Estimating Grain and Straw Nitrogen Concentration in Grain Crops Based on Aboveground Nitrogen Concentration and Harvest Index

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ABSTRACT

Simulating grain (N_g) and straw (N_s) nitrogen (N) concentration is of paramount importance in cropping systems simulation models. In this paper we present a simple model to partition N between grain and straw at harvest for barley (*Hordeum vulgare* L.), wheat (*Triticum aestivum* L.), maize (*Zea mays* L.), and sorghum (*Sorghum bicolor* Moench). The principle of the model is to partition the aboveground N at physiologic maturity based on the relative availability of biomass and N to the grain. The inputs for the model are the harvest index (HI), representing the relative availability of biomass to the grain, and the aboveground N concentration (N_t) at harvest, representing the availability of N. The model has five parameters, of which four (the maximum and minimum achievable grain and straw N concentrations) are readily available; the parameter *C* requires calibration. The model was calibrated and tested for these four species without differentiating genotypes within species. The testing included diverse experiments in wheat; comparing observed and estimated N_g the relative RMSE ranged from 3 to 10% (five experiments) and was 31% in one experiment in which the estimated N_g exceeded consistently the observed values. For barley, maize, and sorghum, the data availability for testing was limited, but the model performed well (relative RMSE values of 7, 7, and 18%, respectively). Therefore, the model proposed seems to be robust. It remains to be determined if the parameters and the method are useful to discriminate genotypic differences in N_g within a species and if the method can be applied to legume crops.

SIMULATING grain (N_g) and straw (N_s) nitrogen (N) concentration is of paramount importance in cropping systems simulation models. N_g is a major quality determinant of cereal and legume crops. For crop simulation models to be useful in helping producers make informed decision regarding N management, they must provide accurate estimates of N_g. In addition, accurate estimates of the N removed with the grain are needed to keep accurate N balances in short- and long-term simulations.

The basic approach to simulate N_g in process-oriented crop models is to allocate dry matter and N to the grain during grain filling depending on the balance between the grain demand and the supply of these two resources. The degree to which the demand is satisfied by the supply depends on environmental and crop conditions affecting photosynthesis and on the N status of the crop. The approach used by Ritchie et al. (1985) in wheat, which was modified by Asseng et al. (2002), assumes that the daily demand of dry matter and N for each grain is independent. The demand is determined by the maximum daily grain growth and N deposition rates, which are empiric functions of temperature. The optimum temperature for N deposition in the grain is higher than that for dry matter, and therefore the simulated N_g tends to increase as temperature increases. The supply of dry matter depends on current photosynthesis and pre-stored reserves, and the supply of N depends on the N concentration of roots, leaves, and stems, which can be depleted until they reach a minimum allowable N concentration. Larmure and Munier-Jolain (2004) proposed a conceptually similar approach to model N_g in peas. This model is not linked to a comprehensive cropping system simulation model and requires considerable input of physiologic parameters to run (number of grains and individual grain growth rate at each reproductive node, rate of progression of the beginning and end of grain filling along the nodes in the stem, and genotype-dependent maximum grain and N deposition rate).

Jamieson and Semenov (2000) followed a slightly different approach. They assumed that the minimum N_g is 15 g N kg^{-1} and that the N harvest index (NHI) increases linearly during grain filling as a function of thermal time, so that the NHI at physiologic maturity is 0.8. An allowance is made for NHI to be greater than 0.8 in the event that the demand of N by the grain is met by postanthesis N uptake. The practical effect is that N_g is basically determined by the supply of total dry matter during grain filling: the lower the supply of dry matter, the higher N_g. None of these models was built as a generic model for grain crops.

The objective of this paper is to present a simple model of N partitioning between grain and straw at harvest. The inputs for the model are the harvest index (HI) and the aboveground biomass N concentration at physiologic maturity (N_t). This information is readily produced by cropping systems simulation models like CropSyst (Stöckle et al., 2003) and EPIC (Williams, 1995), which calculate N_t directly (i.e., independently of N_g and N_s). The model requires minimum calibration to accommodate differences between genotypes or species.

MODEL DESCRIPTION

The basic assumptions of the model are (i) there is a minimum N_g (N_{gn}) and N_s (N_{sn}) that must be satisfied for growth to take place; (ii) there is a maximum N_g (N_{gx}) and N_s (N_{sx}) that cannot be exceeded; (iii) the

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Abbreviations: HI, harvest index; N_g, grain nitrogen concentration; NHI, N harvest index; N_s, straw nitrogen concentration; N_t, N concentration in aboveground biomass at physiologic maturity.

grain (N_{gd}) and straw (N_{sd}) N demands above the minimum concentrations are given by $N_{gd} = N_{gx} - N_{gn}$ and $N_{sd} = N_{sx} - N_{sn}$, respectively; (iv) at harvest, all N above the minimum concentration (N_a) is considered available for allocation to grain or straw; (v) the proportion of N_a allocated to the grain depends on the grain N demand N_{gd} and the total aboveground N demand ($N_{gd} + N_{sd}$). These assumptions have been compiled using the functional equations shown below.

