiency (RUE) is likely the most viable route to increasing yield. As RUE is influenced indirectly by sink strength, it follows that biomass may be increased by increasing grain number. Experiments with high yielding spring wheat lines containing the 7DL.7Ag translocation showed increased grains m⁻² (15%), yield (12%), and biomass (10%) compared with checks. The translocation was also associated with a larger investment in spike mass at anthesis (15%), more grains/spike (11%), and increased photosynthetic rate especially during grain-filling (10%). No effect of the translocation were detected on light interception or canopy architecture, suggesting that increased biomass in 7DL.7Ag lines was largely due to the positive feedback on photosynthesis associated with a larger kernel number. The hypothesis that photosynthesis may respond directly to increased sink was tested experimentally by imposing a light treatment during boot stage. The treatment was associated with a small increase (5%) in the proportion of biomass invested in spike mass at anthesis and 3 extra grains/spike at maturity. Yield and biomass were increased by 20% and 18% respectively compared with checks, while flag-leaf photosynthetic rate during grain-filling was increased by 10%. Results suggest that RUE can be increased indirectly by increasing sink strength and that determination of kernel number is currently a yield limiting process in spring wheat warranting investigation into its physiological and genetic basis.

Introduction

Yield potential (YP) can be expressed in its simplest form as a function of light intercepted (LI), radiation use efficiency (RUE), and the partitioning of biomass to yield, or harvest index (HI):

Equation 1

$$YP = LI \times RUE \times HI$$

Genetic gains in yield over the last 30 years are mainly associated with improved harvest index (HI), while little progress has been made in improving radiation use efficiency (RUE), or light interception (Calderini et al., 1999). Since HI has not increased in approximately 20 years and is approaching its theoretical limit of 60%, there is a clear need to genetically increase biomass if yield gains are to be maintained in the future. Biomass can be increased by increasing light interception or RUE. While there is genetic variation for traits associated with light interception (Richards, 1996), neither genetic nor agronomic treatments that increase light interception have been reported to increase yield in temperate high yield environments. Theoretically, RUE can be increased through modifications to metabolism (Loomis & Amthor, 1999), canopy architecture (Duncan, 1971), or achieving a more optimal source:sink balance (Richards, 1996). Evidence for increasing the metabolic efficiency of photosynthesis is so far theoretical while genetic manipulation of leaf angle has been shown to be associated with modest increases in yield in some backgrounds and has already been adopted quite widely in spring bread and durum wheat (Reynolds et al., 2000). There is strong evidence for sink-limitation in modern wheat lines (Fischer, 1985; Slafer & Savin 1994). Since RUE can respond positively to sink- strength (Fischer, 1985), increased spike-fertility (e.g. a reduction in floret abortion during the booting/heading stage) may provide a mechanism to increase RUE, biomass and thus yield potential. The hypothesis was tested using both genetic (7Ag.7DL near isolines) and physiological (source-sink manipulation) models.

Evidence for sink limitation to RUE from experiments with 7Ag.7DL near-isolines

The 7Ag.7DL translocation from *Agropyron elongatum* was originally introgressed into wheat to introduce Lr19 for leaf rust resistance where it had negligible influence on agronomic type and was found to be associated with increased yield and biomass in one background (Singh et al., 1998). In experiments with six spring wheat backgrounds carrying the 7DL.7Ag translocation yield was increased by on average 13% while biomass was improved in five of the six backgrounds by 10% (Reynolds et al., 2001). To explain the increased biomass, parameters relating to light interception, leaf and canopy photosynthesis, and source-sink balance were measured. There was no evidence for differences in light interception associated with the translocation (Reynolds et al., 2001). However, total biomass measured shortly after flowering was 5% greater than controls, while final biomass was 9% greater (Table 1). In addition, both grain number per spike as well as spike biomass at anthesis were increased by 11% and 15% respectively. This suggested that while RUE may have been increased slightly prior to anthesis at the leaf or canopy level, there was a larger effect associated with a strong post-anthesis sink. This was supported by measurements of leaf photosynthetic rate that were 9% higher during booting, and 21% during grain-filling (Table 1).

