Nitrogen translocation to grain in wheat under elevated carbon dioxide: Why our models need amendment

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Abstract
The effects of elevated atmospheric carbon dioxide on grain quality are well known to be generally negative for human nutrition with reduced concentration of many nutrients such as zinc, iron and proteins. Recent crop simulation models have shown satisfactory performance in terms of growth and yield against experimental data in Australia that have raised the atmospheric CO_2. However, the simulation of the reduced concentration of nitrogen whilst reflecting an apparent dilution masks some more fundamental processes that are not modelled properly. There are over 30 wheat crop simulation models used globally to address various agronomic questions, but few model grain quality parameters. A recent review identified that about half of the 30 models simulated grain N concentration but only two simulated the composition of protein within the grain. The accumulation of grain N is described differently in different models, for example the popular Australian wheat crop model (APSIM-Wheat) allows the rate on N transfer to the grain N to be controlled by factors including high temperature and terminal drought. However, to date elevated CO_2 does not directly influence the rate of N accumulation in the grain in APSIM-Wheat or other commonly used crop models. To model the additional effects of elevated CO_2 on grain N beyond dilution, there is a need to account for the lower demand for N translocation to grain under these conditions. We propose a new mechanistic model that allows such demands to be altered under elevated CO_2 along with other environmental factors.

Keywords
AgMIP, baking quality, gliadin, glutenin, protein.

Introduction

The effect of elevated atmospheric carbon dioxide on crop growth is generally positive increasing growth and yield of harvested grain (Fitzgerald et al. 2016). However, the effects on grain quality are generally negative for human nutrition with reduced concentrations of many nutrients such as zinc and iron and wheat storage proteins, impacting on functional quality traits (Myers et al. 2014; Dietterich et al. 2015). Therefore, in a CO_2-rich atmosphere a universal reduction of grain protein and altered composition may translate to an increase in wheat below the minimum quality standard for bread making. This review examines the known response of wheat to elevated CO_2 conditions and explores the potential changes needed in explanatory models to help advance our understanding and management of grain nitrogen concentration and associated baking quality parameters under elevated CO_2, to maintain the high grain quality of Australian grown wheat.

Review

The current crop models

There are over 30 wheat crop simulation models used around the world to address various agronomic questions, but few model grain quality parameters. A recent review by Nuttall et al. (2017) identified that about half of the 30 models simulated grain N concentration but only two simulated the composition of protein within the grain; SiriusQuality (Martre et al. 2006) and STICS (Brisson et al. 1998). The popular Australian wheat crop model (APSIM-Wheat) accommodates factors controlling grain N such as high temperature and terminal drought, but no account of other quality parameters has been made.

Nitrogen is taken up from the soil in its nitrate or ammonium form in many models and allocated to above-ground parts where subsequent translocation to grain occurs after anthesis. This post-anthesis transfer initially occurs slowly but increases near linearly at a near maximum rate after the initial lag-phase is passed. In APSIM-Wheat and APSIM-Nwheat (Asseng et al., 2002; Keating et al. 2003) and an earlier Australian wheat model (OLEARY-CONNOR (OLC), O'Leary and Connor 1996) the demand for N within the developing grain is greatest early in the grain filling period, and a longer duration of grain filling causes a dilution of grain N as grain biomass increases. This emergent property is typically seen in observed and simulated data. The rate at which N is transferred to the grain within the models is affected by a range of variables which differ between models (e.g. Figure 1).