The actual N_g depends on how much of N_a is allocated to the grain and on HI as follows:

$$N_g = N_{gn} + N_a \times P_g/\mathrm{HI} \quad [1]$$

where N_a is the N available for allocation expressed as a concentration quantity:

$$N_a = N_t - [\mathrm{HI} \times N_{gn} + (1 - \mathrm{HI}) \times N_{sn}] \quad [2]$$

where N_t is the aboveground biomass N concentration at physiologic maturity, and P_g is a grain partitioning factor computed as

$$P_g = \{\mathrm{HI} \times N_{gd}/[\mathrm{HI} \times N_{gd} + (1 - \mathrm{HI}) \times N_{sd}]\}^R$$
$$= [1 + (1 - \mathrm{HI}) \times N_{sd}/(\mathrm{HI} \times N_{gd})]^{-R} \quad [3]$$

Multiplying N_a from Eq. [2] by the aboveground biomass gives the N mass in excess of that required to satisfy the minimum concentration of grain and straw and is therefore available for allocation to grain or straw. The term within brackets in the first line of Eq. [3] represents fractionally what would be the partition of N_a to the grain if N_{gx} and N_{sx} are met; under such conditions $R = 1$ as explained below. Similarly, multiplying N_g from Eq. [1] by the grain yield gives the grain N mass. The power R is computed as follows:

$$R = \{N_a/[\mathrm{HI} \times N_{gd} + (1 - \mathrm{HI}) \times N_{sd}]\}^C \quad [4]$$

The term within brackets represents the fraction of the N needed to reach the maximum concentration in the aboveground biomass that is satisfied by N_a and can be interpreted as the degree of "saturation" on N of the aboveground biomass. If the aboveground N biomass satisfies only N_{gn} and N_{sn}, then $R = 0$ because $N_a = 0$; if it is sufficient to satisfy N_{gx} and N_{sx}, then $R = 1$. The power C is a dimensionless empiric factor that allows adjusting P_g for cultivar or species effects: the higher the value of C, the higher the priority of the grain as a sink for N_a. The grain partitioning factor P_g is therefore the partitioning of N_a to grain if grain and straw reach their maximum N concentration, adjusted through R by the actual availability of N.

The parameters N_{gx}, N_{gn}, N_{sx}, and N_{sn} are considered constants that depend on the species or cultivar. Therefore, to compute N_g based on Eq. [1], the only inputs required are N_t and HI. Once N_g has been determined, N_s can be calculated from:

$$N_s = (N_t - \mathrm{HI} \times N_g)/(1 - \mathrm{HI}) \quad [5]$$

MATERIALS AND METHODS

Data from numerous sources for wheat, barley, maize, and sorghum were collected and used to calibrate and test the model. The specific information collected was HI, N_t, N_g, and N_s. The criteria for selecting data were that besides having available HI, N_t, N_g, and N_s, the data showed a reasonable range of variation in HI, N_g, or both. Data sets with the widest range of variation in one of these variables were favored for calibration. The parameters N_{gx} and N_{gn} were not calibrated but were derived from an analysis of several data sets showing the apparent biological boundaries of these parameters for each species. For wheat and barley, the parameter C was calibrated using a data set from the Cook Agronomy Farm (46°47′ N, 117°5′ W, elevation 773–815 m) located 8 km north east of Pullman, WA, in the years 1999 and 2001 (spring wheat) and 2000 (spring barley) (Huggins, unpublished data). For maize, the parameter C was calibrated using a limited data set given in Huggins et al. (2001) and Derby et al. (2005). For sorghum, the parameter C was calibrated using a limited data set given in Kamoshita et al. (1998a). For testing purposes, we used several data sets collected for our own team or retrieved from the literature. The optimization was performed by setting an algorithm seeking the least square difference between observed and predicted N_g by changing the parameter C.

Depending on the choice of parameters and on the values of HI and N_t, the computed N_g can exceed the allowable maximum (N_{gx}) or fell below the allowable minimum (N_{gn}) in extreme cases, when dealing with very high or very low N_t or HI. Similarly, P_g can exceed unity in the computations. Therefore, if in the computation $N_g > N_{gx}$, then N_g is set to N_{gx}; if $N_g < N_{gn}$, then N_g is set to N_{gn}. Similarly, if $P_g > 1$, then P_g is set to 1.

RESULTS

Calibration

We analyzed information on N_g and N_s to define objectively N_{gx}, N_{gn}, N_{sx}, and N_{sn} for these crops. Selected results are shown in Table 1. For wheat and barley, N_{gx} seems to be between 35 and 40 g kg^{-1} and N_{gn} between 11 and 12 g kg^{-1}. For comparison, N_g of soybean is typically 60 g kg^{-1} (e.g., Huggins et al., 2001). It is likely that there is genotypic variation in these parameters; however, the information reviewed prevents drawing definite conclusions in that regard. For straw, N_{sn} and N_{sx} are in the order of 2 and 14 g kg^{-1}. Larmure and Munier-Jolain (2004) discussed the possibility that crops well nourished with N can have higher N_{gn} than crops with low N status. We explored the impact of changing N_{gn} and other parameters of the model in the sensitivity analysis presented in the Discussion section.

Maize and sorghum have generally lower N_g than wheat or barley. We found difficulties in finding relatively high N_g or N_s in experiments with these crops. For maize, the N_g of hybrids typically grown by producers rarely exceeds 15 g kg^{-1} in field conditions (Table 1). Uribelarrea et al. (2004) presented useful information on the biological aptitude of maize to produce grains with high or low N_g by using hybrids generated from the Illinois Protein strains, obtained under several cycles of selection for low and high N_g. They showed N_g ranging from 7 to 29 g kg^{-1} (Table 1). The minimum values are in accord with those presented by Bodley (2004) and Derby et al. (2005). Wyss et al. (1991) presented a surprisingly high value of N_g of 47 g kg^{-1} for the Illinois Protein strain line selected for high protein, a major difference compared with values from hybrids. Kamoshita

Table 1. Selected information on grain and straw maximum and minimum nitrogen concentration at harvest (N_{gx}, N_{gn}, N_{sx}, N_{sn}, respectively) of wheat, barley, maize, and sorghum.

