Rice Yield Variability in Australia in Relation to Cool-Temperature Damage, N Fertilizer and Water Depth

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ABSTRACT

The Australian rice industry is concentrated in a relatively small region at latitude 35-37°S. Yield variability in the region, associated with low temperatures, is the major weather-related problem for the industry and has led to yield reductions of 20-30% in at least one year in ten. A model describing the problem in terms of floret sterility, delayed development and a generalised reduction in assimilation was presented in the report from the previous meetings of the Pacific Rim group. This model showed that during the nineteen eighties, despite relatively high mean annual temperatures, there were several years with low minimum temperatures during the sensitive phases of the rice crop, and relatively low yields.

In recent years, the almost universal adoption of semi-dwarf varieties and increasing adoption of deep (~20cm) water at the sensitive stages, has led to marked increases in yield, compared to the tall varieties and shallow (~5cm) water. For example the national mean yield was 10 t ha^{-1} in 1992 despite temperatures being around average. The expected yield, based on the previous model, was 8 t ha^{-1}. In addition, some growers now apply high rates of N fertilizer (>150 kg N ha^{-1}) to crops growing in deep water and achieve yields approaching 14 t ha^{-1}. Such rates were previously unthinkable for either tall varieties or shallow water, because they led to massive sterility in all but the warmest seasons. The advantage of deep water is to cover the developing florets at the microspore stage and so protect them from low night temperatures.

A linked program of experiments and simulation modelling is investigating the interaction of temperature, water depth and N status on rice yield. The model is used to extrapolate the results through time using a long run of historical weather data. The model simulates the yield reductions with high N applications found when rice is grown in shallow water and the occasional catastrophic yield reductions in cool years. However, for rice grown in deep water, the model suggests that long-term mean yields and yield response to applied N are higher than when rice is grown in shallow water. The frequency of catastrophic yield reductions is also reduced for rice grown in deep water, even at high N levels.

The model shows how linked adjustments in management and genotype may offset possible long-term climatic or other environmental change.

INTRODUCTION

The Australian rice industry is concentrated in a semi-arid part of south-eastern Australia in the Murray and Murrumbidgee valleys where it is fully irrigated from the rivers using water stored in dams in the headwaters. The total rice area in recent years has been 100,000 - 120,000 and production has been 750,000 - 1,000,000 tonnes. The region has few pests or diseases, the level of solar radiation is exceptionally high (>28 MJ m^{-2} d^{-1}), mild temperatures (mean summer temperature of 24°C) and hence potential yield is very high The main environmental constraints to yield is low temperature (Angus and Lewin 1991).

Potential yields

In situations when there is no low-temperature damage, for example in the warm, north-east part of the region and in warm seasons, very high yields can be obtained with semi-dwarf varieties, with many commercial crops yielding >12 t ha^{-1}, experimental crops yield >14 t $ha^{-1}$and in 1992, a district average for the variety Amaroo of 10 t ha^{-1}. Although these amounts seem high, larger potentials have been discussed. For example, in the tropics, a region which has normally produced lower yields than the Riverina, Akita (1989) suggested that a yield of 15 t ha^{-1} was possible. Presumably in the environment of the Riverina with high radiation and relatively mild temperatures the potential may be higher than previously considered.

Nitrogen status

The key to obtaining high yields is large applications of N fertilizer, particularly at the time of permanent flooding (PF) (Bacon 1990). Despite this, commercial practice has been split application with only part of the N applied at PF and supplementary N applied at panicle initiation (PI), the latest stage when N is used efficiently for yield. A advisory service supports this is based around a tissue test for N, using near infra red reflectance (Batten *et al.* 1991). The evidence supporting split application is from the research of Heenan and Lewin (1982), Bacon and Heenan (1984) and Bacon (1985) which showed large yield responses to applied N, and no significant difference in yield response for N applied at PF and PI. Other studies by Humphries *et al.* (1987) showed a small yield advantage for N application at PI over application at PF. More recent studies with semi-dwarf varieties grown at high yield levels (Bacon *et al.* 1987) have shown that the response to N applied at PF far exceeds the response at PI.

