



## Opinion paper

# The importance of water-soluble carbohydrates in the theoretical framework for nitrogen dilution in shoot biomass of wheat



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## ABSTRACT

Breeding for yield has increased the concentration of reserve water-soluble carbohydrates (WSC) in wheat from dry, low yielding environments of Australia to wet, high-yielding environments of the UK. This generalized increase in WSC can reduce the concentration of nitrogen (N) in shoots and consequently reduce the crop critical N concentration (%N<sub>c</sub>: the minimum concentration of N to achieve maximum growth rates). This may cause errors when assessing a crop's N status using N dilution curves which relate critical N concentration (%N<sub>c</sub>) and shoot biomass (W), i.e. %N<sub>c</sub> = aW<sup>-b</sup>. Inaccurate diagnosis of a crop's N status will have negative environmental and economic consequences such as N losses to the environment and yield gaps. Here, we (i) outline the drivers of variation in WSC, (ii) discuss the implications of WSC on wheat N status, (iii) propose an adjustment of the theoretical N dilution framework that makes explicit a WSC compartment, and (iv) provide estimates of the range of error derived from the current two-compartment model.

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## 1. Introduction

Nitrogen (N) is one of the most important inputs in agriculture; in 2007, almost 85 million t of N fertilizer was applied worldwide and 60% of that was used for cereals (Raun et al., 2009). The amount and timing of N application are important decisions for farmers to avoid yield gaps, manage financial risk and reduce the likelihood of damaging N losses to the environment (Galloway and Cowling, 2002; Monjardino et al., 2015). Nitrogen fertilization and N use efficiency are thus major subjects in agricultural research (Cassman et al., 2002; Chalk et al., 2014; Dalgaard et al., 2014; Gastal et al., 2015; Lemaire, 2015). Breeding and agronomic avenues to improve N use efficiency require rigorous quantification of crop N status to account for the allometric relationship between N concentration and biomass.

The dynamics of shoot N concentration in a growing crop can be described by a N dilution curve. The process of N dilution has wide empirical support (Caloin and Yu, 1984; Greenwood et al., 1990) and was described in a theoretical framework by Lemaire and Gastal (1997). The framework defines the shoot biomass (W) of a crop as the sum of a structural component (W<sub>s</sub>) with a low and

constant N concentration (%N<sub>s</sub>) and a metabolic component (W<sub>m</sub>) with a higher N concentration (%N<sub>m</sub>). Total biomass is thus:

$$W = W_m + W_s \quad (1)$$

and the N concentration of the biomass is then defined as:

$$\%N = (\%N_m \times W_m + \%N_s \times W_s) / W \quad (2)$$

At the start of the growing season, when total biomass is small, shoots consist mostly of metabolic tissue (i.e. leaves) and thus have a relatively high N concentration. As the crop grows, more structural biomass (i.e. stems) with a lower N concentration is produced which dilutes the N<sub>c</sub> in the shoots. The dilution of N as the crop grows is assumed to be driven by the allometric relationship between W<sub>m</sub> and W:

$$W_m = kW^\alpha \quad (3)$$

in which *k* is a growth coefficient. Then, the decline in shoot N concentration with crop biomass can be described by:

$$\%N = k(\%N_m - \%N_s)W^{\alpha-1} + \%N_s \quad (4)$$

values for %N<sub>m</sub> have been estimated as 6.5% for C3 crops and 4.8% for C4 crops, and a common value for %N<sub>s</sub> of 0.8% has been derived for both C3 and C4 crops (Lemaire and Gastal, 1997). A simplified empirical equation to describe the N dilution curve has been proposed by Greenwood et al. (1990):

$$\%N_c = aW^{-b} \quad (5)$$

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in which  $\%N_c$  is the critical N concentration, i.e. the minimal N concentration required for maximum growth rate,  $a$  is the crop N concentration when  $W = 1 \text{ t ha}^{-1}$  and  $b$  is the ratio between the relative decline in  $\%N$  and the relative crop growth rate. For wheat (*Triticum aestivum* L.), the curve developed by Justes et al. (1994) is the most commonly used reference, where  $a = 5.35$  and  $b = 0.442$ .

Using a crop-specific critical N dilution curve to account for the allometry of N and biomass, the N nutrition index (NNI, Lemaire and Meynard, (1997); Lemaire et al., (2007)) can be calculated which defines the N status of a crop:

$$\text{NNI} = \%N_{\text{actual}} / \%N_c \quad (6)$$

in which  $\%N_{\text{actual}}$  is the actual, measured N concentration of the crop under investigation. A NNI lower than 1 means the crop is N deficient (i.e. maximum growth rates are not reached). A NNI higher than 1 means 'luxury' consumption of N (i.e. additional N is taken up but maximum growth rates are already reached), and NNI equal to 1 means the crop N concentration maximizes growth without excess N. The NNI is a robust tool to quantify the N status of crops because it relates N concentration to the actual crop biomass, thus accounting for factors other than N, e.g. genotype or water supply, that may affect biomass (Sadras and Lemaire, 2014).