Source	N_{gx}	N_{gn}	N_{sx}	N_{sn}	Source of variation
	g kg^{-1}				
			Wheat		
McDonald (1992)	40.1	15.1	13.8	2.5	site, N fertilization rate; Southern Australia
Huggins, unpublished	31.4	18.7	7.0	2.4	within-field variation; year 1999; Pullman, WA
Huggins, unpublished	28.4	16.4	7.2	2.2	within-field variation; year 2001; Pullman, WA
Halvorson et al. (2004)	33.4	13.8	9.5	2.0	year, N fertilization rate, rotation; Akron, CO
Bonfila et al. (2004)	37.6	15.6	NA	NA	irrigation level, Israel
Rao and Dao (1992)	26.9	NA	13.9	NA	year, N placement, tillage; El Reno, OK
Stoddard (1999)	36.0	NA	NA	NA	cultivar, sink manipulation; pot experiment
Sofield et al. (1977)	35.0	21.4	NA	NA	cultivar, temperature; pot experiment
Mi et al. (2000)	33.3	12.2	NA	NA	cultivar, N fertilizer rate; pot experiment
			Barley		
Voltas et al. (1997)	34.0	12.5	NA	NA	cultivar, sink manipulation; Spain
Birch et al. (1997)	32.0	11.2	NA	NA	site, N fertilizer rate; Queensland, Australia
Bulman and Smith (1993a)	24.6	17.8	14.5	5.6	year, N fertilizer rate; Quebec, Canada
Huggins (unpublished)	26.4	11.2	8.7	2.5	within-field variation; year 2000; Pullman, WA
			Maize		
Wyss et al. (1991)	47.7	6.6	10.5	10.0	inbreed lines; Urbana, IL
Uribelarrea et al. (2004)†	28.8	6.5	NA	NA	year, genotype, N fertilizer rate; Champaign, IL
Derby et al. (2005)	14.8	7.7	7.6	2.9	year, N fertilizer rate, irrigation; Oakes, ND
Bodley (2004)	15.8	12.9	4.1	1.8	year, N fertilizer rate and timing; Pullman, WA
			Sorghum		
Kamoshita et al. (1998a)	26.4	10.8	13.9	3.5	N fertilizer rate, irrigation; Queensland, Australia
Kamoshita et al. (1998b)	16.5	9.5	8.6	3.6	hybrids, N fertilizer rate; Queensland, Australia

† Uribelarrea et al. (2004) reported protein concentration; we converted to nitrogen concentration using the factor 6.25 g protein g^{-1} N.

et al. (1998a) presented data for sorghum showing that N_g can reach values comparable to those of wheat or barley (29 g kg^{-1}), albeit in crops with extreme post-anthesis stress and ample N supply. This value is similar to that reported for maize (Uribelarrea et al., 2004). We assumed that N_{gn} reported for maize applies for sorghum as well. Maximum and minimum N_s values for sorghum straw are similar to those reported for barley and wheat (ca. 14 and 2 g kg^{-1}) (Table 1), and we assume that they also apply to maize. Our choices for N_{gx}, N_{gn}, N_{sx}, and N_{sn} for these four crops are presented in Table 2.

We used a set of experiments for each crop to estimate the parameter C. The results of the calibration are shown in Fig. 1. For spring wheat, we used information collected in Pullman, WA, in which the source of variation was N fertilization rates and within-field spatial variation. The agreement between predicted and observed values was reasonably good ($C = 0.72$, $r^2 = 0.92$, $n = 336$, RMSE = 0.8 g kg^{-1}). In the case of barley, the information was also collected in Pullman, WA, and, similar to wheat, the calibration yielded very good results ($C = 0.19$, $r^2 = 0.86$, $n = 139$, RMSE = 0.9 g kg^{-1}). In both cases, there was a tendency for the results obtained with the calibrated model to overestimate the lower N_g and to underestimate the higher N_g values, as reflected by the slopes between predicted versus observed (ca. 0.9) reported in Fig. 1. For maize and sorghum, we do not have the abundance of data we have for wheat and barley. Therefore, we combined information from Derby et al. (2005) and Huggins et al. (2001) to calibrate the parameter C for maize and used one experiment reported in Kamoshita et al. (1998a) to calibrate the parameter for sorghum. The range of N_g in the case of maize was fairly narrow. Nevertheless, for maize and sorghum, the results of the calibration were satisfactory (Fig. 1). The values of C obtained in the calibration are summarized in Table 2.

Table 2. Grain and straw maximum and minimum nitrogen concentration at harvest (N_{gx}, N_{gn}, N_{sx}, N_{sn}, respectively) and the optimized value for the parameter C of wheat, barley, maize, and sorghum used to estimate grain and straw nitrogen concentration at harvest.