Cold damage

Low temperatures produce three forms of damage: direct injury to microspores causing pollen sterility, reduced growth and a delay in development. The mechanism of direct injury to microspores has been extensively described but is not fully understood (Satake 1976). The symptoms of this injury are deformed microspores and sterile pollen following a period of cool weather, particularly minimum temperatures below 10-15°C at the stage of microspore formation, which occurs about 12-16 days before anthesis, depending on temperature. The effect of low temperatures on reduced growth appears to be a process common to all plants in which the assimilation process is reduced; however in rice it may also include a component of photoinhibition. The yield reduction associated with delayed development appears to be due to prolonging the period over which low temperatures can affect the other processes.

High N-status is known to greatly increase the severity of cold damage, particularly through its effect on pollen sterility (Heenan 1984). At very high N status, the effect can be so devastating that low temperatures at the microspore stage can lead to total sterility and zero yield. Until recent years the level of applied N on commercial crops has been low because of the risk of loss, particularly on long-grain, tall varieties (Bacon and Heenan 1984).

Large amounts of fertilizer N applied early in development appears to lead to greater cold injury than equivalent amounts applied at PI. Ricegrowers thus face a dilemma of needing to apply large amounts of N at an early stage of crop development in order to achieve high yield potential and efficient use of N, and risking cold damage to crops of high N-status.

The only crop management approach to cold damage is to increase the depth of floodwater at the microspore stage to ~20 cm. It is known that, in low-temperature conditions, crops growing in deep water yield much higher than those in a normal depth of ~5 cm.

Modelling approach

In order to evaluate the benefits and risks, a modelling approach has been commenced. It builds upon the simple model of Angus and Lewin (1990) to forecast yield in relation to temperature. This model operates at a whole-region scale and is based on empirical relationships for the variety Calrose for a period of 25 years over five rice-growing regions, and the variety Inga for two regions over 10 years. Since that model was developed, new varieties have replaced Calrose and Inga. These varieties are semi-dwarf and have been shown to yield 13-15% more than Calrose in field experiments. The higher yields were accurately forecast simply by correcting for this genetic advantage. However, by the early 1990's the district yields appeared to be higher even than predictions made from the linear corrections to the Calrose yield. The likely reason is that a greater proportion of growers are increasing water depth at the time of microspore development, and it is possible that the microspores were covered by water at the stage when cold damage was most likely.

Added to this approach is a more conventional model of rice growth and yield in relation to weather and N status, based on the approach of Angus *et al.* (1990). This model is calibrated to a set of experimental data describing a high-yield crop.

MATERIALS AND METHODS

An experiment with drill-sown crop of the variety Amaroo was conducted at Yanco Agricultural Institute in 1988-89 in order to determine the growth and N relations of a high-yielding crop. Details of the experiment and the plant measurements are reported by Bacon *et al* (1988).

In addition to measuring plants, we made estimates of net ammonification using a modification of the method of Raison *et al.*(1987). The method used was to sample the top 10 cm of soil between the rows of rice plants at the time of each harvest so as to determine the level of ammonium-N in three situations: (1) in the unconfined soil (2) in soil confined by a tube (5 cm diameter, inserted to a depth of 10 cm in the soil) which prevented root uptake of nutrients (3) in another tube in which a slick of paraffin was added to the floodwater to restrict O_2 entry and hence denitrification. By subtracting the mass of ammonium-N in the unconfined soil at one sampling from the mass in the confined soil at the next sampling, it was possible to calculate the rate of net ammonification. Similarly, by subtracting the amount in the confined tube at one sampling from the amount in the +paraffin tube at the subsequent sampling it was possible to estimate losses, presumably denitrification.

