A model of protein accumulation and composition in wheat.

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Introduction

Recently published work on nitrogen uptake by wheat plants and its redistribution among plant tissue has shown that transfer of N to grain (Jamieson & Semenov, 2000) is dominated by N supply from vegetation rather than demand by grain. Protein composition depends on how the N translocated from plant tissue or from post-anthesis soil N uptake is partitioned into the various protein fractions (Martre *et al.*, 2003). The analysis strongly suggests that modelling must concentrate on defining the genetic variation in the size of pools of N that are available for translocation to the grain, and how these interact with grain growth duration to determine grain protein content. This brief paper reports on work to be published in full elsewhere. We used the wheat model Sirius to investigate how varying the capacity of one of the two main vegetative pools of translocatable N affects grain protein content at harvest, and to test the extension of Sirius developed by Martre *et al.* (2003) with several cultivars.

The version we based our work on was Sirius 2000, an update on the model described by Jamieson & Semenov (2000). Sirius has predicted grain protein content accurately over a substantial range for several cultivars in widely varying conditions (Jamieson & Semenov, 2000; Martre *et al.*, 2003, Armour *et al.*, 2004). It allocates the N taken up before anthesis into three main pools. These are a "green" pool that contains N at a constant specific concentration per unit green area (1.5 g/m2), stem pools that contain structural (unrecoverable) N at 0.003 kg N / kg (DM), and labile N with a storage capacity of 0.012 kg N / kg (DM). After anthesis, all non-structural N (i.e., "green" and labile N pools) is available for translocation to grain, and is moved at a constant rate in thermal time to be in the grain at physiological maturity in unstressed conditions. Available soil N is used in preference to N from premature senescence of green area. Hence potential final grain N concentration can be varied only by varying either the duration of grain filling (so that grain mass is lowered for the same N content) or by increasing the size of the N pools available for translocation to the grain.

Model Development

The model was extended in two ways in separate exercises in New Zealand and France. Martre *et al.* (2003) modified the model code slightly to allow grain uptake of N from anthesis for structural proteins – essentially building the structures that would hold carbohydrates and protein accumulated during grain filling. Because the target for these is mainly cell walls, and is therefore controlled by the number of cells being constructed, this part of the process is sink regulated. From the beginning of linear grain filling, the extra N available on a daily basis is partitioned into storage protein components, and this is assumed to be source-regulated in the way suggested by Jamieson and Semenov (2000). A further hypothesis was that the allocation of storage N between gliadin and glutenin fractions during grain growth is constant. Because storage proteins are by far the bulk of proteins accumulated, the whole process of grain protein accumulation is dominated by the source within the crop. The detail of the study involved a single cultivar, Thésée.

In the New Zealand exercise, the capacity of the labile pool was varied to influence capacity to build protein, but without reference to protein fractions. In Sirius 2000, the capacity of the labile N pool was fixed at 0.012 kg N / kg (DM), assuming upper (Nm) and lower limits of stem N concentration of 0.015 and 0.003 kg N / kg (DM). To investigate the effects of varying N pool sizes on final grain N

concentration, Nm was varied between limits of 0.010 – 0.017 kg N / kg (DM) with other parameters held constant using cultivars descriptions for Belfield and Claire.

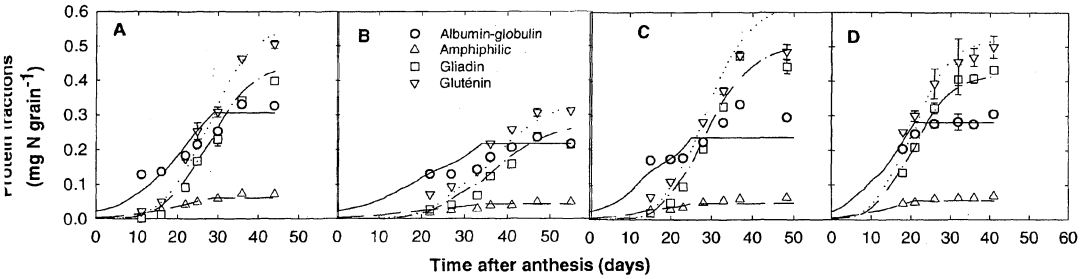

Figure 1. Observed (symbols) and simulated (lines) quantity of albumin-globulin (—), amphiphilic (— —), gliadin (—·—), and glutenin (·····) protein fractions versus the number of days after anthesis for grain of *T. aestivum*. A, Arche; B, Récital; C, Renan; D, Tamaro. Crops were grown in the controlled environment close-top chamber under ambient temperature (19°C/14°C, day/night air temperature) and with non-limited water supply. Experimental data are mean ± 1 SE (n = 2).

Methods

In France an experiment was conducted to test whether the theory developed for Thésée applied to other cultivars. Four cultivars of winter wheat, Arche, Récital, Renan, and Tamaro were grown outside in 2 m^2 containers under non limiting water and N supplies until anthesis. From anthesis, one container of each cultivar was subjected to water shortage, and received only 20 % of the control; another was transferred into controlled environment closed-top chambers, where day/night temperatures were regulated at 28 °C/15°C. The same cultivars were also grown in the field with no N fertilisation or with 250 kg N / ha. An intermediate N fertilisation treatment was obtained on a plot where Lucerne was previously grown, providing ca. 70 kg N / ha.

