

# The puzzling role of water-soluble carbohydrates in the algorithm of wheat yield

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## Abstract

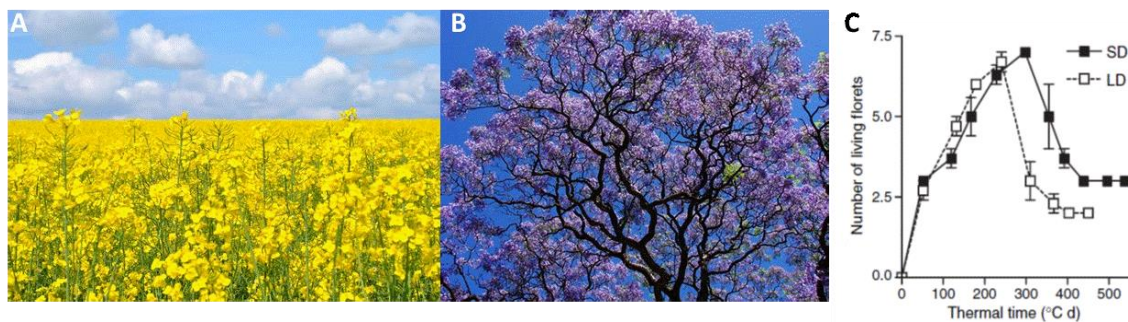
Annual plants accommodate environmental variation through grain number. Correlations between yield and grain number in the range from crop failure to yield potential have typical  $r^2 \sim 0.8$ . This correlation was interpreted as cause-and-effect until Tom Sinclair and Pete Jameson stirred the pot with their yield-beer metaphor in 2006. At the 13<sup>th</sup> Australian Agronomy Conference in Perth, we outlined an evolutionary perspective of Charles Edwards algorithm relating resources, grain number and grain size. Since then, our conceptual model has evolved to account for hierarchies in plasticity of yield components and genomic conflict. Water-soluble carbohydrates (WSC) remain a gap in our model because WSC may buffer grain size but are largely unrelated to yield and involve trade-offs with grain number and root growth. We then asked if labile carbohydrates might have a hidden role beyond the trophic. At the 20<sup>th</sup> Australian Agronomy Conference in Toowoomba, we speculate that high concentration of labile carbohydrates in plant may challenge the osmotic homeostasis of aphids thus providing a working hypothesis that connects WSC with aphid resistance in cereals. It is suggested that the amount and concentration of labile carbohydrates should be regarded as functionally different traits, with amount relevant to the carbon economy of the crop, and concentration playing a substantial osmotic role in plant defence against aphids and viruses.

## Keywords

aphids, osmotic potential, sugars, trade-off, allocation

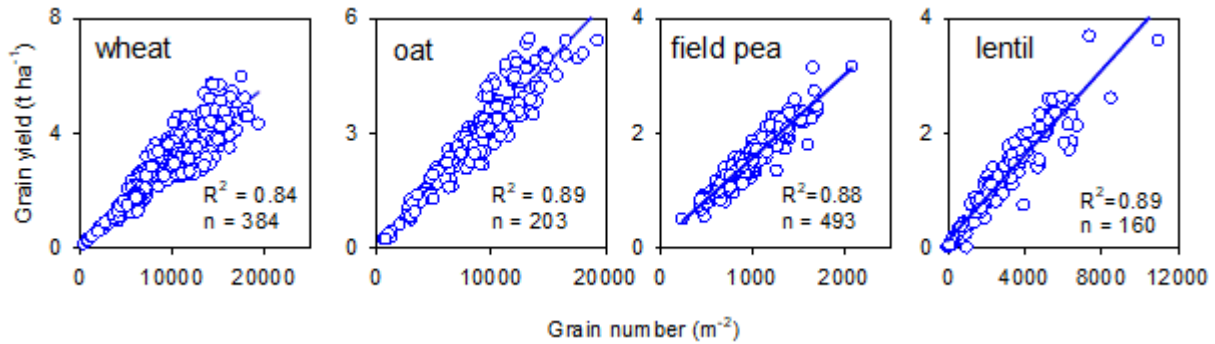
## Crops overproduce flowers and accommodate environmental variation through grain number

Angiosperms overproduce flowers (Figure 1); this is universal. There is a handful of hypotheses to explain why a plant would produce 100 flowers to set 40 fruit. Next, we observe annual crops accommodate environmental variation through grain number (Figure 2); exceptions are rare.