RESULTS

Agronomic summary

Detailed results are presented by Bacon *et al* (1989). Fig. 1 shows yield response to applied N. The response to N applied at PF was greater than for the split application which was greater than for the PI application (Fig 1a). The apparent recovery of applied N in the above-ground parts of the crop are shown as the slopes of the lines in Fig 1b. These show that the apparent recovery of the PF application was greater than for the PI application. The yield in relation to N taken up at maturity (Fig. 1c) for six of the seven treatments fall on a single line with a slope of 70 kg grain per kg N. The one aberrant point refers to the PI application of 200 kg N ha^{-1}. Here, it appears that the N taken up was not all utilised in assimilation.

Data on growth and plant-N are shown later along with the simulations.

Ammonification *in-situ*

Fig 2a shows the rate of ammonification of soil receiving no N fertilizer over the life of the crop. The maximum rate was 1.7 kg ha^{-1} d^{-1}. The increased rate in the first part of the season is presumably due to increasing temperatures. The decline later in the season occurred despite a constant temperature and did not appear to be due to any other environmental constraint. It appears that the reaction at least partly followed first-order dynamics, reflecting a depletion of the organic-matter substrate during the course of the season.

The cumulative ammonification shown in Fig 2b reached a total of 150 kg N ha^{-1} during the season, almost double the plant uptake. The cumulative ammonification measured where the floodwater was covered with a slick of paraffin was 160 kg N ha^{-1}, suggesting a loss of only 6%. However the N uptake for the crop which received no N fertilizer was only 80 kg N ha^{-1}. The losses assessed by the *in situ* incubation method are clearly not enough to explain the discrepancy. We speculate that there may have been nitrification/denitrification losses associated with the oxidation of the rhizosphere via the aerenchyma in the roots.

MODEL

Formulation

The approach to simulating rice growth in relation to weather and N is generally similar to the approach used for tropical rice by Angus *et al.* (1990). The derivation of the model is not discussed in detail here but a symbolic description is presented in Table 2, including the system of nine equations used in simulating growth, the three equations used in simulating development and two equations used to simulate soil-N dynamics.

A difference from the previous model is that assimilation is calculated in relation to intercepted radiation, because of access to data on leaf area index (LAI) in this experiment. However, because of the importance of interception by the panicles, particularly after "turning" (the time when panicles droop because of the weight of grain), we included an empirical equation which simulated full interception at the top of the canopy by panicles carrying >600 g m^{-2} of grain, and proportionately less interception with less grain.

Another difference is that soil N dynamics are simulated. One pool of organic N and one pool of mineral N are considered. Ammonification from the organic to the mineral pool is simulated as a function of temperature and the efficiency of recovery of the native soil ammonium is assumed to be the same as for ammonium derived from fertililizer..

Parameter estimation

The approach to modelling here aims for the most simple formulation compatible with describing the mechanisms. The computer program which represents the model contains only about 150 lines of code and 11 parameters. The simple approach enables the values of the few parameters to be estimated by an objective procedure using an optimiser.

The unique advantage of the combination of a simulation model and an optimiser is that unsuitable functional forms and incorrect parameters can be distinguished. The optimiser estimates the parameters which produce the best-fitting model. If that fit is unsatisfactory, the functional forms of the model must be changed. If the fit is satisfactory, it is then necessary to decide whether the parameter values are biologically reasonable. The estimated parameter values are shown in Table 3, along with explanations of the state variables and driving inputs.

Model fit

The model is fitted to the data, first using best-guess parameter values obtained from the literature or from direct observation. After iteration to select the optimal parameter values the optimiser returns the best fit obtainable with the model as formulated. In practical terms the optimiser can fit only five parameters at a time so that the procedure must be repeated with several groups of parameters varied together.

The model was fitted to values of dry matter, grain dry matter, above-ground N, grain N, LAI and ammonification of soil which received no fertilizer N. The diverse attributes were fitted by weighting the values with the inverse of the variance of each.

The summary of the fit is presented in Table 4, the fit of the model to the data for yield and dry matter is in Fig 3, and for all attributes measured for two of the treatments (Fig 4).