Crop	N_{gx}	N_{gn}	N_{sx}	N_{sn}	C
	g kg^{-1}				
Wheat	40	12	14	2	0.72
Barley	35	11	15	2.5	0.19
Maize	30	7	15	2	−0.12
Sorghum	30	7	15	2	0.18

Model Testing

Several data sets independent from those used in the calibration were used for model testing. Figure 2 shows the testing results for six different experiments with wheat. An overall evaluation indicates an excellent performance of the model across a range of localities, N fertilization rates, water availability, rotations, and cultivars. The N_g data reported by Fischer (1993) and Fischer et al. (1993) for spring wheat, corresponding to several N rates and application timing, were satisfactorily estimated by the model, except for one point that was overestimated. This point corresponded to the maximum N application rate of the experiment (240 kg N ha^{-1}). The observed N_t and HI were 13 g kg^{-1} and 0.35, respectively, for which the model predicts N_g of 27.5 g kg^{-1} (NHI = 0.74), whereas the observed value was 23.5 g kg^{-1} (NHI = 0.63). McDonald (1992) reported the average N_g for three spring wheat cultivars at four different sites and with different N fertilization rates. The agreement between estimated and observed N_g was excellent (Fig. 2); the model captured the effect of the environ-

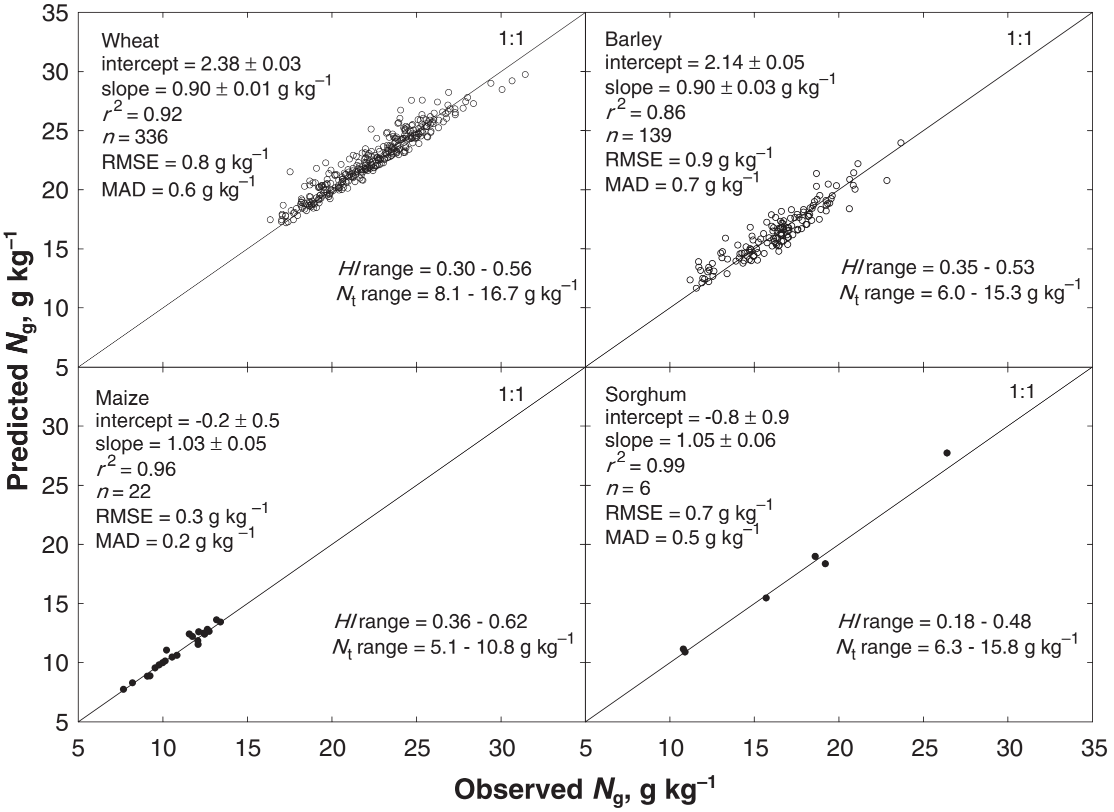

Fig. 1. Calibration of the parameter C for wheat, barley, maize, and sorghum. For wheat and barley, the data are from Pullman, WA; for maize, data are from 1 yr from Derby et al. (2005) and from Huggins et al. (2001); for sorghum, data are from Kamoshita et al. (1998a). Wheat average harvest index (HI) and aboveground nitrogen concentration (N_t) were 0.42 (range 0.30–0.56) and 11.5 (range 8.1–16.7 g kg^{-1}); barley average HI and N_t were 0.43 (range 0.35–0.53) and 9.6 (range 6–15.3 g kg^{-1}); maize average HI and N_t were 0.55 (range 0.36–0.68) and 8.3 (range 5.1–10.8 g kg^{-1}); sorghum average HI and N_t were 0.37 (range 0.18–0.48) and 10.4 (range 6.3–15.8 g kg^{-1}). RMSE and MAD are RMSE and mean absolute difference between observed and predicted N_g.

ment and the effect of the fertilization rate in each site. Halvorson et al. (2004) presented data for winter wheat for 9 yr with five N fertilization rates. Although the parameter C was calibrated for spring wheat, we tested the model for their winter wheat data as well. The overall agreement between estimated and observed N_g was good, with a tendency of the model to overestimate N_g at the higher end. Within each year, the model represented correctly the increase in N_g with increasing N application rate. Except for one year, the estimated N_g was within 10% of the observed value.