Table 1. Main effect of 7DL.7Ag translocation on the wheat cultivars Angostura, Star and Yecora, spring wheat season, NW Mexico, 2000 (adapted from Reynolds et al., 2001 & 2004).

	Yield	Biomass	Harvest index	Grains/spike	Kernel weight	Biomass Zadok-35	Biomass at anthesis	Spike biomass at anthesis	Photosynthesis booting	Photosynthesis Grainfill
	(g m ⁻²)	(g m ⁻²)	(%)		(mg)	(g m ⁻²)	(g m ⁻²)	(g m ⁻²)	(μmol m ⁻² s ⁻¹)	(μmol m ⁻² s ⁻¹)
Control	680	1,700	40.0	32.5	40.3	400	930	275	21.5	16.5
+ 7DL.7Ag	760	1,850	41.1	36.0	39.0	370	980	315	23.5	20.0
% effect	12%	9%	3%	11%	-3.5%	7%	5%	15%	9%	21%
LSD	68	138	2.1	3.3	2.1	85	79	35	3.2	2.9
P value	0.01	0.05	0.10	0.05	0.10	0.25	0.05	0.05	0.10	0.05

It appears that the 7Ag.7DL translocation is associated with increased spike fertility manifested as larger investment in spike mass at anthesis and a larger number of competent grains/spike, generating an increased demand for assimilates throughout grain-filling associated with increased leaf photosynthetic

rate and a greater final biomass. The results presented here are consistent with a large body of literature indicating that yield is sink limited in wheat (Fischer, 1985; Slafer & Savin, 1994; Calderini et al., 1999), although in previous studies no effect of sink on final biomass was observed. The data suggest that photosynthetic rate per unit leaf area is apparently underutilized in modern cultivars (under the relatively optimal conditions in which these experiments were conducted) and that if grain number can be improved, RUE during grain-filling can be increased in response to the need for more assimilates, permitting simultaneous increases in final biomass and yield. These hypotheses were tested in high yield wheat cultivars using a treatment that increased sink strength.

Evidence for excess photosynthetic capacity from manipulation of grain number per spike

High yield wheat cultivars were grown in 4-row plots, and during booting stage a sink treatment was applied to increase grain number whereby light penetration to the inner rows was increased by bending outer rows away from inner ones during the day. At the end of the treatment rows naturally assumed a vertical position for the duration of grain-filling. The effect of the pre-anthesis sink treatment was to increase biomass at anthesis by 150 g m^{-2} and the proportion of assimilates invested in spikes of primary tillers by 5%. At maturity the sink treatment was associated with an extra 365 g m^{-2} of biomass and approximately 3 extra grains/spike, while average kernel weight and harvest index were not affected (Table 2). Leaf photosynthetic rate measured at different times during grain-filling were on average 10% higher in plots that had experienced the pre-anthesis sink treatment (Table 2). The data confirmed the hypothesis that photosynthetic rate is apparently underutilized in modern cultivars and that RUE during grain-filling can be increased through increasing number of grains per spike. The evolutionary basis of this is not clear, however, under in the wild there would be a clear advantage in having an excess photosynthetic capacity at flowering to increase the chances of seed filling and maturation in an unpredictable environment.

Table 2. Main effect of increasing light penetration into a wheat canopy for 15 days during booting stage on growth traits averaged for three bread wheat cultivars (Siete Cerros, Baviacora, Baviacora+Lr42) and the durum cultivar, Atill, Obregon, NW Mexico, 2001 & 2002.