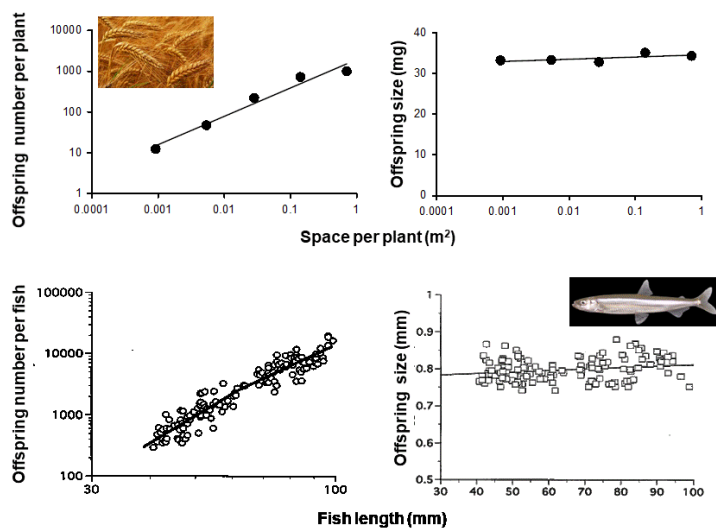
**Figure 1. (A-B) Angiosperms overproduce flowers; fruit-to-flower ratio is low. (C) Dynamics of floret survival in wheat illustrate overproduction and mortality. SD is short day and LD is long day, suggesting the plant might be using photoperiod to anticipate grain fill conditions. Source: Ghiglione et al. (2008).**

The correlation between yield and grain number has been misinterpreted as cause-and-effect until Sinclair and Peterson (2006) challenged this view. Their proposition had gaps and triggered controversy (Fischer 2008), but had the merit to motivate further interpretations of the yield-number correlation. Why would a plant adjust number and keep seed size stable, and not the other way around?



**Figure 2. Annual crops accommodate environmental variation through grain number.**

An excursion into ecological and evolutionary territory showed a striking similarity between crop and fish (Fig. 3). The question changed fundamentally – we were now asking, what do wheat and salmon have in common (Sadras 2006). Answers to this question progressed in a series of theoretical studies of grain yield in annuals (Sadras 2007; Sadras and Denison 2009; Sadras and Slafer 2012; Slafer *et al.* 2014).



**Figure 3. Wheat (top) and pond smelt (bottom) conserve offspring size and adjust offspring number in response to availability of resources. Wheat and pond smelt are both semelparous. Note the log scale necessary to capture the variation in number. Source: Puckridge and Donald (1967) for wheat, and Katayama (2001) for pond smelt (*Hypomesus nipponensis*).**

### Water-soluble carbohydrates in the algorithm of crop yield

The simplest model accounting for the simultaneous determination of grain number (GN) and potential grain size (GS) is

$$\frac{R}{GS} \approx GN \quad \text{eq. 1}$$

where R is crop resources. The rationale of this model involves three elements outlined before (Sadras 2007; Sadras and Slafer 2012). Briefly, the first assumption is that plants are able to account for past, current and future environmental conditions by combining memory mechanisms including epigenetics, proximate environmental cues such as direct sensing of water and nutrient availability in

soils, and cues such as photoperiod that allow for future conditions (see for example Figure 1C). Second, conserved offspring size GS is adaptive; it is under strong genetic control, with heritability typically above 0.7. Third, the plant accommodates environmental variation by allowing for the allocation of a variable amount of resources R to GN grains of target size GS; resources are difficult to estimate but crop growth rate in the critical period of grain set is a sound approximation (Andrade *et al.* 2005).