Wuest and Cassman (1992) and Huggins (1991) presented experiments in which the timing of N application was varied to favor N uptake during grain filling. The Wuest and Cassman (1992) experiments were conducted in irrigated wheat with the N applied pre-planting and at anthesis. The Huggins (1991) experiment was conducted in a Mediterranean climate where precipitation after anthesis is scarce. Therefore, N was applied at planting and in the fall of the previous year to allow N to penetrate deep in the profile with the infiltrating water during winter and early spring. Results of estimated versus observed N_g for both experiments are shown in Fig. 2. In the experiment of Wuest and Cassman (1992), the model overestimated N_g but correctly represented the increasing N_g at increasing N fertilization rates. Similarly, timing and rate of N fertilization affected N_g in the Huggins (1991) experiment, and the model correctly represented the effect of both variables on N_g (Fig. 2). Adding all or a fraction of the N in fall, as opposed to adding all the N in spring, caused increases in N_t and N_g at harvest of 15 and 10%, respectively, averaged over all N fertilization rates. A second experiment reported by Huggins (1991) involved tillage (no-till versus conventional tillage), preceding crop (Austrian winter peas or winter wheat), and N fertilization rates (range 0–200 kg N ha^{-1}). The model correctly represented the increase in N_g with increasing fertilization rate (Fig. 2).

Diseases affect yield and the deposition of N in the grain. Dimmock and Gooding (2002) reviewed the effect of diseases on N_g and concluded that rusts (*Puccinia* spp.) and powdery mildew (*Erysiphe graminis*) infections decrease N_g and increase N_s, but *Septoria* spp. infections tend to increase N_g, with exceptions. We can speculate that N_g data obtained from plots affected by rusts or powdery mildew will be overestimated by the model. Olesen et al. (2000) presented 2 yr of data for winter wheat grown in Denmark. Treatments included irrigation and N fertilization timing. We compared the N_g reported by these authors with that estimated with our model and found a gross overestimation of N_g (Fig. 2). The absolute N_g values reported were relatively

