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Response of winter wheat to N-fertiliser: Dynamic model

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Abstract. A concise computer simulation model is described for calculating the growth and N-content of winter-wheat. The validity of the model was tested by means of a new application of statistical theory against the results of nationwide fertiliser experiments having different designs. There was agreement within the limits of experimental error between the measured and simulated values of both total plant and of grain dry weight over the entire range of N-fertiliser treatments in the different experiments. The model also gave good estimates of the %N in the grain provided N-fertilizer levels were not high. Response curves, calculated from the model for grain yield, grain %N, are given for different combinations of potential yield, mineralisation rate and the distribution of inorganic-N down the soil profile.

Introduction

Simulation models have been developed that give good descriptions of N-response of, for instance, potatoes [11] and rice [1]. Some of the concepts behind these models and the intrinsic equations in them, appear to be so general that they could apply to widely different crops. Other equations and coefficients that are specific for winter wheat are described in the previous paper. We therefore attempted to develop a dynamic model for N-response for winter wheat.

The most favoured approach for testing the validity of models is based on comparing the best estimate of the optimal N level for each site with that deduced from the model. A serious drawback of this approach is that there is usually a massive error in determining the optimum from field experimental data and it is seldom clear how far differences between experimentally-determined and measured optima result from shortcomings in the model or from experimental error [23]. A novel application of statistical theory has been introduced to overcome these problems [23]. It is based on systematic inspection of the differences between simulated and observed yields obtained with each level of N-fertiliser in each experiment. Differences that are of sufficient size and cannot be accounted for in terms of experimental error are identified and trends in these differences evaluated. This paper describes the model and tests of its validity with the new statistical procedures. The model is also used to predict the effects of N-fertiliser on yield and %N in the grain of winter wheat and the predictions are compared with the results of independent experiments reported in the literature.

Description of the model

The model makes separate calculations for each experiment. First it calculates a growth rate coefficient to define the way in which the plant mass increases with time in the absence of N-stress. Simulations of the growth of crops are then carried out separately for each experimental treatment. Essentially the growth period is divided into daily intervals, and for each day the increment of plant dry matter is calculated from the growth rate coefficient, the %N in the dry matter at that time and the minimum %N needed to permit maximum growth rate.

The soil is visualised as consisting of 18 5-cm-thick layers and all the inorganic-N is assumed to exist as nitrate. For each day and each layer the model calculates the soil water content, after taking account of rainfall and evapotranspiration, and the nitrate content after taking account of leaching, mineralisation and uptake by the roots.

For each day the model calculates,

(a) the increment in plant mass
(b) the depth of rooting
(c) the N-uptake by the crop
(d) the evapotranspiration and soil water content
(e) the leaching of nitrate down the soil profile
(f) the mineralisation of soil organic matter.

After these calculations the model updates the %N in the plant, the total plant weight, the distributions of water and nitrate down the soil profile. When the period of simulation is complete (i.e. at the time corresponding to maturity) the model partitions total dry matter and nitrogen between straw and grain. The main equations are given below and the most important symbols are defined in Table 1.

Time of maturity

From U.K. work [24] it may be deduced that winter wheat matures after a cumulative thermal time from the end of February of 1860 day degrees above 0 °C. According to this criterion, the date of maturity varied from day (Julian) 207 to 216. In the model the date of maturity was always assumed to be day 210.

Growth rate coefficient

The growth rate coefficient K_2 was calculated for each experiment from the growth of dry weight obtained with the level of fertiliser-N that gave the largest

Table 1. Principal symbols and their definitions.

Symbol	Definition
E_O	Evaporation from an open water surface (mm)
E_C	Transpiration from crop canopy (mm)
E_S	Evaporation from bare soil (mm)
E_T	Evapotranspiration from bare soil plus crop (mm)
f_r	Fraction of the soil surface covered by the crop
G_F	Growth rate factor to correct for growth rate being reduced by sub-optimal %N in the plant
K_1	Growth coefficient ($\mathrm{t\,ha^{-1}}$)
K_2	Growth coefficient ($\mathrm{t\,ha^{-1}\,d^{-1}}$)
N_S	Amount of inorganic-N in the top 90 cm of soil in early spring
N_F	Amount of fertiliser-N applied ($\mathrm{kg\,N\,ha^{-1}}$)
M_N	Total amount of N apparently mineralised in the top 90 cm of soil ($\mathrm{kg\,N\,ha^{-1}}$)
P_G	%N in grain dry matter
P_M	Minimum %N in the dry matter of the above ground parts of the plant that is needed to permit maximum growth rate
P_W	%N in the above ground parts of the plant
Q	Coefficient for the decline in mineralisation rate with depth down the soil profile ($\mathrm{cm^{-1}}$)
R	Rainfall (mm)
T	Time (Julian days)
W	Dry weight of plant mass excluding fibrous roots ($\mathrm{t\,ha^{-1}}$)
W_M	Maximum dry weight of plant mass excluding fibrous roots that can be obtained with any level of N fertilizer ($\mathrm{t\,ha^{-1}}$)
W_G	Weight of grain dry matter ($\mathrm{t\,ha^{-1}}$)
W_S	Weight of straw dry matter ($\mathrm{t\,ha^{-1}}$)
x	Depth from soil surface (cm)