Treatment	Grain number	Biomass at maturity	Harvest index	Kernel weight	Grain /spike	Spike number	Biomass at anthesis	Tiller number at anthesis	Spike:cul biomass at anthesis	Photosynthesis Grainfill
	(g m^{-2})	(g m^{-2})	(%)	(mg)		(m^{-2})	(g m^{-2})	(m^{-2})	(%)	$(\mu\text{mol m}^{-2} \text{s}^{-1})$
?									?	
Check	791	1790	44.0	42.8	40.3	469	1020	540	27.7	25.9.
Sink-Tmt	949	2155	44.8	42.5	43.3	524	1170	640	29.1	28.6
?% effect	20%	18%	2.0%	-1%	7%	12%	15%	18%	5%	10%

?LSD	75	183	2.8	3.1	4.0	53	149	113	0.24	2.0
P value	0.01	0.01	ns	ns	0.03	0.01	0.01	0.01	0.01	0.01

Traits for increasing spike-fertility

The evidence outlined in the previous sections clearly indicates a need to improve understanding of the genetic basis of spike fertility so that these genes can be targeted in both conventional and molecular approaches to breed for increased grain number. In the meantime improvement of spike-fertility related traits can be incorporated as objectives in empirical breeding approaches using available genetic variation in traits that may influence spike fertility. One example is the multi-ovary (MO) trait shown to increase grain number when introgressed into improved spring wheat backgrounds (Figure 1). Other traits associated with spike fertility have been tested in spring backgrounds by comparing trait expression with yield in unselected progeny of three crosses whose parents contrasted in (i) growth rate during spike-growth stage, (ii) partitioning of biomass to spike at anthesis, (iii) relative duration of spike-growth stage (iv) relative duration of pre-anthesis period. Preliminary data indicate that partitioning of biomass to the spike and a relatively longer pre-anthesis period were best associated with yield (Reynolds et al., 2004).

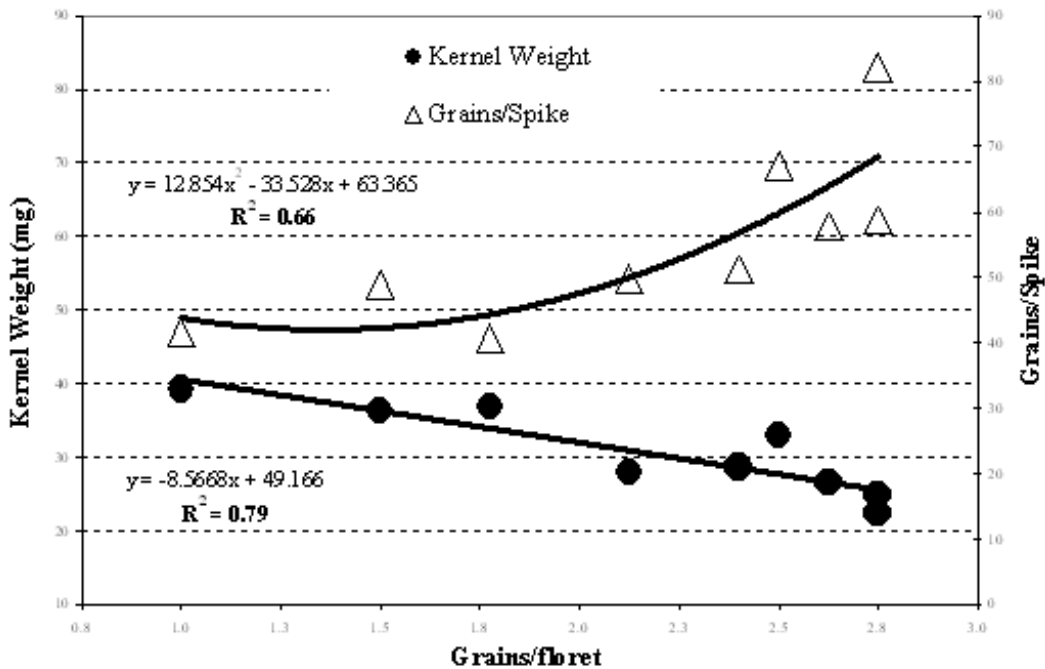


Fig. 1. The relationship between the number of grains/floret and (i) kernel weight (● closed circle) and (ii) grains/spike (Δ open triangle), in eight genotypes expressing the multi-ovary (MO) trait, and the average value of eight lines not expressing the MO trait, for progeny of crosses between an MO source and five elite spring bread wheat cultivars, NW Mexico, 2001. (from Reynolds et al., 2004)