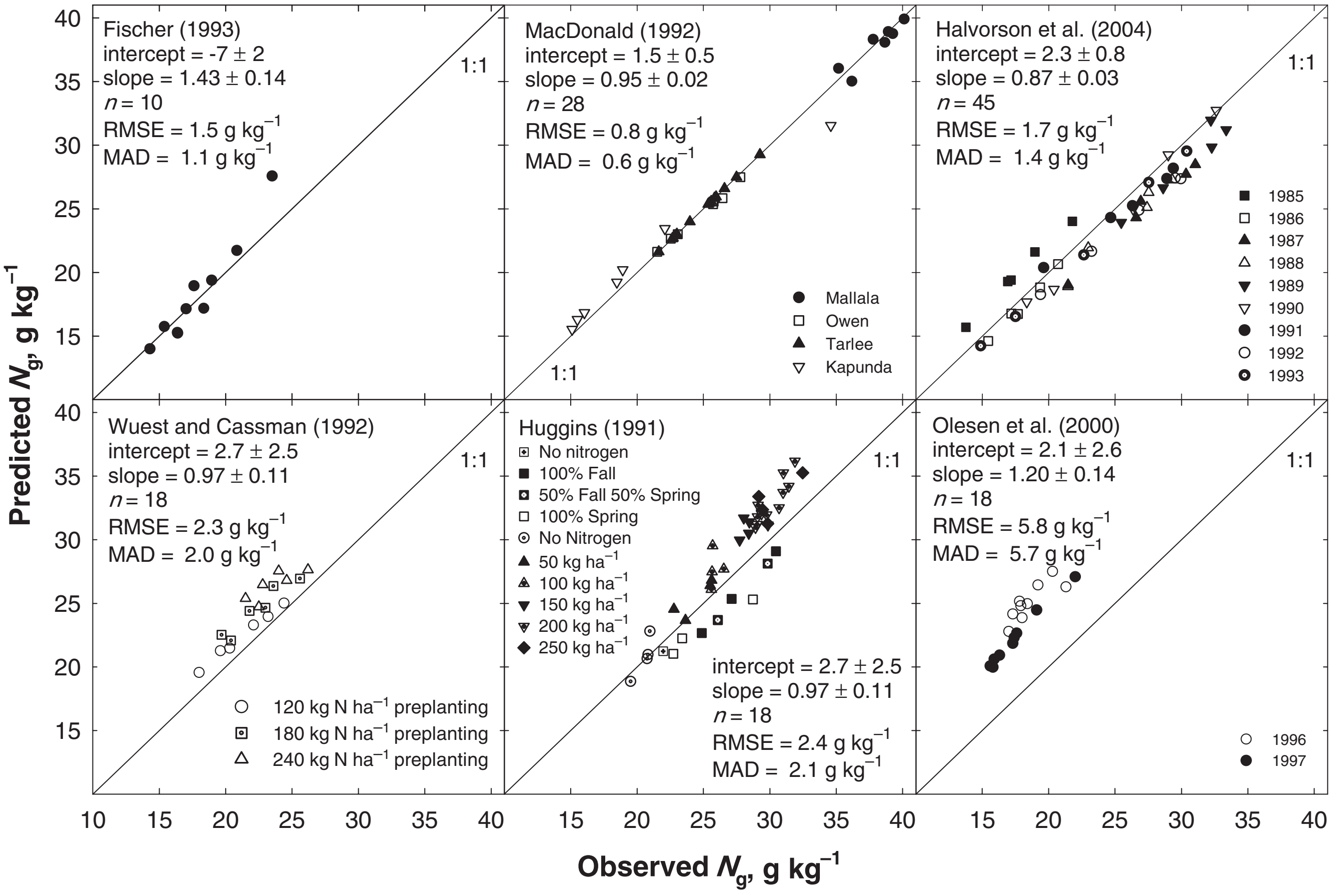

Fig. 2. Testing of the model for wheat. Fischer (1993), Olesen et al. (2000), and Wuest and Cassman (1992) treatments were nitrogen (N) fertilization rate and timing in irrigated experiments. Olesen et al. (2000) experiments were affected by powdery mildew and *Septoria* spp. McDonald (1992) treatments were N fertilization rates and site. Halvorson et al. (2004) treatments were fertilization rate, rotation, and year in dryland winter wheat in Akron, CO. Huggins (1991) treatments were N fertilization rates and timing in dryland spring wheat in a Mediterranean climate (Pullman, WA).

low (average 18.6 and 17.5 g kg^{-1} for 1996 and 1997, respectively), but the average N_s values were high (average 9.9 and 7.5 g kg^{-1} for 1996 and 1997, respectively). The authors indicated that a serious infestation of mildew was present in 1996 and that an infestation of *Septoria* was present in 1997. Therefore, we surmise that the overestimation by the model is due to the effect of mildew, which limits more the N yield than the total yield and thus decreases N_g. However, the argument is weakened when one considers that the effects of *Septoria* are ambiguous (Dimmock and Gooding, 2002). The application of fungicide in that experiment, which decreased the magnitude of the infections but failed to eliminate them, caused an increase in N_g in both years, consistent with the idea that diseases may explain a portion of the departure of the predicted N_g with respect to the observed. The model seemed to overestimate N_g in all of the irrigated experiments (Fig. 2; one case in Fischer et al., 1993; Wuest and Cassman, 1992; Olesen et al., 2000).

We tested the model for spring barley using data collected by Huggins (unpublished) at the Cook Agronomy Farm and data presented by Bulman and Smith (1993b) for three cultivars. We tested the model for winter barley using data from Delogu et al. (1998). The testing shows good agreement for the Pullman data (Fig. 3). For the Bulman and Smith data, the model correctly predicted an increase in N_g as the N fertilization rate increased but increasingly overestimated N_g as the fertilization rate increased. For the control with no N applied, the model predicted N_g correctly. We do not have an explanation for the overestimation, but it is plausible that the parameters used were inappropriate for the condition of their experiment. It is worth noting that they reported the average for three cultivars, not the data by cultivar. The averaging could be masking genotypic differences not considered in the model parameters. The N_g data for winter barley of Delogu et al. (1998) were very well estimated by the model (Fig. 3).

For maize, the testing was performed using the data presented by Bodley (2004), Derby et al. (2005) (data from a different year than that used in the testing), and Mehdi et al. (1999) (Fig. 3). The model underestimated N_g from Bodley's (2004) data but represented well the tendency of N_g to increase with increasing fertilization rate. Similarly, the model slightly underestimated the values given by Derby et al. (2005); however, the predicted values were within 10% of the observed N_g, except for one case that departed 13% from the observed. The N_g data presented by Mehdi et al. (1999) were very well estimated by the model. The two clusters of data