Plants were sampled from anthesis to grain maturity. Grains were ground to wholemeal flour and the protein fractions were sequentially extracted, and their N content was determined using the Kjeldahl method (Triboï *et al.*, 2003).

In experiments in Canterbury, New Zealand, (Armour *et al.*, 2002; 2004, Jamieson *et al.*, 2004) replicated experiments on five farms over two years had treatments with varying N supplies. Four varieties were used, two sites with Claire, and one each of Savannah, Regency and Centaur. At harvest grain samples were analysed for grain protein content, and these values were compared with predictions from Sirius 2000 using the original Nm value of 0.015 kg N / kg (DM).

In addition to simulations to match experimental treatments, a set of simulations were run using weather and soil data for Lincoln, New Zealand. Chosen cultivars were Belfield, a bread wheat with no vernalisation response, and Claire, a European feed wheat.. The same sowing date (8 May 2003) was used for both. N inputs were high, irrigation was either supplied or not, and deep and shallow soils were used in the simulations.

Results

French Experiments

Under non-limiting water supply and outside temperature, the model gave good simulations of the timing and rates of accumulation of the different protein fractions for the four cultivars (Fig. 1). Similar agreement was observed for the 5 other treatments (data not shown). The quantity of storage proteins varied more than 3-fold, and there was a good agreement between simulated and observed quantities of gliadins and glutenins (data not shown). However, the range of structural protein contents varied over a small range and, even though absolute amounts were reasonably well matched, correlations were poor (data not shown).

New Zealand experiments and simulations

Over a wide range, there was good agreement between measured and simulated protein concentrations (Jamieson *et al.*, 2004). The following simulations are an attempt to explore the mechanism of cultivar variation.

In well watered conditions, there was strong feedback between achieved yield and Nm, with high protein achieved at the cost of yield. In water stressed conditions yield was unaffected although grain protein concentration varied with labile pool size. Achieved grain proteins varied with management and phenology, as well as with Nm. For instance, at Nm = 0.017 kg N / kg (DM), phenological differences, management and soil variations caused grain protein to vary from 10.9-14.0 % (Fig. 2).

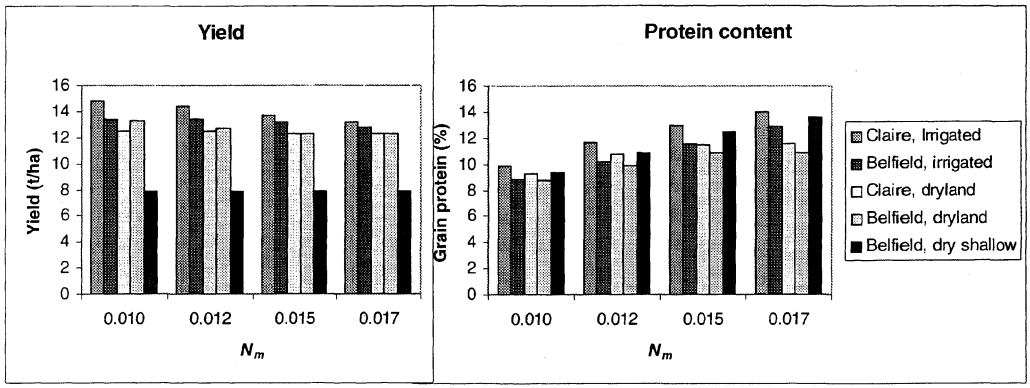

Figure 2. Simulated variation in yield and protein content in response to changes in cultivar, labile N pool capacity and water management in a Canterbury environment.

Discussion

Although there was very good agreement between observed and simulated storage protein contents across environments and cultivars, it was less good for structural proteins. The lack of correlation here may be due mostly to the small range of variation, but also arises from a lack of response in the model of structural protein accumulation to N fertilisation and post-anthesis water deficit. This may be because there is feedback of N availability on grain demand for structural N, which was not allowed for. Nevertheless, the total content and composition is dominated by the larger fractions, so there is a reduced importance of the errors in structural protein

content. The model of Martre *et al.,*. (2003) was based on analysis of one variety. The analysis in fig. 1 shows the partitioning rules are similar among the four varieties tested here.

Further work comparing more extremely differing cultivars is required to confirm whether this is universal. Figure 2 provides some evidence of cultivar variation in inherent ability to produce protein. Here we generated this sort of variation by allowing the capacity of one of the main shoot N pools to vary with cultivar. We were able to mimic the sorts of differences observed among cultivars of different end uses. These overlie variations caused by changes in environment and management. Although we have targeted the labile N pool in our simulations, the variation in source strength may involve both major retranslocatable N pools in the shoot. Further experimental work should aim to quantify the pool capacities

Conclusions

The model used here gives a simple mechanistic framework that explains environmental and genotypic effects on grain protein content and composition. Our assumptions that grain protein composition is a direct function of the total quantity of N per grain, and that N partitioning is not affected by the growing conditions appeared to hold for the four cultivars over a significant range of N fertilisation and post-anthesis temperature and water supply. From this study, we suggest that the variations of protein composition for winter wheat are due to different quantity of N per grain.

Recent evidence favours the shoot as the main determinant of grain protein concentration, so research into genetic factors controlling grain protein should concentrate there rather than on the grain itself. We have suggested one avenue of research – quantification of differences in N pool capacities among cultivars – as a good place to start.

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