value of plant mass, W_H, in $\mathrm{t\,ha^{-1}}$ of dry matter, at time T_H (time of harvest in Julian days). It was calculated from the previously [9] derived equation:

$$K_2 = (K_1 \ln W_H + W_H - K_1 \ln W_0 - W_0)/(T_H - T_0) \tag{1}$$

where K_1 is the growth rate coefficient which always has a value of $1\ \mathrm{t\,ha^{-1}}$, W_0 is the dry weight at the start of simulation, day T_0. W_0 was set equal to $0.13\ \mathrm{t\,ha^{-1}}$ and T_0 to Julian day 84.

Increment in the weight of dry matter

The increment in the weight of dry matter, ΔW, of plant mass for each day during the growing period was calculated from

$$\Delta W = \frac{K_2 W}{K_1 + W} * \Delta T * G_F \tag{2}$$

where the value K_2 was calculated separately for each experiment by means of equation (1), K_1 was set equal to $1\ \mathrm{t\,ha^{-1}}$, and G_F was a growth factor to correct for the influence of %N in the plant biomass on growth rate. Errors of integration were minimised by setting W equal to its value at the start of the day plus half its increment during the previous day.

On the basis of previous evidence (12) G_F was calculated from,

$$G_F = P_W/P_M \tag{3}$$

where P_W is the %N in the dry matter of the above ground parts of the plant and P_M is the minimum %N at which growth rate is maximum. P_M is calculated for each day by,

$$P_M = 1.35\,(1 + 3e^{-0.26\,W_M}) \tag{4}$$

where W_M is the maximum attainable weight of dry plant biomass on that day. Equation (4) was found to define P_M during the growth of wheat at least up to anthesis in Siman's experiments [22]. W (the weight of the mass of that particular treatment on that day) was used in previous work with potatoes [11] but in this work on winter wheat W_M gave better estimates of yields and N-contents than W.

Root depth

At the start of simulation of crop growth the depth of soil containing 90% of roots was set equal to 60 cm on the basis of the results of past experiments [25]. Thereafter the depth in cm was taken to be $60 + 20 * W$ with W expressed in $\mathrm{t\,ha^{-1}}$ until the depth equalled 90 cm because rooting depth often increases by about 20 cm for every $1\,\mathrm{t\,ha^{-1}}$ increase in plant weight.

N-uptake by the crop

The treatment was based on the following premises: that all the inorganic-N in soil is nitrate, that plant roots are able to absorb all the nitrate at a concentration greater than $0.18\,\mathrm{kg\,N\,ha^{-1}\,cm^{-1}}$ [13] to a depth of 90 cm; that nitrate is never absorbed below a depth of 90 cm; and that only 80% of the N absorbed from the soil is recovered in the plant mass (see equation (1) ref. [13]); the remainder is in the roots or lost from the soil/plant system by processes such as leaching from the leaves.

For each day the potential maximum increment in plant N was calculated as $P_M * W$ less the plant-N on the previous day. The actual increment is equal to the potential maximum if there is adequate available NO_3—N to the depth of rooting. As only 80% of the amount of N that disappears from soil is recovered in the crop, the soil to depth of rooting needs to contain an amount of available NO_3—N (i.e. all the NO_3—N at a concentration of more than $0.18\,\mathrm{kg\,N\,ha^{-1}\,cm^{-1}}$) that exceeds (1/0.8)* (the potential maximum N-increment) for the potential maximum amount to be absorbed. Otherwise uptake is taken as being equal to 0.8 * (the available NO_3—N in soil to the depth of rooting).

Crop roots are considered to remove nitrate from the uppermost layer, then the next and so on down the soil profile.

Evapotranspiration and soil water content

Evapotranspiration was calculated as the sum of the water lost by evaporation from the soil surface and that transpired from the crop. Methods of calculation were based on those described previously [2, 4, 16, 21].

The fraction, f_r, of the soil surface covered by crops was considered to be 0.6 when $W = 0.13\,\mathrm{t\,ha^{-1}}$ and to increase in proportion to W until $W = 2.5\,\mathrm{t\,ha^{-1}}$ when f_r is set equal 0.9 (cf. ref. [14]). Total daily evapotranspiration E_T was calculated as:

$$E_T = f_r \times E_C + (1 - f_r)E_S \tag{5}$$

where E_C is the transpiration per unit area of crop and E_S is the evaporation per unit area of soil.