This model overlooks allocation to roots and storage of labile carbohydrates in shoot, which is concurrent with the determination of grain number and potential grain size (Dreccer *et al.* 2009). Hence, using crop growth rate between stem elongation and anthesis (CGR,  $\text{g m}^{-2} \text{d}^{-1}$ ) to estimate resource availability, we can rewrite eq. 1:

$$\frac{\text{CGR}}{\text{GS}} \cdot E_{\text{GR-GN}} \approx \text{GN} \quad \text{eq. 2}$$

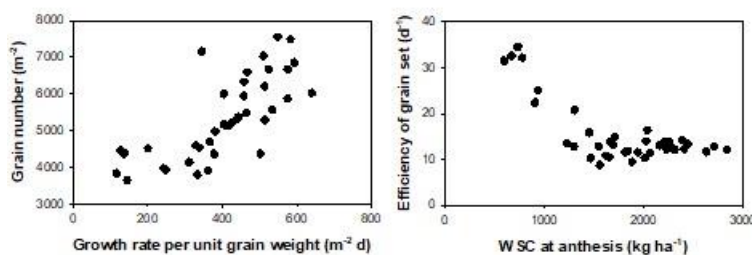
where  $E_{\text{GR-GN}}$  is the efficiency of conversion of growth rate per unit grain size into grain number ( $\text{d}^{-1}$ ). Crops with more resources allocated to carbohydrate reserves will have lower efficiency to produce grain, hence the expected inverse function

$$E_{\text{GR-GN}} \approx f(\text{WSC})^{-1} \quad \text{eq. 3}$$

where WSC is the amount of water-soluble carbohydrates stored in shoots at anthesis ( $\text{g m}^{-2}$ ). Likewise,  $E_{\text{GR-GN}}$  is expected to decline with increasing allocation of resources to root. Fruiting efficiency, defined as the number of grains per unit spike dry matter at anthesis is an important source of variation in grain number (Ferrante *et al.* 2012) and could be expected to contribute to  $E_{\text{GR-GN}}$

$$E_{\text{GR-GN}} \approx f(\text{fruiting efficiency}) \quad \text{eq. 4}$$

We tested eq. (2) and eq. (3) with data from a trial with 13 historic wheat varieties adapted to winter-rainfall environments grown in two locations; eq. (4) remains to be tested. Figure 4 shows data conform to expectations: high allocation to labile carbohydrates reduces efficiency of grain set  $E_{\text{GR-GN}}$ . Many independent studies further support the conclusion that carbohydrate reserves are, in most cases neutral or negative for yield (Sadras *et al.* 2020). Hence, we ask why selection for yield has favoured higher amount and concentration of labile carbohydrates in wheat (Figure 5A).

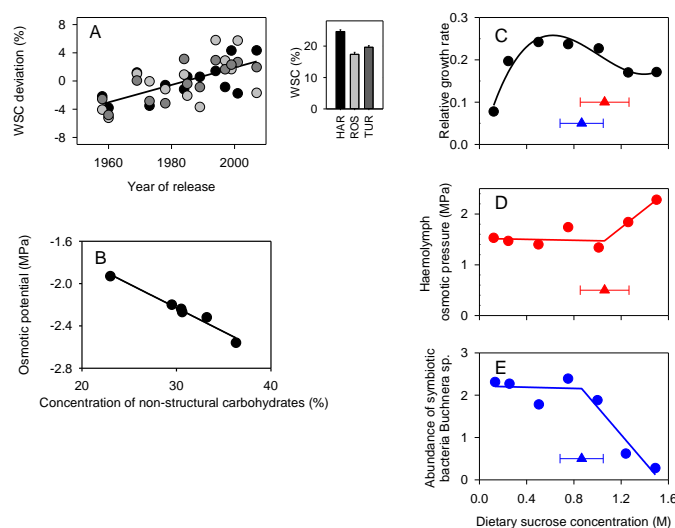


**Figure 4** Wheat grain number is proportional to growth rate per unit grain weight as expected from eq. (2), and the efficiency of grain set is inversely related to WSC as expected from eq. (3). Data from a historical set of 13 varieties released between 1958 and 2006 grown in two locations