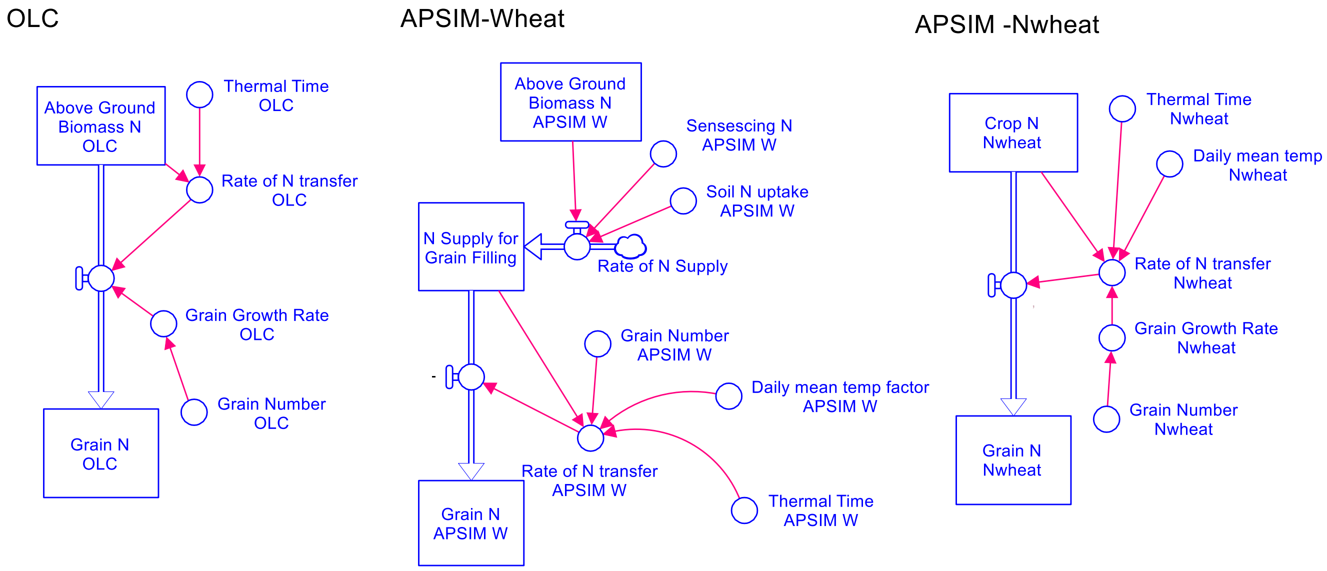

Figure 1. Diagrammatic representation of the OLC, APSIM-wheat and APSIM-Nwheat grain N models, showing the State variables (rectangles) and modifying variables (circles) which define the rate of N movement to grain.

Effects of elevated CO_2

Elevated CO_2, consistently reduces grain protein and N concentrations, through reduced concentrations of N in the above ground biomass, but also through changes to the timing and rate of N remobilisation during leaf senescence and grain filling (Nuttall et al. 2017). However, while changes in N supply for grain filling are captured within the models (Figure 1), in none of the models is the timing or rate of N transfer to the grain directly influenced by elevated atmospheric CO_2.

Predicting Grain N under elevated CO_2

Recently, crop simulation models have shown satisfactory performance in terms of their ability to predict growth and yield against experimental data in Australia where crops have been grown with elevated atmospheric CO_2 (O'Leary et al. 2015). However, to date there has been relatively little testing of the capacity of crop models to simulate the effects of elevated CO_2 with respect to grain N or other quality parameters. Therefore, we tested three crop models (OLC, APSIM-Wheat and APSIM-Nwheat) on data from the Australian Grains Free Air Carbon-dioxide Enrichment (AGFACE) experiment at Horsham (O'Leary et al. 2015; Fitzgerald et al. 2016), to determine how well they accounted for the effects of elevated CO_2 on grain nitrogen concentration. The comparison covered cultivar Yitpi over three years 2007, 2008 and 2009. The models were run without tuning to the yield and grain quality data.

These three models account for the effects of elevated CO_2 increasing water use efficiency and radiation use efficiency. These effects cause a dilution of N in the grain. The general response was below the 1:1 line showing the dilution effect of elevated CO_2 but the simulated values were slightly higher than observed for OLC and lower for APSIM-Nwheat despite similar range for these two models. The slope of the observed data forced through zero was 0.937 (with 95% confidence range 0.912-0.962), OLC producing 0.944 (0.925-0.963), APSIM-Wheat 0.993 (0.981-1.00) and APSIM-Nwheat 0.990 (0.976-1.00). Relative to the observed field data, OLC over-predicted the mean grain N by around 14% under elevated CO_2 ($P < 0.05$), APSIM-Nwheat under-predicted it by 7% ($P < 0.05$) and APSIM-Wheat was close to the observed mean within 2% and not statistically different. The performance of the models were similar under ambient CO_2 conditions with OLC over-predicting the mean grain N by 14% ($P < 0.05$), APSIM-Nwheat under-predicted it by 12% ($P < 0.05$) and APSIM-Wheat was close to the observed mean within 3% and not statistically different (Figure 2).