Calculation of E_C and E_S was based on previously reported approaches. E_C was assumed to be the potential maximum transpiration rate, E_O, when the soil moisture deficit was less than a critical value and to decline linearly with increasing deficits until an upper critical deficit is reached when transpiration ceased. The critical deficits, per cm of rooting depth, were respectively, 0.146 and 0.156 cm for the loamy sands, 0.202 and 0.212 cm for the loams and sandy loams and 0.111 and 0.171 cm for the clays.

Daily evaporation E_S, from the bare soil surface was calculated from E_O by the following formula,

$$E_S = E_O e^{-AT'} \tag{6}$$

where A is a coefficient and T' days is the effective time of evaporation [21]. It is the period from the time the soil is at field capacity for which the soil surface would have had to be sujected to a constant evaporative demand, E_O, before the soil moisture deficit would have reached its current value. Minor corrections were made to account for the effects of intermittent small quantities of rain. Each day the soil moisture deficit was recalculated as the moisture deficit on the previous day plus the excess evapotranspiration over rainfall. To permit these calculations A was set equal to $0.08\,\mathrm{d^{-1}}$ for the loamy sands, $0.05\,\mathrm{d^{-1}}$ for the sandy loams and loams and $0.44\,\mathrm{d^{-1}}$ for the clay soils.

Leaching of nitrate down the soil profile

Whenever soil was at field capacity (zero deficit) and there was an excess of rainfall over evapotranspiration leaching of nitrate down the soil profile occurred. It was calculated for each day from the excess rainfall over evapotranspiration, the amounts of nitrate in each of the layers and the volumetric water content at field capacity. The volumetric water content at field capacity was taken to be 0.24 $cm^3 cm^{-3}$ for the loamy sands, 0.32 $cm^3 cm^{-3}$ for the loams and sandy loams and 0.49 $cm^3 cm^{-3}$ for the clays. The procedure was as described by Burns [5] with the exception that no correction was made for upward movement of nitrate.

Mineralisation of soil organic matter

The mineralisation rate (dM_N/dt) over the entire profile was considered to remain at the same value for each experiment throughout the period of simulation. Mineralisation rate to depth x, $(dM_N/dT)_x$ was considered to be

$$(dM_N/dT)_x = (dM_N/dT)(1 - e^{-Qx}). \qquad (7)$$

The treatment was based on the view that mineralisation rate is dominated by microbial breakdown of root residues from past crops. Q was taken to be 0.0738 cm^{-1} as described previously [11].

Partition of assimilate and nitrogen between grain and straw

The daily calculations of soil nitrate increments in growth, etc., ceased at the day corresponding to the date of maturity. The model then partioned the plant mass W(t ha^{-1}) into weight of grain W_G and W_S the weight of straw by an equation referred to previously [13].

$$W_G = 16.82 + 0.9021\, W_S - 0.03387\,(E_O)_{3\text{-}7} - 0.01469\, R_{60} \qquad (8)$$

where $(E_O)_{3\text{-}7}$ is the evaporation (mm) from an open water surface from March–July inclusive and R_{60} is the rainfall in mm during the last 60 days before harvest.

The model included equation (9) below, to calculate the percent N, P_G in the grain dry matter. The derivation of this equation was largely based on the argument presented in the previous paper [13]. P_G was considered to depend on what the %N in the whole plant would have been if there had been no losses of N from the plant during senescence. As the minimum %N in the plant (P_M) needed to permit maximum growth rate declined as plant mass per unit area got larger a relationship was developed between P_G and P_W/P_M. An additional term was included to take account of the effects (13) of evaporation in mm $(E_O)_{5\text{-}7}$ from an open water surface (May–July inclusive). Equation (9) is

$$P_G = 0.172 + 1.023\,(P_W/P_M) + 0.002273\,(E_O)_{5\text{-}7}. \qquad (9)$$

Values of the coefficients in equation (9) were obtained by regression analysis using inputs of P_W and P_M that were obtained by a preliminary simulation with the model described in this paper.

When it is specifically stated that simulations are for average conditions equations (8) and (9) in the model were replaced with,

$$W_G = 1.206 + 0.9527\,W_S \tag{10}$$

and

$$P_G = 0.8238 + 1.0716(P_W/P_M). \tag{11}$$

(see ref. [13])

Inputs

Apart from the parameter values given in the forgoing section, the model required inputs, the values of which varied from experiment to experiment. These inputs are,

(i) the average mineralisation rate during the main growing period. These were between 0.22 and 0.88 $\mathrm{kg\,N\,ha^{-1}\,d^{-1}}$ and are summarised in Table 1 of [13];
(ii) the measured distribution of inorganic-N to a depth of 90 cm in spring and the time of such measurement (see Table 1 of [13]);
(iii) the maximum weight of straw plus grain at maturity with any level of N fertiliser. It varied between 11.0 and 18.3 $\mathrm{t\,ha^{-1}}$;
(iv) the daily rainfall and monthly potential evapotranspiration.

