Linking wheat grain quality to environmental processes

Garry O'Leary[1], Cassandra Walker[1], Joe Panozzo[1], Thabo Thayalakumaran[2], Malcolm McCaskill[3], James Nuttall[1], Kirsten Barlow[4], Brendan Christy[4] and Senthold Asseng[5]

[1] Agriculture Victoria, 110 Natimuk Road, Horsham, VIC 3400 garry.oleary@ecodev.vic.gov.au gjoleary@yahoo.com

[2] AgriBio, 5 Ring Road, Bundoora, VIC 3083

[3] Agriculture Victoria, 915 Mount Napier Road, Hamilton, VIC 3300

[4] Agriculture Victoria, 124 Chiltern Valley Road, Rutherglen, VIC 3685 Australia Present address: Precision Agriculture, 113 High Street Rutherglen, VIC 3685

[5] University of Florida, Gainesville, FL 32611-0570, USA

Abstract
Maintaining high quality grain from Australian dryland production systems is under threat from three main environmental factors. These are rising atmospheric CO_2 concentrations, increasing frequency of drought and higher temperatures both as average increase and more frequent heat waves. For wheat, we propose a new hypothesis and simulation model for predicting the environmental effects on the synthesis of glutenin and gliadin proteins, two important quality parameters which control end-use properties. This model is applicable for the diverse environments encountered in Australia and France. Mechanistically linking changes in composition of these rheologically-important proteins to environmental conditions should support targeted breeding selection of suitable genes to help maintain grain quality in wheat and provide a marketing edge for Australian grain.

Key Words
crop, gliadin, glutenin, protein, transpiration, water use

Introduction
Various measures of wheat quality have been defined and are dependent on the intended end use. One of the most basic quality parameters is grain protein content. This is relatively cheap and quick to measure, and general lineal relationships have been shown to exist between protein content and many complex quality parameters (Ferrise et al 2015; Békés et al 2016). The key environmental factors affecting grain protein are water availability during the growing season, particularly during the post-anthesis period, high temperatures and elevated atmospheric CO_2 concentration, while crop nutrition, especially nitrogen and sulphur also affect grain protein and quality (Naeem et al 2012; Williams and Diepeveen 2019). For rising atmospheric carbon dioxide associated with climate change there is a consistent effect of reducing grain protein concentration in grain as well as glutenin and gliadin properties (Fitzgerald et al 2016). The effects of high CO_2 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). Therefore, in a CO_2-rich atmosphere a universal reduction of grain N concentration (protein) and altered protein composition may translate to an increase in wheat below the minimum quality standard for bread making (Walker et al 2017).

Protein content of grain is generally well modelled across diverse present-day environments with a relative accuracy similar to grain yield (Asseng et al 2019). Biophysical modelling helps us to clarify in a methodical way the known effects of environment on crop and grain growth and quality (Nuttall et al 2017). While modelling is a mechanistic approximation of the real world it helps to refine our theories in complex environments involving multiple interactions and feedback effects not easily tested in thought experiments. Glutenin and gliadin are two important proteins necessary in defining end-use quality, in particular bread-baking quality. The quantities of these are known to be strongly associated with properties such as dough extensibility, dough strength and loaf volume (MacRitchie 2016). We review how these two grain-quality proteins can be modelled as affected by key environmental variables important in Australia.

Review
The storage proteins, glutenin and gliadin, have been well known to be important parameters in determining bread quality since the early 1970's in Australia (MacRitchie 2016; Békés et al 2016). High glutenin and low gliadin levels are considered desirable for bread and pasta making. These proteins are synthesised as

long chain polymers of varying lengths (>400kD) comprising of different proportions of high and low molecular weight glutenin subunits, respectively. Each of these proteins are synthesised at different rates as grain filling progresses, and the relative rates are affected by environmental conditions resulting in large differences in the resultant mass of these proteins between diverse locations (Panozzo et al 2001; Martre et al 2003).

In Australian (Victoria) experiments of gliadin synthesis was shown to be more rapid with glutenin reaching its maximum rate of synthesis 6 to 8 days after gliadin reached its maximum rate (Panozzo et al 2001). Gliadin reached its maximum rate at around 14 days after anthesis). The size of both these polymers increased as the grain matured resulting in approximately 1:1 ratio, with a higher proportion of glutenin attributed to drier conditions in a non-irrigated environment (Panozzo et al 2001). In France, the timing of the maximum rate of synthesis of glutenin and gliadin are seen to be almost identical (both around 28 days after anthesis) with a resultant larger production of glutenin with typical glutenin:gliadin ratios around 1.5–2:1 (Martre et al 2003). The grain water content was proposed as an important parameter to model glutenin and gliadin synthesis. Our original testing of Martre's SIRIUSQUALITY model (Martre et al 2006) over simulated the glutenin production in Victoria, which is consistent with the above expectation of grain grown in France (data not shown). The absolute differences in the days to maximum production of glutenin and gliadin between locations is primarily attributed to temperature differences of which is readily modelled. However, the large final ratio difference and difference between glutenin and gliadin maximum rate timing poses significant challenges in modelling these proteins at the different global locations with the same model.