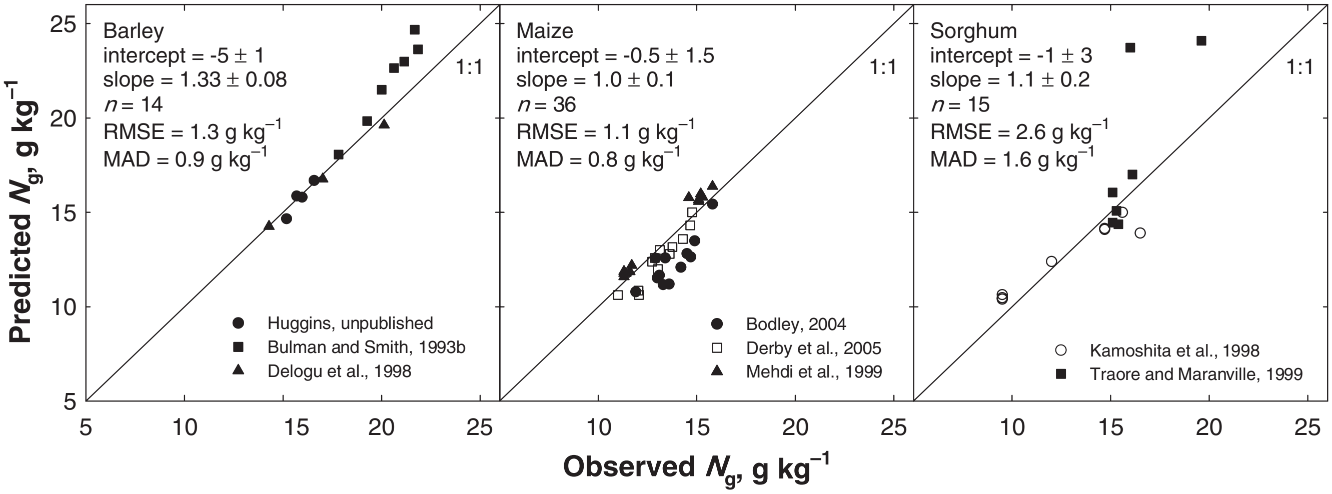

Fig. 3. Testing of the model for barley, maize, and sorghum. The data for spring barley are from Pullman, WA (Huggins, unpublished) and from Bulman and Smith (1993b) in an experiment in Canada; their data is the average of three cultivars. Data from Delogu et al. (1998) are for winter barley growing at three nitrogen (N) fertilization rates (0, 80, and 140 kg N ha^{-1}); each point is the average of 2 yr. Data for maize are from Bodley (2004) and Derby et al. (2005) for maize grown at different N fertilization rates in Pullman, WA and Oakes, ND, respectively. Data from Mehdi et al. (1999) correspond to 2 yr and different tillage practices. The data for sorghum from Kamoshita et al. (1998b) are from three hybrids grown at 0 and 240 kg N ha^{-1}, and data from Traore and Maranville (1999) are for different genotypes adapted to the experimental area (Nebraska) or adapted to tropical growing conditions.

belong to different years. The estimated N_g was within 5% of the observed N_g. In general, N_g of maize is between 10 and 15 g kg^{-1}, a relatively narrow range compared with that of wheat or barley (Fig. 1–3).

For sorghum, the testing was performed using data from Kamoshita et al. (1998b) for three hybrids grown at 0 and 240 kg N ha^{-1} and from Traore and Maranville (1999) for different genotypes adapted to the experimental area (Nebraska) or adapted to tropical growing conditions (Fig. 3). For both data sets, the model estimated the observed N_g reasonably well. However, for two points from Traore and Maranville (1999), the model overestimated N_g by 14 and 25%. In one case (14%), the overestimation corresponds to a line adapted to the experimental area growing conditions, and the reasons for the overestimations are not clear. The case in which the overestimation was the greatest (25%) corresponds to a genotype adapted to tropical conditions. In the experiment, the reported HI for that genotype was 0.07, an extremely low value for sorghum. The model seems to have difficulties handling extreme conditions. No data regarding the environmental and agronomic conditions of the plots were provided, and events such as frost could have affected grain filling in this tropical genotype.

DISCUSSION

The method proposed to estimate N_g is simple and requires minimal inputs. The principle of the model is similar to that used in mechanistic models: It is based on the relative availability of carbon or total biomass and N. The HI represents the "availability" of biomass for the grain, and N_t represents the availability of N. The allocation of N to the grain is made at harvest, not on a day-by-day basis, as is done in mechanistic models with daily time-step. It can be argued that daily (or even hourly) information generated during the simulation is not efficiently used when the final decision on how much N is allocated in the grain is made at harvest.

The meaning of HI and N_t in the model is illustrated in Fig. 4, where N_g is shown as a function of N_t and HI. For a given HI, N_g increases as N_t increases. For a given N_t, N_g decreases as HI increases, reflecting the dilution effect of increasing HI on N_g. The parameter C effect is also illustrated in Fig. 4 using the parameters calibrated for wheat and maize. For both crops, we fixed HI to 0.45 and graphed the change in N_g as a function of N_t. Wheat, which has a C constant greater than that of maize, tends to favor the grain as N sink rather than the straw. In maize, the priority given to the grain is moderated compared with that of wheat. The reasons for such difference in the physiology of these two crops are not clear. Elucidating the reasons could help in developing cultivars for high or low N_g. The model clearly shows that increasing HI while keeping N_t unchanged leads to a decrease in N_g. This is not desirable in crops like hard red spring wheat, for which the objective is to achieve N_g above approximately 20 g kg^{-1}, but it is a logical way of keeping low N_g in malting barley, where N_g above approximately 20 g kg^{-1} is detrimental to the malt quality.

Table 3 presents a sensitivity analysis of the parameters based on the calibration for wheat. All the parameters were increased or decreased by 20%, and the relative change in N_g was tabulated for several combinations of HI and N_t. The parameter that affected the N_g estimations the most was N_{gx}. One reason for that is that it is numerically the parameter with the maximum absolute value. In all cases, changing the parameters by 20% produced changes in N_g of less than 20%. In the worst case, changing N_{gx} by 20% changed N_g by 13% (Table 3). The parameter C showed relatively low sensitivity, with changes in N_g of less than 4% in response to changes in C of 20%. If cultivars or species vary in the values of the parameters, detecting differences in just