APPLICATION OF THE MODEL TO N x COLD-INJURY

As indicated in the Introduction, there are qualitative descriptions of the interaction of N-status and cold injury but no hard data on the processes involved. The following attempt at simulation is based on the best descriptive information available on cold injury and some speculations on the effect of N status. Cold injury leads to floret sterility, primarily becasue of pollination failure. It is most efficient to simulate the process through the number of florets, but since the model in Table 2 does not explicitly simulate floret number, it is expressed as a loss of a proportion of the florets, depending on the timing an duration of damaging temperature.

The timing of the cold-sensitive stages of microspore development and anthesis can be simulated with reasonable accuracy using the development equations in Table 2. Injury in the field has been estimated by Angus and Lewin (1991) from a simple model applied to long term data. This estimate is for a loss of 8 kg grain ha^{-1} for each 1°C of minimum temperature below 20 °C. This estimate however applies to crops of district average yield level and N-status. Presumably florets are sterilised in proportion to the intensity of cold damage, so a proportion of florets equivalent to the yield loss is deleted in the proportion found in the previous study.

The mechanism for the interaction of N-status on cold damage is unknown, so an empirical approach was used. The first attempt was to use the state-variable for the tissue nitrogen status, RNC (Table 2). The interaction of timing and nitrogen status was estimated by scaling the effect in relation to the timing of the microspore stage, as shown in Fig. 5

The combined model was then run with data on radiation and temperature for Griffith from 1954-55 until 1981-82, assuming a crop sown on 15 October, with a starting amount of 40 kg N ha^{-1} of soil ammonium-N, and with various levels of N fertilizer. All other parameters were as for the previous simulation.

The "predicted" outcomes for various years are shown in Fig. 6. These show responses varying from the sort obtained in the experiment reported above, to situations in which N was clearly unprofitable because of cold injury. However the "predictions" show none of the catastrophic losses which are known to occur at high N-status. The suspected reason for the failure of this model is that the state variable RNC does not effectively represent the effect of N-status on cold damage. The values of RNC at the simulated microspore stage showed little variation between high and low-N crops. Examination of measured values of above-ground tissue of high-N and low-N crops confirmed this.

This presents a puzzle of how a crop "senses" its N status at this time. If it is not the N-concentration, what is the attribute that most accurately represents N status? It may be the N-concentration of the growing panicle, but we have no data on which to base a simulation. The only other variable at our disposal is the total mass of N in the above-ground parts of the plant, so we have used the variable, CROPN, as an indicator of N-status. We assume a 0.1% reduction in floret number for each 1°C of minimum temperature below 20°C at the most sensitive stage, for a crop with a reference N-uptake of 5.0 g N m^{-2}, based on the percentage yield reduction (0.1% based on the 8 kg ha^{-1} per cold °C for an 8 t ha^{-1} crop) found in the study by Angus and Lewin (1991), as shown in Fig. 5. The increasing reduction in floret number in relation to N status was simulated with by scaling CROPN relative to the reference level, (CROPN/5.0).

The estimated yields based on this model for weather data at Griffith are shown in Fig 7a. They represent, qualitatively at least, the expected pattern of yield reductions and failures of high-N crops. Another simulation was run with minimum temperatures representing those found in deep water, which is, on average 5°C warmer than air temperature. The results for this simulation, shown in Fig 7b, suggest that deep water leads to consistently higher and more reliable yields than for high-N crops.

DISCUSSION

The present version of the model is not yet sufficiently validated to use in making predictions which are significant for the industry, and experiments are continuing to test the predictions. Based on the preliminary simulations, we are becoming optimistic about the long-term possibility of overcoming the deleterious effects of cold damage at high N status by using a combination of deep water and semi-dwarf varieties. Given the diverse range of systems in which rice is grown in the region, we can envisage two general approaches to managing N and the risk of cold damage:

Scenario 1: Present situation

The current system for applying N is for most to be applied by drill prior to sowing, with a possible supplementary application at PI, depending on measurements made at that time such as shoot density or N%. This system should apply to sensitive or tall varieties, and be attractive to growers who are averse to the risk of cold damage. It may also have a place if for some reason deep water at the microspore stage cannot be provided.