A new conceptual glutenin and gliadin model

The synthesis of protein requires carbon and nitrogen substrates. For modelling the total protein levels this is typically achieved by modelling both the carbon and nitrogen rates of production and accumulation. The carbon rate is achieved by modelling the rate of plant and crop biomass production, whereas the protein content is typically determined by multiplying the grain nitrogen content by a conversion factor, which is 5.7 kg protein per kg N for wheat grain. The level of independence between carbon and nitrogen varies between models but mostly achieves satisfactory performance (Asseng et al 2019). The effects of environmental stress include the typical factors that reduce crop growth (e.g. frost, cold and high temperature, water shortage, leaf growth, grain set).

The idea that grain water content will help model glutenin and gliadin production is attractive for biochemical elegance (e.g. glass transition of the polymers, Ferreira et al 2012) and is robust across different locations. There are very large differences between these locations and this points to certain fundamental processes that are not captured in Martre's et al (2003) model. For example, Ferreira et al (2012) showed that irrespective of temperature effects, grain filling was arrested when the grain water content dropped below ~46% and that glutenin polymerisation greatly increased when the grain water content dropped below 32% for vitreous grains in durum wheat. These observations can be modelled by including polymerisation driven by grain water content. However, some inconsistencies remain where greater polymerisation of glutenin (rather than gliadin) appears in bread wheat in France by 30 days after anthesis when grain water content is well above 50% (Martre et al 2003). Grain water contents in Australian experiments are typically 50% around 30 days after anthesis, where polymerisation of gliadin is largely completed (higher than glutenin) and glutenin polymerisation continues at a decreasing rate after 30 days.

This complex behaviour at the different locations may be better modelled with respect to water stress as the triggers to senescence, grain drying and protein polymerisation. Figure 1a shows how such a model may be constructed in a rate and state model diagram. If the crop is unstressed then an optimal unlimited glutenin and gliadin synthesis rate is set to be maximised at a fixed thermal time after anthesis, e.g. equivalent to 25 days after anthesis in this illustrated example (Figure 1b). If the crop is stressed, e.g. with a transpiration ratio of 0.5 for the whole grain filling period, then a delay in the unlimited glutenin synthesis rate compared to the unstressed condition occurs (Figure 1c and Figure 2). The unlimited gliadin rate remains unchanged under stressed conditions because of its smaller molecular mass (Figure 1c). If the available storage amino acids are insufficient to meet the unlimited demand for glutenin and gliadin synthesis, then the actual rate is reduced to meet the supply available. Some supply constants may be necessary to buffer coarse time steps. For a typical simulation in Victoria using weather data the expected near 1:1 ratio of glutenin to gliadin is achieved (Figure 2).