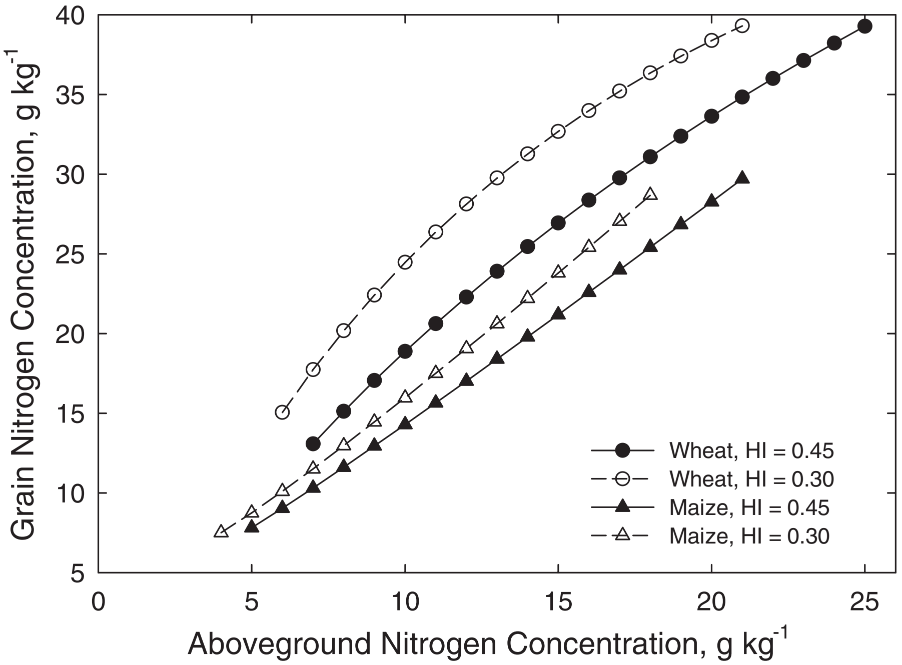

Fig. 4. Modeled variation of the grain nitrogen (N) concentration in response to aboveground biomass N concentration at harvest and to the harvest index using the parameters fitted for wheat and maize.

one parameter could be challenging. Genetic differences in N_g have been suggested in wheat (Sofield et al., 1977). Perhaps the Illinois Protein strain lines of maize represent the most striking case of genotypic differences in N_g and variables related to the N and carbon metabolism within a species (Dudley and Lambert, 2004). It seems clear that the model correctly discriminates physiologic differences among species, as illustrated by the differences in the parameters among the four crops. It remains to be proven if the parameters of the model are able to capture differences among genotypes within a species.

As presented, the model does not consider differences on how the final HI and N_t are achieved. For example, the effect of N uptake timing, if any, is not represented in the model. It can be proposed that two crops with identical HI and N_t, but with one acquiring all the N preanthesis and the other acquiring a sizable fraction of the N postanthesis, would differ in the final N_g. Data by Huggins (1991) and Wuest and Cassman (1992) strongly suggest that all the effect is contained in N_t and that timing per se does not affect N_g unless N_t is affected. The data analyzed for wheat also suggest that for irrigated crops the model tends to overestimate N_g (the model was validated for dryland spring wheat). A plausible explanation is that crops without water stress rely mostly on current photosynthesis for grain filling instead of reserves remobilization (Gallagher et al., 1975). The remobilization of reserves to the grain includes N compounds, whose remobilization is limited if grain filling is performed mostly with current photosynthesis. If that is the case, the model could accommodate this by making the parameter *C* a function of a water stress index during grain filling: the lower the water stress, the lower the value of *C*.

A disadvantage of this method is that the potential contribution of N remobilized from the roots is not represented in the model. We have tried this method only in nonlegume crops, but it would be relevant to calibrate the parameters or modify the method for a legume crop like soybean. Given that legumes are self-sufficient in N

Table 3. Sensitivity analysis of the model parameters. The parameters calibrated for wheat and shown in Table 2 were changed by plus or minus 20%, and the relative change in grain nitrogen concentration (N_g) with respect to original calibration is reported for three harvest index (HI) and aboveground nitrogen concentration (N_t) values. N_{gx}, N_{gn}, N_{sx}, N_{sn} are the maximum and minimum, grain and straw nitrogen concentration, respectively; *C* is an empirical parameter of the model.

			N_{gx}		N_{gn}		N_{sx}		N_{sn}		*C*	
HI	N_t	N_g	+20%	−20%	+20%	−20%	+20%	−20%	+20%	−20%	+20%	−20%
	—g kg^{-1}—		%									
0.20	8	25.7	4.5	−5.1	3.2	−2.6	−0.6	0.9	−3.0	2.4	3.7	−3.4
	12	33.3	9.1	−9.7	2.0	−1.6	−1.2	1.8	−1.2	0.9	3.7	−3.1
	16	37.8	13.2	−13.6	0.9	−0.7	−1.7	2.6	−0.4	0.3	2.0	−1.6
0.35	8	18.2	1.3	−1.7	2.3	−2.1	−0.4	0.5	−3.1	2.6	1.2	−1.3
	12	26.0	4.1	−5.2	2.3	−1.8	−1.3	1.5	−1.5	1.2	2.1	−1.9
	16	32.0	6.9	−8.4	1.5	−1.2	−2.2	2.5	−0.7	0.6	1.8	−1.6
0.40	8	16.5	0.8	−1.0	1.8	−1.8	−0.3	0.3	−3.0	2.5	0.8	−0.8
	12	24.0	3.1	−4.1	2.1	−1.7	−1.1	1.2	−1.5	1.2	1.7	−1.6
	16	30.2	5.5	−6.9	1.5	−1.2	−2.0	2.2	−0.8	0.6	1.6	−1.4

acquisition, we hypothesize that differences in N_g derive mostly from differences in HI. A major advantage of this model is the transparency with which N_g is determined. In a crop simulation model, it would be meaningless to expect, or even to obtain, a correct estimate of N_g, when the simulated N_t or HI depart from reality.

CONCLUSIONS

The method proposed here to partition N between grain and straw at harvest in grain crops seems to be robust. Four out of the five parameters in the model were obtained from field experiments, and one was calibrated based on observed values of HI, N_t, and N_g, which suggests that this model can be easily parameterized for other species or, if necessary, growing conditions. It remains to be determined if the parameters and the model are useful to discriminate genotypic differences in N_g within a species and if the model can be applied to legume crops.

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