Scenario 2: For well managed semi-dwarfs apply all N early

From the experiment reported here, from several similar experiments with semi-dwarf varieties, and from the results of a simulation, it can be concluded that high and reliable yields can be obtained large amounts of N applied at PF, provided there is deep water at the microspore stage. The optimal strategy for N application should be to identify responsive fields prior to sowing and apply the then apply the optimal amount of N. As Bacon *et al* (1987) concluded there is a need is to refine pre-sowing tests to predict the optimal N application..

A more general conclusion can be drawn from this example. This study showed it was possible to overcome a serious environmental constraint with a suitable combination of management practices. This opportunity arose in this case because existing yields were well below potential. As technology lifts actual yields towards potential, there is less opportunity to overcome the effects of envionmental constraints. In regions where other environmental stresses such as high temperatures limit production or may do so in the future, there may be combinations of management practices which overcome the limitation.

REFERENCES

Akita, S. 1989. Improving yield potential in tropical rice. p41-73 In: Progress in Irrigated Rice Research, IRRI, Los Banos.

Amthor, J.S. 1984. The role of maintenance respiration in plant growth. *Plant Cell Environ.* **7**, 561-569.

Angus, J.F, Sudjadi, M., Fazekas de St.Groth, Nanan Sri Mulyani, Hadiwahyono, Damdam, M. and Wetselar. 1990. Simulating nitrogen response of irrigated rice. *Pl. Soil* **127**, 219-229.

Angus, J.F. and Lewin, L.G. 1991. Forecasting Australian Rice Yields. p1-8 In: Shu Geng and Casey Walsh Cady (Eds.). Climatic Variations and Change: Implications for Agriculture in the Pacific Rim. University of California, Davis.

Bacon, P.E. and Heenan, D.P. 1984. Response of Inga rice to application of nitrogen fertilizer at varying growth stages. *Aust. J. Exp. Agric. Anim. Husb.* **24**, 250-254.

Bacon, P.E. 1985. The effect of nitrogen application time on Calrose rice growth and yield in south-eastern Australia. *Aust. J. Exp. Agric.* **25**, 183-190.

Bacon, Peter, Laing, Graham, Heenan, Damian, McCaffrey, Don, Welsh, Tina, Lacy, John, Batten, Graeme, Fowler, John, Beale, Peter, Mallise, Simon and Dunstan, Penny. 1987. Effect of N topdressing on yield of M7 receiving a range of N rates prior to flooding. p13-20 In: Rice Research 1987. NSW Agriculture and Fisheries.

Batten, G.D., Blakeney, A.B., Glennie-Holmes, M., Henry, R.J., McCaffrey, A.C., Bacon, P.E. and Heenan, D.P. 1991. Rapid determination of shoot nitrogen status in rice using near infra red spectroscopy. *J. Sci. Food Agric.* **54**, 191-197.

Humphries, E., Muirhead, W.A., Melhuish, F.M. and White, R.J.G. 1987. Effects of time of urea application on combine-sown Calrose rice in south-east Australia. I Crop response and N uptake. *Aust. J. Agric. Res.* **38**, 101-112.

Raison, R.J., Connell, M.J. and Khanna, P.K. 1987. Methodology for studying fluxes of soil mineral-N in situ. *Soil Biol Biochem.*, **19**, 521-530.

Satake, Tetsuo. 1976. Determination of the most sensitive stage to sterile-tpe cool injury in rice plants. Research Bulletin No 113, Hokkaido National Agricultural Experiment Station.