Start of simulation

For each experiment the start of simulation was the day when the inorganic N in soil was measured. Crop growth simulation was started later, on day 84. The model permitted inclusion of different levels and times of application of N-fertiliser top dressing. It was assumed all the fertiliser-N behaved as if, at the instant of application, it consisted entirely of NO_3—N and was distributed uniformly in the uppermost 5 cm layer.

The experiments

These are described in Table 1 of the previous paper [13].

Evaluation of the model

The model was run to simulate the plant mass, the grain dry weight and the grain %N for each treatment of each experiment. Simulated and measured values of these parameters are given in Fig. 1. Visual inspection suggests that the model gave a good description of the data.

A statistical analysis was carried out. The $\sqrt{\mathrm{MSE}}$ was calculated from the deviations between the simulated and measured values of the various parameters. For seven of the experiments $\sqrt{\mathrm{MSE}}$ calculated in this way compared

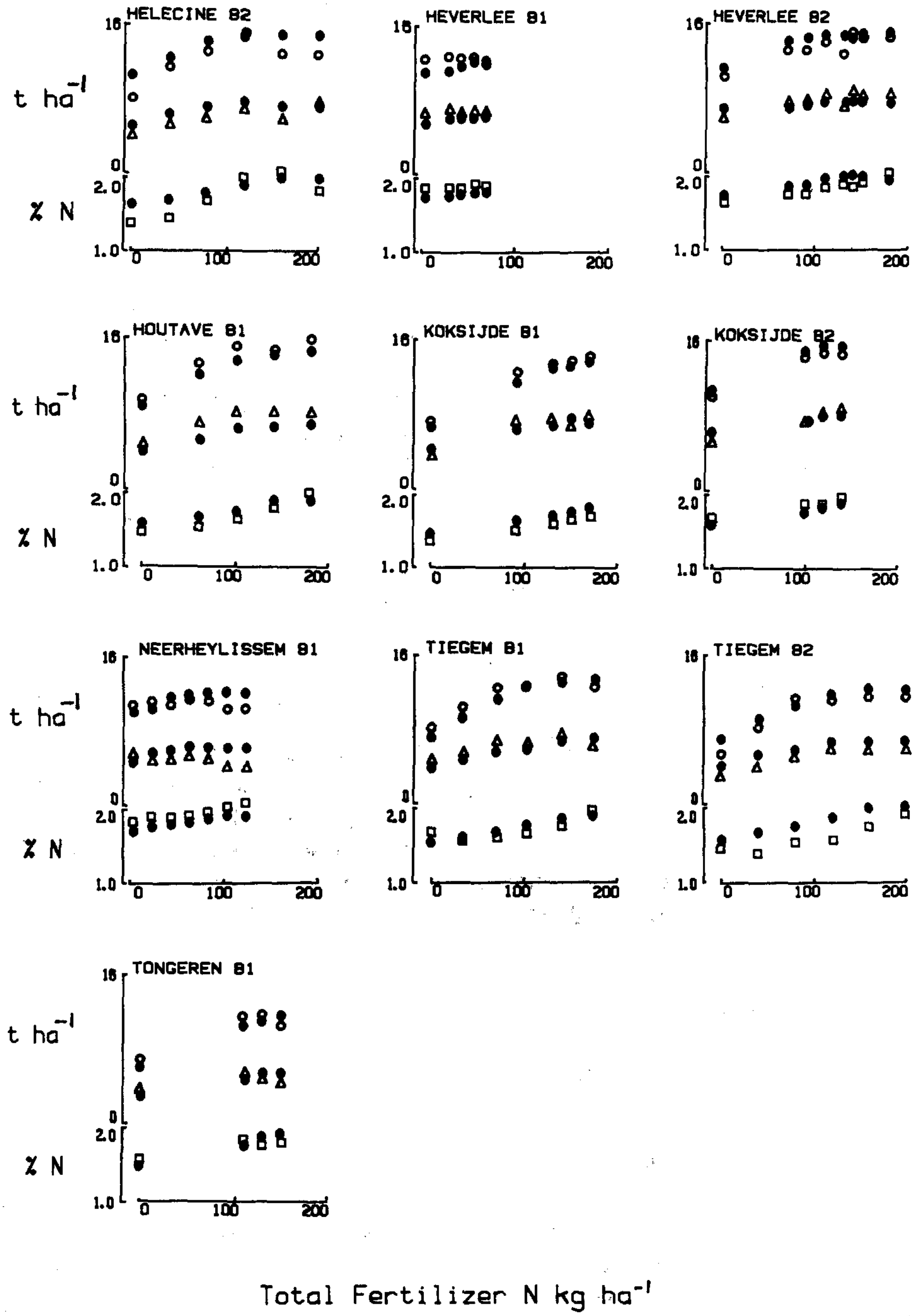

Fig. 1. Measured dry weight of plant mass (straw plus grain), t ha^{-1}, 0; measured dry weight of grain t ha^{-1} Δ; measured %N in grain dry matter, □; and the corresponding simulated values ●; for different total fertiliser-N applications. Measured values are averaged over varieties.