Conclusions

Physiological data collected in well managed high yield environments indicate that grain number m^{-2} (sink) is the current primary rate limiting step for yield potential in spring wheat, and that excess photosynthetic capacity (source) exists during grain-filling even in the highest yielding cultivars. Improvement of RUE at the crop level should, therefore, be tackled both indirectly through increasing our

understanding of the genetic and physiological basis of spike fertility, as well as directly at the level of canopy photosynthesis and photosynthetic metabolism. To reflect its complexity, a model for describing yield potential needs to incorporate the fact that RUE varies over the crop cycle in response to both environment and source: sink balance. The following modification to equation 1 is suggested:

$$YP = HI \times \int_e^m (RUE \times LI) \quad (\text{Equation 2})$$

where e and m represent emergence and maturity respectively. The equation derives from an analysis of dry matter accumulation presented by Monteith (1977) but in Equation 2 dry matter is expressed as the product of LI and RUE integrated over the crop cycle to recognize the fact that both RUE and LI have developmental components. The idea that the RUE of a genotype can be differentiated according to crop stage is extremely relevant to its genetic dissection. Physiological models tend to consider average effects of RUE (S. Chapman, personal communication) overlooking evidence that genetic expression of yield and biomass are determined by interactions between phenological stage and environment (Fischer, 1985; Abbate et al., 1995; Reynolds et al., 2002). The theoretical upper limit to crop yield and biomass (Loomis & Amthor, 1999) implies a constant upper value for RUE which, though difficult to imagine being achieved, nonetheless defines the ultimate goal of manipulation of the crop genome.

References

- Abbate PE, Andrade FH and Culot JP (1995). The effects of radiation and nitrogen on number of grains in wheat. *Journal of Agricultural Science*. (Cambridge) 14, 351-360.
- Calderini DF, Reynolds MP and Slafer GA (1999). Genetic gains in wheat yield and main physiological changes associated with them during the 20th century. In 'Wheat: ecology and physiology of yield determination'. (Ed. EH Satorre and GA Slafer) (New York: Food Products Press).
- Duncan WG (1971). Leaf angles, leaf area, and canopy photosynthesis. *Crop Science* 11, 482-485.
- Fischer RA (1985). Number of kernels in wheat crops and the influence of solar radiation and temperature. *Journal of Agricultural Science* 108, 447-461.
- Loomis RS and Amthor JS (1999). Yield potential, plant assimilatory capacity, and metabolic efficiencies. *Crop Science* 39, 1584-1596.
- Monteith JL (1977). Climate and the efficiency of crop production in Britain. *Phil Trans Royal Soc. London*. 281, 277-294.
- Reynolds MP, van Ginkel M and Ribaut JM (2000). Avenues for genetic modification of radiation use efficiency in wheat. *Journal of Experimental Botany* 51, 459-473.
- Reynolds MP, Calderini DF, Condon AG and Rajaram S (2001). Physiological basis of yield gains in wheat associated with the *LR19* translocation from *Agropyron elongatum*. *Euphytica* 119, 137-141.
- Reynolds MP, Trethowan R, Sayre KD and Crossa J. 2002. Physiological factors influencing genotype by environment interactions in wheat. *Field Crops Research* 75, 139-160.
- Reynolds MP, Pellegrineschi A and Skovmand B (2004). Sink-limitation to yield and biomass: a summary of some investigations in spring wheat. *Annals of Applied Biology* (in press).
- Richards RA (1996). Increasing the yield potential of wheat: manipulating sources and sinks. In 'Increasing Yield potential in wheat: Breaking the barriers'. (Ed. MP Reynolds, S Rajaram, A. McNab) (Mexico: CIMMYT).

Singh RP, Huerta-Espino J, Rajaram S and Crossa J (1998). Agronomic effects from chromosome translocations 7DL.7Ag and 1BL.1RS in spring wheat. *Crop Science* 38, 27-33.

Slafer GA and Savin R. 1994. Sink-source relationships and grain mass at different positions within the spike in wheat. *Field Crops Research* 37, 39-49.