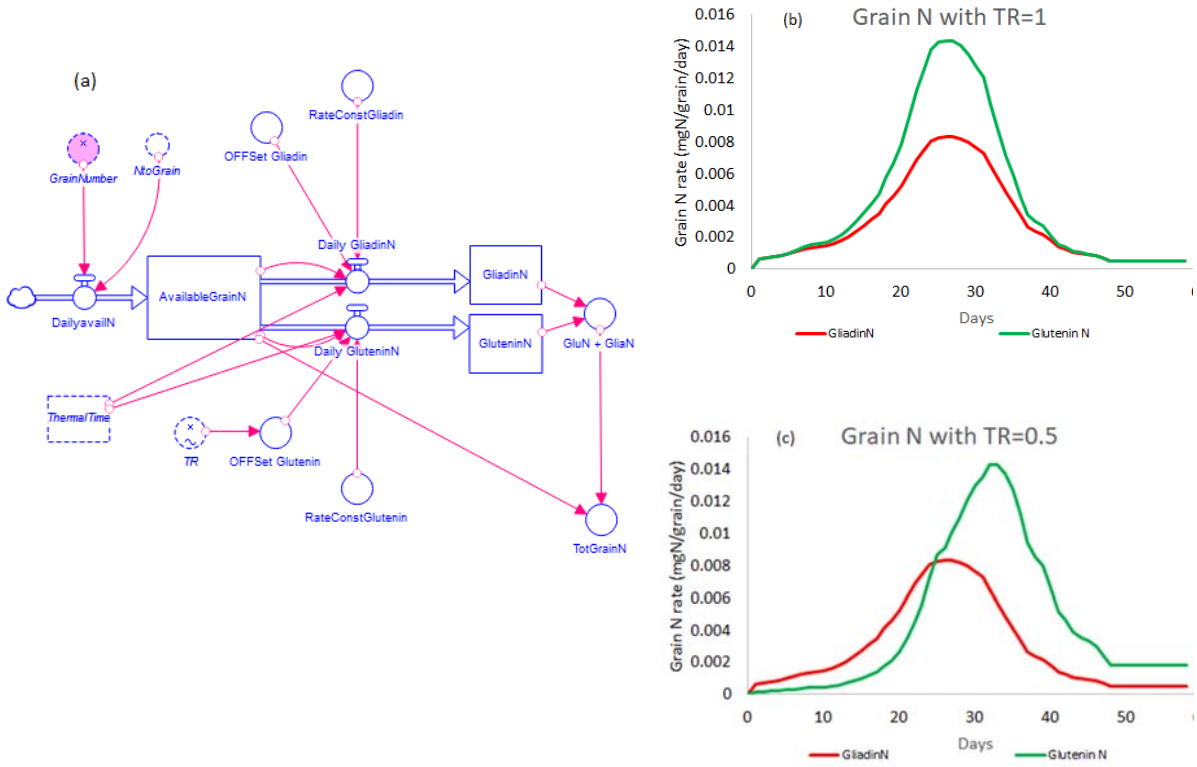

Figure 1. Diagrammatic representation of key state and rate variables to simulate glutenin and gliadin protein synthesis in wheat (a) as affected by amino acid supply, thermal time (temperature and time) and transpiration ratio (TR, an indicator of acute water stress). Unstressed (b) and stressed (c) daily maximum glutenin and gliadin synthesis rate with an example TR=0.5 for the stressed condition.

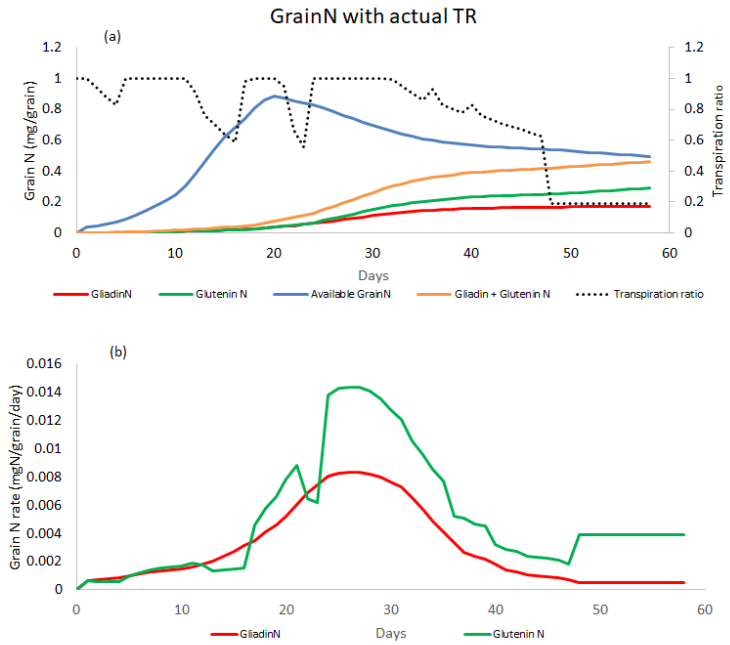

Figure 2. Simulated grain N attributed to glutenin and gliadin, available N and transpiration ratio (a) and daily maximum rate of synthesis for glutenin and gliadin N (b) during grain filling.

Conclusions

Modelling the synthesis of important grain quality proteins, glutenin and gliadin, is challenging due to the complexity of linking multiple environmental variable to these more complex quality parameters. The larger

molecular mass and longer chains of glutenin compared with gliadin may mean that a differential transpiration effect may be enough to model the large differences seen between these proteins for growing condition occurring in both Australia and France. Rather than grain water content, daily transpiration is more sensitive to subtle environmental changes like vapour pressure deficit and water supply during the post-anthesis period and may offer a more robust model than the current buffered grain water content approach.

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