with $\sqrt{\hat{\sigma}_E^2}$ the estimated residual sum of squares of the untransformed data after taking account of the main effects of variety and fertiliser level. Although the method of calculation of $\sqrt{\hat{\sigma}_E^2}$ probably overestimates $\sqrt{\hat{\sigma}_E^2}$, $\sqrt{\text{MSE}}$ is with few exceptions greater than $\sqrt{\hat{\sigma}_E^2}$. This means that the model failed to account for some of the variability in the various parameters.

A summary of the biases obtained with the simulation model are given in Tables 2, 3, 4 and 5 with significance calculated as in [23]. One data point in each experiment, that corresponding to the maximum yield of biomass was used as an input for the simulations. This value and the corresponding values of grain dry weight and %N in the grain have been excluded from the results presented in Tables 2, 3, 4 and 5. We consider that any bias significantly greater that 5% of the true mean at the 5% probability level indicates a weakness in the model. The extent to which the biases are related to the level of N-fertiliser have been tested with a rank correlation test which compares the ranks of the biases with ranks of the levels of applied N. When the biases increase (or take lower positive values), the values of rank correlation are near 1 and when they decrease the values of rank correlation are near -1.

The model tended to over-predict slightly the plant mass at low levels of N-fertiliser at Tiegem 82 and to over predict slightly at high levels Neerheylissem 81 (Table 3). There is some evidence that the model does not predict grain weight very well at one site (Neerheylissem 81, data set 23–25). With this exception, however, the data in Tables 3 and 4 indicate that the model defines the total dry weight and grain weights without appreciable bias at all levels of N-fertiliser on all sites.

The model was, however, less satisfactory for predicting the %N in the grain when the levels of N-fertiliser were high (Table 5). There was an important over-prediction at Koksijde 81 (data set 3–12) and Tiegem 82 (data set 29–32) and a tendency to over-predict at Tongeren 81 (data set 33–36).

According to the foregoing criteria there is no evidence that in general application, the model prediction would exceed 5% of the mean for plant mass or grain weight over the entire range of N-fertiliser treatments. It is also calculating the %N in the grain with a bias of less than 0.2 (of %N).

Table 2. Deviations of values estimated by the model from those measured experimentally

Experiment[a]	No. of deviations	Weight of plant mass		Dry weight of grain		%N in grain dry weight	
		$\sqrt{\text{MSE}}$[b]	$\sqrt{\sigma^2}$ (d.f.)	$\sqrt{\text{MSE}}$[b]	$\sqrt{\sigma^2}$ (d.f.)	$\sqrt{\text{MSE}}$[b]	$\sqrt{\sigma^2}$ (d.f.)
Heverlee 81	8	0.86	0.26 (3)	0.81	0.28 (3)	0.11	0.031 (3)
Koksijde 81	40	0.65	0.49 (27)	0.41	0.26 (27)	0.13	0.172 (27)
Koksijde 82	30	0.70	0.59 (45)	0.37	0.32 (45)	0.10	0.048 (45)
Neerheylissem 81	18	1.06	0.61 (10)	0.98	0.32 (10)	0.12	0.058 (10)
Tiegem 81	15	0.52	0.32 (8)	0.52	0.23 (8)	0.09	0.051 (8)
Tiegem 82	20	0.98	0.59 (12)	0.76	0.39 (12)	0.23	0.052 (12)
Tongeren 81	12	0.44	0.55 (6)	0.43	0.37 (6)	0.11	0.099 (6)

[a] Further details of experiment given in Table 3.

[b] Calculated from deviations between predicted and measured values.

Table 3. Test of the validity of the model for calculating the dry weight of plant mass.

Data set[a]	Experiment	N-levels	No. of biases	Significant $d > -5\%$		biases $d > 5\%$		Spearman rank correlation[c] coefficient	
				No.	Ranks[b]	No.	Ranks[b]		
1	Heverlee 81	0, 26, 39, 52, 65	4	1	1			−0.80	NS
2			4					−0.80	
3	Koksijde 81	0, 90, 130, 150, 170	4					0.20	NS
4			4					−1.00	
5			4	1	2			0.20	
6			4					−1.00	
7			4					1.00	
8			4					−0.68	
9			4					0.40	
10			4					0.40	
11			4					−1.0	
12			4					0.20	
13	Koksijde 82	0, 100, 120, 140	3					−0.50	NS
14			3			1	3	−0.50	
15			3					−1.0	
16			3			1	3	−0.50	
17			3					0.50	
18			3					0.88	
19			3					0.12	
20			3					0.50	
21			3					1.00	
22			3					1.00	
23	Neerheylissem 81	0, 20, 40, 60, 80, 100, 120	6					−0.83	*
24			6					−0.63	
25			6			2	5, 6	−0.83	
26	Tiegem 81	0, 35, 70, 105, 140, 175	5	1	3			−0.40	NS
27			5					−0.10	
28			5					−0.60	