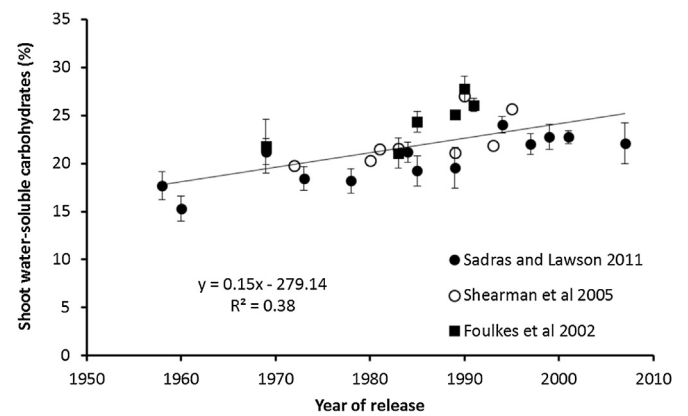
The N dilution framework assumes that plants produce only stems and leaves (metabolic and structural tissue) and no storage organs such as grains or tubers. However, vegetative wheat crops can accumulate large amounts of reserve (non-structural) water-soluble carbohydrates (WSC). The concentration of WSC in crop biomass will affect the shoot N concentration, because WSC does not contain N. High concentration of WSC can thus dilute the N in the biomass, hence the need for a WSC compartment in the N dilution model as suggested by Errecart et al. (2014) and Sadras and Lemaire (2014). Errecart et al. (2014) found a reduction in  $\%N_c$  under water deficit compared with well watered tall fescue and one of their hypotheses was that this was due to an increase in WSC concentration under drought stress. However WSC was not measured in the study.

There is a large intra-specific variation in WSC of wheat and this trait is also responsive to growing conditions including supply of water and N (Shearman et al., 2005; Dreccer et al., 2009; Sadras and Lawson, 2011). Thus, not accounting for WSC can result in misdiagnosis of crop N status. Here, we (i) outline the drivers of variation in WSC, (ii) discuss the implications of WSC on wheat N status, (iii) propose an adjustment of the theoretical framework that makes explicit a WSC compartment, and (iv) provide estimates of the range of error derived from the current two-compartment model.

## 2. Drivers of water soluble carbohydrate accumulation

In wheat crops, water-soluble carbohydrates are stored mostly in stems and a small amount in leaf and spike (van Herwaarden et al., 1998). Most WSC are accumulated before anthesis (50–75%, Ehdai et al., 2006) and accumulation can continue up to about half way through grain filling (Ehdai et al., 2006; Dreccer et al., 2009). They can contribute up to 25% of total aboveground shoot biomass (van Herwaarden et al., 1998; Sadras and Lawson, 2011). During grain filling, WSC are partially translocated to the grain. The contribution of WSC to grain yield varies greatly with cultivar and growing conditions, ranging from 10 to 30% in non-stressed crops (Gebbing et al., 1999; Foulkes et al., 2002) to 50–90% in stressed crops (van Herwaarden et al., 1998; Yang et al., 2001).

Several factors modulate WSC accumulation in wheat crops. It is well established that the shoot N concentration correlates negatively with WSC accumulation (e.g. Bänziger et al., 1994; van Herwaarden et al., 1998; Tahir and Nakata, 2005). For example,



**Fig. 1.** Breeding and selection for yield increased the concentration of water-soluble carbohydrates in shoots of Australian and UK wheat varieties. Sources: Australia: Sadras and Lawson (2011), mean of eight replicates; UK: Foulkes et al. (2002), mean of three replicates, and Shearman et al. (2005), single replicate. Error bars represent standard errors of the replicates.

Bänziger et al. (1994) found that N application at heading caused a negative linear correlation such that an increase of  $1 \text{ mg g}^{-1}$  N in the shoot was associated with a reduction of  $8.5 \text{ mg g}^{-1}$  WSC. Hoogmoed et al. (unpublished) applied different N rates at tillering and found a reduction of  $20.5 \text{ mg g}^{-1}$  WSC for each  $1 \text{ mg g}^{-1}$  increase of shoot N. Thus, crops grown under low N supply will likely have higher concentrations of WSC than crops grown under high N conditions. Two explanations for this effect are proposed. First, a common pool of reduced carbon and energy is used to produce both nitrogen compounds and WSC (van Herwaarden et al., 1998; McIntyre et al., 2011), leading to a reduction in WSC accumulation under high concentrations of N. Second, plant N deficiency has a greater effect on carbohydrate use than on leaf photosynthesis, leading to a decrease in tissue expansion, and a relative increase in WSC accumulation (Gastal et al., 2015).

While much work has been done on the effect of drought on remobilization of WSC to the grain during grain filling (e.g., Wardlaw and Willenbrink, 2000; Yang et al., 2001; Foulkes et al., 2002), only a few studies have assessed the effects of drought on the actual concentration of WSC before remobilization occurs. Overall, it appears that the concentration of WSC in wheat is reduced under drought (Foulkes et al., 2002; Ehdai et al., 2006; Foulkes et al., 2007; Rebetzke et al., 2008). In addition, Karsten and MacAdam (2001) found a reduction in WSC concentration under drought for some pasture species (*Lolium perenne* L., *Festuca arundinacea* Schreb. and *Trifolium repens* L.). However, some have found an increase in WSC concentration under drought (Zhu et al., 2009; Saint Pierre et al., 2010). Part of the discrepancies may be related to the severity of the drought and time scales of the responses. In the short term, or under less severe water deficit, tissue expansion is reduced while photosynthesis continues, leading to accumulation WSC in plant tissue (Muller et al., 2011). More specific studies on how drought affects the concentration of WSC are much needed, in particular the scaling from short to long-term responses at the whole-plant level.

Genetic variation in WSC concentration is large (Foulkes et al., 2002; Ehdai et al., 2006; Ruuska et al., 2006). For example, Ruuska et al. (2006) tested 22 varieties that differed in their WSC concentration (measured at anthesis) from  $<100 \text{ mg g}^{-1}$  dry weight to  $260 \text{ mg g}^{-1}$  dry weight. Though there was a small but significant genotype x environment interaction, the genotypes generally maintained their relative rankings across the environments. Selection for yield has indirectly increased WSC concentration of wheat in both dry, low yielding environments of Australia and wetter, high yielding environments of the UK (Fig. 1), and irrigated systems in

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