### Aphid resistance: an overlooked role of labile carbohydrates in cereals?

We started a new excursion into ecological territory to explore alternative roles of labile carbohydrates in cereals. We speculate that high concentration of labile carbohydrates in plant may challenge the osmotic homeostasis of aphids (Figure 5B-E), thus providing a testable hypothesis that connects WSC with aphid resistance in cereals (Sadras *et al.* 2020). It is suggested that the amount and concentration of labile carbohydrates should be regarded as functionally different traits, with amount relevant to the carbon economy of the crop, and concentration playing an osmotic role. A

companion paper in this conference advances an experimental test of the putative connection between labile carbohydrates in wheat and feeding behaviour and fitness of aphids.



**Figure 5.** (A) Selection for yield over five decades steadily increased the concentration of WSC in wheat adapted to winter-rainfall environments of Australia. Inset is the average across varieties in three locations, HAR: Hart, ROS: Roseworthy, TUR: Turretfield and the scatterplot is the deviation of each variety relative to the environmental mean. The fitted line is the least-square regression ( $r = 0.66$ ,  $p < 0.0001$ ). (B) Correlation between the osmotic potential and concentration of non-structural sugars (fructan + sucrose) of wheat plants in a factorial experiment comparing 3 cultivars (Froid, Brawny, PI 372129) infested with Russian wheat aphid (*Diuraphis noxia*) and uninfested controls. The fitted line is the least-square regression ( $r = -0.98$ ,  $p < 0.001$ ). (C) Relative growth rate of the pea aphid *Acyrtosiphon pisum* as a function of sucrose concentration in artificial diet. Growth rate is  $\log_e(\text{day-8 mass}/\text{day-6 mass})/2$ , with each aphid weighed on day 6 and day 8 to the nearest  $\mu\text{g}$ . (D) Osmotic pressure of the haemolymph of 8-day-old aphids reared on diets with varying concentration of sucrose. (E). Abundance of symbiotic bacteria *Buchnera spp.* in 8-d-old aphids on diets of varying concentration of sucrose. Abundance is  $10^{-6}$  x the number of copies of *Buchnera dnak* gene per ng total DNA. Compiled by Sadras et al. (2020).

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## References

- Andrade FH, Sadras VO, Vega CRC, Echarte L (2005) *Journal of Crop Improvement* **14**, 51-101.  
 Dreccer MF, van Herwaarden AF, Chapman SC (2009) *Field Crops Research* **112**, 43-54.  
 Ferrante A, Savin R, Slafer GA (2012) *Field Crops Research* **136**, 52-64.  
 Fischer RA (2008) *Field Crops Research* **105**, 15-21.  
 Ghiglione HO et al (2008) *The Plant Journal* **55**, 1010-1024.  
 Katayama S (2001) *Fisheries Science* **67**, 401-407.  
 Puckridge DW, Donald CM (1967). *Australian Journal of Agricultural Research* **18**, 193-211.  
 Sadras VO (2006) On wheat and salmon: the trade-off between seed size and number. In 'Proceedings of the 13th Australian Agronomy Conference, Australian Society of Agronomy '  
 Sadras VO (2007) *Field Crops Research* **100**, 125-138.  
 Sadras VO, Denison RF (2009) *New Phytologist* **183**, 565-574.  
 Sadras VO et al. *Frontiers in Plant Science* **11**, 937.  
 Sadras VO, Lawson C (2011) *Crop and Pasture Science* **62**, 533-549.  
 Sadras VO, Slafer GA (2012) *Field Crops Research* **127**, 215-224.  
 Sinclair TR, Jamieson PD (2006) *Field Crops Res* **98**, 60-67.  
 Slafer G, Savin R, Sadras VO (2014) *Field Crops Research* **157**, 71-83.