29	Tiegem 82	0, 40, 80, 120, 160, 200	5	1	2	0.60	*
30			5			0.60	
31			5			0.50	
32			5	1	1	0.50	
33	Tongeren 81	0. 110, 130, 150	3			0.50	NS
34			3			−0.50	
35			3			−1.00	
36			3	2	5, 6	−1.00	

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[a] A different data set number is allocated to the data obtained for each variety in each experiment.

[b] Refers to the lowest level of applied N-fertiliser, 2, 3 etc., to successively increasing levels.

[c] Rank correlations marked * are significant at 5% level; NS signifies not significant.

Table 4. Test of the validity of the model for calculating grain dry weights.

Data set[a]	No. of biases	Significant $d < -5\%$		biases $d > 5\%$		Spearman rank correlation coefficient[c]	
		No.	Ranks[b]	No.	Ranks[b]		
1	4	1	1			−0.80	NS
2	4					−0.15	
3	4					0.20	*
4	4					0.20	
5	4					0.20	
6	4					0.80	
7	4					0.40	
8	4					0.20	
9	4					0.40	
10	4					1.00	
11	4			1	1	0.20	
12	4					0.20	
13	3					−0.50	NS
14	3					0.50	
15	3					−1.00	
16	3					0.50	
17	3					0.50	
18	3					0.50	
19	3					0.50	
20	3					0.50	
21	3					1.00	
22	3					1.00	
23	6			1	6	−0.83	*
24	6			1	6	−0.49	
25	6			3	3, 5, 6	−0.83	
26	5	1	3			0.68	NS
27	5	1	3			−0.10	
28	5					−0.50	
29	5			2	1, 2	0.60	*
30	5					0.30	
31	5					0.60	
32	5			1	1	0.50	
33	3					−0.50	NS
34	3					−0.50	
35	3					−1.00	
36	3					−1.00	

[a] Data set is defined in Table 2.

[b] 1 refers to the lowest level of applied N-fertiliser; 2, 3 etc., to successively increasing levels.

[c] Rank correlations marked * are significant at 5% level; all others are not significant.

It was not possible to calculate $\sqrt{\hat{\sigma}_E^2}$ for three experiments. Nevertheless, the $\sqrt{\mathrm{MSE}}$ calculated for these experiments were similar to those calculated for the other 7 experiments (table 6). The indication is that the degree fit for the two sets of experiments is similar.

Table 5. Test of the validity of the model for calculating the %N in the grain.

Data set[a]	No. of biases	Significant $d < -5\%$		biases $d > 5\%$		Spearman rank correlation coefficient[c]	
		No.	Ranks[b]	No.	Ranks[b]		
1	4					0.95	NS
2	4					−0.80	
3	4					0.95	*
4	4			1	3	−0.40	
5	4					−0.40	
6	4					0.40	
7	4					−0.60	
8	4			2	3, 4	−0.80	
9	4			1	2	−0.40	
10	4			2	2, 4	−1.00	
11	4					−1.00	
12	4					−0.95	
13	3					−0.88	NS
14	3					−0.50	
15	3					0.12	
16	3					−1.00	
17	3	1	2			−0.50	
18	3					0.50	
19	3					−1.00	
20	3					0.12	
21	3					−0.50	
22	3	1	2			0.12	
23	6					−0.81	NS
24	6					−0.54	
25	6	3	4, 5, 6			0.83	
26	5					0.30	NS
27	5					0.30	
28	5					−1.00	
29	5			4	2, 3, 4, 5	−0.78	*
30	5			3	2, 4, 5	−0.80	
31	5			4	2, 3, 4, 5	−0.58	
32	5			3	3, 4, 5	−0.98*	
33	3					−1.00	*
34	3					−1.00	
35	3					−1.00	
36	3					0.50	

[a] Data set is defined in Table 2.

[b] 1 refers to the lowest level of applied N-fertiliser; 2, 3 etc., to successively increasing levels.

[c] Rank correlations marked * are significant at 5% level; NS signifies not significant.

Total amount of N in the grain plus straw

The predicted total amounts of N in the above-ground parts of the plant were generally linearly related to the measured amounts. When N-fertiliser was witheld the average predicted content was 4% greater than the measured value.

Table 6. Comparison between model prediction and measurement for experiments with only one variety.

Experiment	$\sqrt{\text{MSE}^a}$ (d.f.)		
	Plant mass	Grain dry weight	%N in grain
Helecine 82	1.57 (4)	1.07 (4)	0.217 (4)
Heverlee 82	1.11 (7)	0.52 (7)	0.049 (7)
Houtave 81	1.07 (3)	0.52 (3)	0.111 (3)

[a] Calculated from differences between measured and predicted yields.