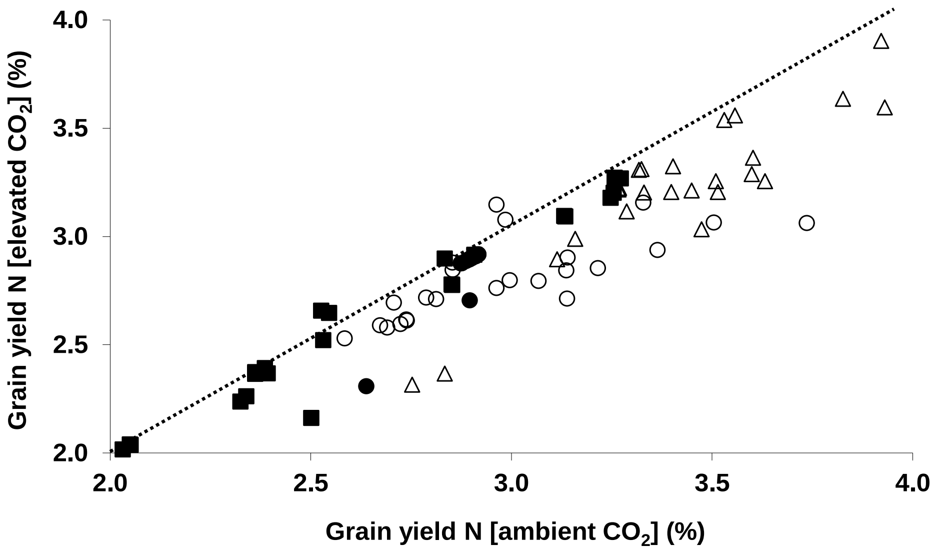

Figure 2. The effect of elevated CO_2 (550 ppm) on grain N concentration (%) observed in a FACE experiment at Horsham (○) and equivalent simulated values from the OLC model (Δ), APSIM-Wheat (●) and APSIM-Nwheat (■). The 1:1 dotted line indicates where eCO_2 has no effect on grain N.

The simulation of the reduced N concentration in grain, whilst reflecting the apparent dilution of plant nitrogen status, does not elucidate all of the fundamental processes linked with protein content and composition (i.e. major storage proteins gliadin and glutenin) within the models. Additional effects of elevated CO_2, include increasing leaf nitrogen use efficiency and the effects of elevated CO_2 on the flux of N into the developing grain. Once these effects are incorporated we expect the effect of elevated CO_2 on grain N effect to be more accurate with increased utility.

Relationships to baking quality

Statistical analyses of grain quality data show the dominance of crude protein content and cultivar for defining parameters such as loaf volume or dough rheology (McCaskill et al. 2016). However, in the presence of elevated CO_2 the negative effects in terms of loaf volume and dough rheology were significantly greater at lower protein levels, with a non-linear interaction. Opportunity to better predict such end use properties may also be linked with modelling protein composition (gliadin and glutenin) where these properties control viscoelastic properties of wheat dough (Martre et al. 2006).

The simulation of complex processes such as the synthesis of protein within the developing grain requires sound explanatory mechanisms of the process as well as observed measurements of various states of the process. Without this feature, models may be little more than a statistical reflection of the observed data. That is, the model is tuned to the data without reflecting the underlying mechanisms of grain protein formation. A lack of measured data of the component states of N risks obtaining the "right answer for the wrong reason" to the extent of the mechanisms included in the model.

The missing links

The ability for many contemporary crop models to simulate grain quality parameters is typically restricted to average grain size and grain-N content (protein concentration) and lack the capacity to predict more detailed whole-grain physical characteristics, protein composition or functional properties. To model the additional effects of elevated CO_2 on grain N beyond dilution, accounting for the lower demand for N translocation to grain is needed. We propose a mechanistic model be pursued that allows such demands to be altered under elevated CO_2 and other factors like light, water or nitrogen stress. Their utility could be extended by accounting for properties which more directly reflect grain functional and end-use value. Such models will provide a powerful tool for developing adaptation strategies, both agronomic and breeding, for combating the impacts of climate change to arable crop production and grain quality

Next steps

Our analyses and recent reviews of modelling grain quality point to the need to include additional baking quality parameters. We plan to advance a new grain quality model employing the State and Rate variable approach of the STELLA modelling software. There remains, however, uncertainty in what parameters are of most interest to the baking industry.

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