Nevertheless, when N-fertiliser was applied the predicted values were greater than the measured values and the difference increased with increasing fertiliser application. On average the difference was 12% with the mean application of N-fertiliser and 19% with the highest level.

Discussion

The model did not include a term for the loss of N from cereal crops during senescence which could explain why the total N content of cereal grain plus straw is higher than the measured values. Some support for this view is provided by previous work [8, 12, 26] which showed that such losses did occur even in Europe and that their magnitude increased with the level of N-nutrition.

If most of the increase in plant mass and grain growth occurred before loss of N, as is suggested in the previous paper, this weakness in the model should not have influenced its ability to estimate the weights of plant mass, cereal grain and, to a lesser extent, %N in the grain. These exceptions are born out by the data in Fig. 1 and the analyses in Tables 2, 3, 4, 5 and 6. They indicate that as far as it is possible to determine, in view of the inevitable experimental errors, the model is estimating the effects of N-fertiliser on dry weight of plant mass and dry weight of grain without bias. There is also quite good agreement between calculated and measured values of %N of grain. This degree of agreement may, in part, be a consequence of the fact that some of the equations in the model were derived from the same data that were used for testing it which is unsatisfactory but inevitable at this stage of model development. Also the mineralisation rate of soil organic matter and the maximum final yield were required as inputs for each experiment. Even so, with these caveats in mind it is worth discussing the practical implications of the model. Figure 2 gives predicted response curves of the foregoing features of the crop plotted against the Sollwert (the total amount of inorganic-N in the top 90 cm of soil on day 90 plus the amount of N-fertiliser applied) for soils having different mineralisation rates. These are chosen to broadly correspond with the U.K. Advisory Service's N index system which is largely based on previous cropping. We believe [10] the soil with the lowest mineralisation rate 0.4 kg N ha^{-1} d^{-1} roughly corresponds to one which has been continuously cropped with cereals (ADAS N-index of 0) [19]. The soil

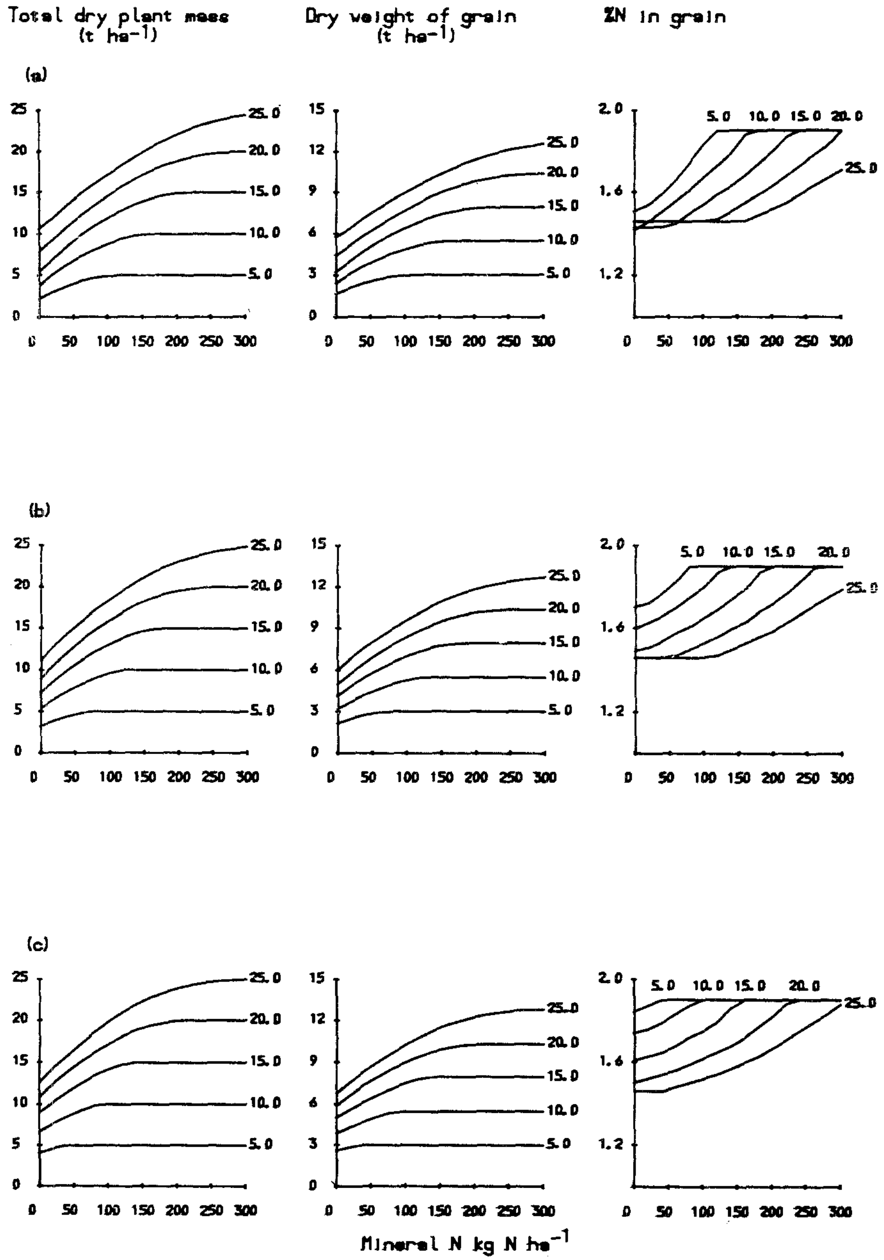

Fig. 2. The simulated total dry plant mass (straw plus grain), the simulated dry weight of grain and the simulated %N in the grain plotted against total amounts of inorganic-N in the top 90 cm of soil, N_S, at the start of the growing season plus the applied fertiliser-N, N_F, on soils with mineralisation rates of (a) 0.4 kg N ha^{-1} d^{-1}, (b) 0.7 kg N ha^{-1} d^{1} and (c) 1.0 kg N ha^{-1} d^{-1}. Numbers at the end of each graph are the potential maximum dry weight of grain plus straw when N is not limiting.

Table 7. Measured N-fertiliser requirements of winter wheat.

Grain yield ($t\,ha^{-1}$ dry weight)	'Sollwert' Total inorganic plus fertiliser-N needed to give maximum yield[a] ($kg\,N\,ha^{-1}$)	Estimated mineralisation rates during growing period $kg\,N\,ha^{-1}\,d^{-1}$	Reference
5.6	160	0.7–1.6[b]	Dilz et al. [6]
6.1	200	0.7–1.6[b]	Dilz et al. [6]
4.0[f]	140[f]	–	Gustafson & Mattson [15]
5.4[f]	210[f]	–	Gustafson & Mattson [15]
7.2	190	0.55[d]	Jungk & Wehrmann [17, 18] Kohler
6.2[c]	200[e]	–	Ris et al. [20]

[a] Includes second dressing.

[b] Estimated for period May to August from measurements made after the second cereal crop in the rotation potatoes, cereals, cereals, potatoes [11].

[c] Average wheat yields 1975–1983 in the Netherlands (Food and Agriculture Organisation of the United Nations) [7].

[d] Estimated over period March–July inclusive.

[e] Value used for farm advice.

[f] Derived from published graphs.

with the highest mineralisation rate broadly corresponds to one which has received large and frequent dressings of farmyard manure or slurry (ADAS N-index of 2). The predictions are for average weather conditions, and are calculated with equations (10) and (11) substituted for (8) and (9) in the model. They are also for conditions where there is no leaching.

One interesting consequence of the model is that the %N in the grain is related to N-fertiliser level by near parallel lines for crops with different yield potentials grown on a soil having the same mineralisation rate. According to these relationships an increase of 0.1%N in the grain will be induced by a fertiliser application of 30 $\mathrm{kg\,N\,ha^{-1}}$ when the average mineralisation rate is about 0.4 $\mathrm{kg\,N\,ha^{-1}\,d^{-1}}$ and by about 40 $\mathrm{kg\,N\,ha^{-1}}$ when the average mineralisation rate is about 0.7 $\mathrm{kg\,N\,ha^{-1}\,d^{-1}}$. It is notable that the values of 30 and 40 $\mathrm{kg\,N\,ha^{-1}}$ are remarkably similar to the range of 29 to 40 quoted by Benzian et al. [3]. The model also predicts that the value would be on average 50 $\mathrm{kg\,N\,ha^{-1}}$ if the mineralisation rate was 1 $\mathrm{kg\,N\,ha^{-1}\,d^{-1}}$. Few values of this magnitude have been reported for winter wheat soils.

Some of the reported values for Sollwert — the minimum total amount of inorganic-N in the soil plus fertiliser-N needed for maximum grain yield — are given in Table 7. The grain yields with the optimum level of N-fertiliser are also given and in two cases it has been possible to include an estimation of the mineralisation rate.

If it is assumed that those cases where no mineralisation rates were measured the rates exceeded 0.4 $\mathrm{kg\,N\,ha^{-1}\,d^{-1}}$, then in all instances whether mineralisation rates were measured or not, the experimentally determined value of Sollwert is rather higher than that expected from Fig. 1. This bias might be expected because the model was run for conditions when there was no leaching or denitrification. If either of these two processes had occurred the model would have been expected to underestimate N-fertiliser requirement. The model clearly gives predictions that are at least in semi-quantitative terms in agreement with the results of these sets of data wich are entirely independent of those used for developing the model.

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