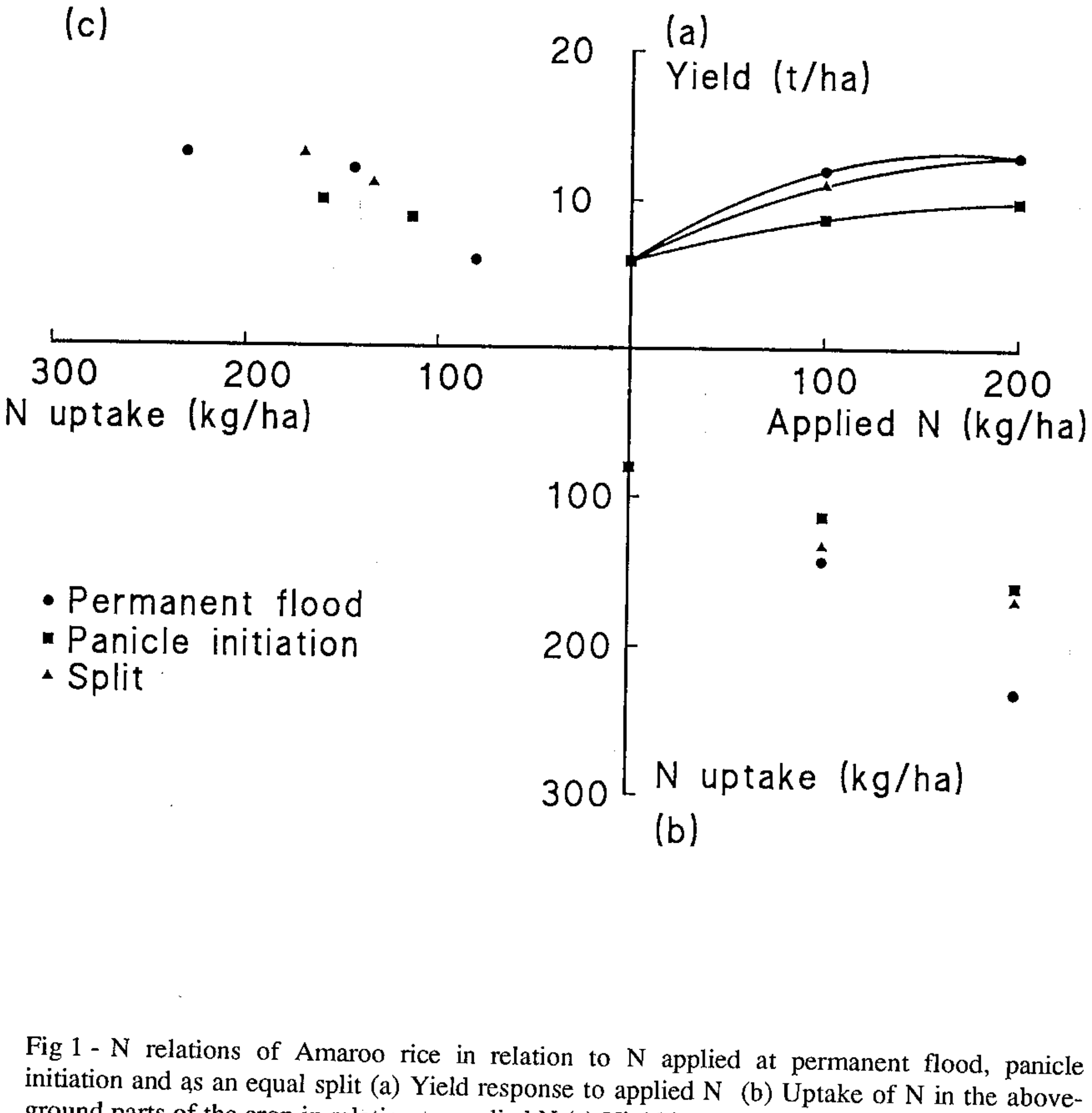

Fig 1 - N relations of Amaroo rice in relation to N applied at permanent flood, panicle initiation and as an equal split (a) Yield response to applied N (b) Uptake of N in the above-ground parts of the crop in relation to applied N (c) Yield in relation to N-uptake.

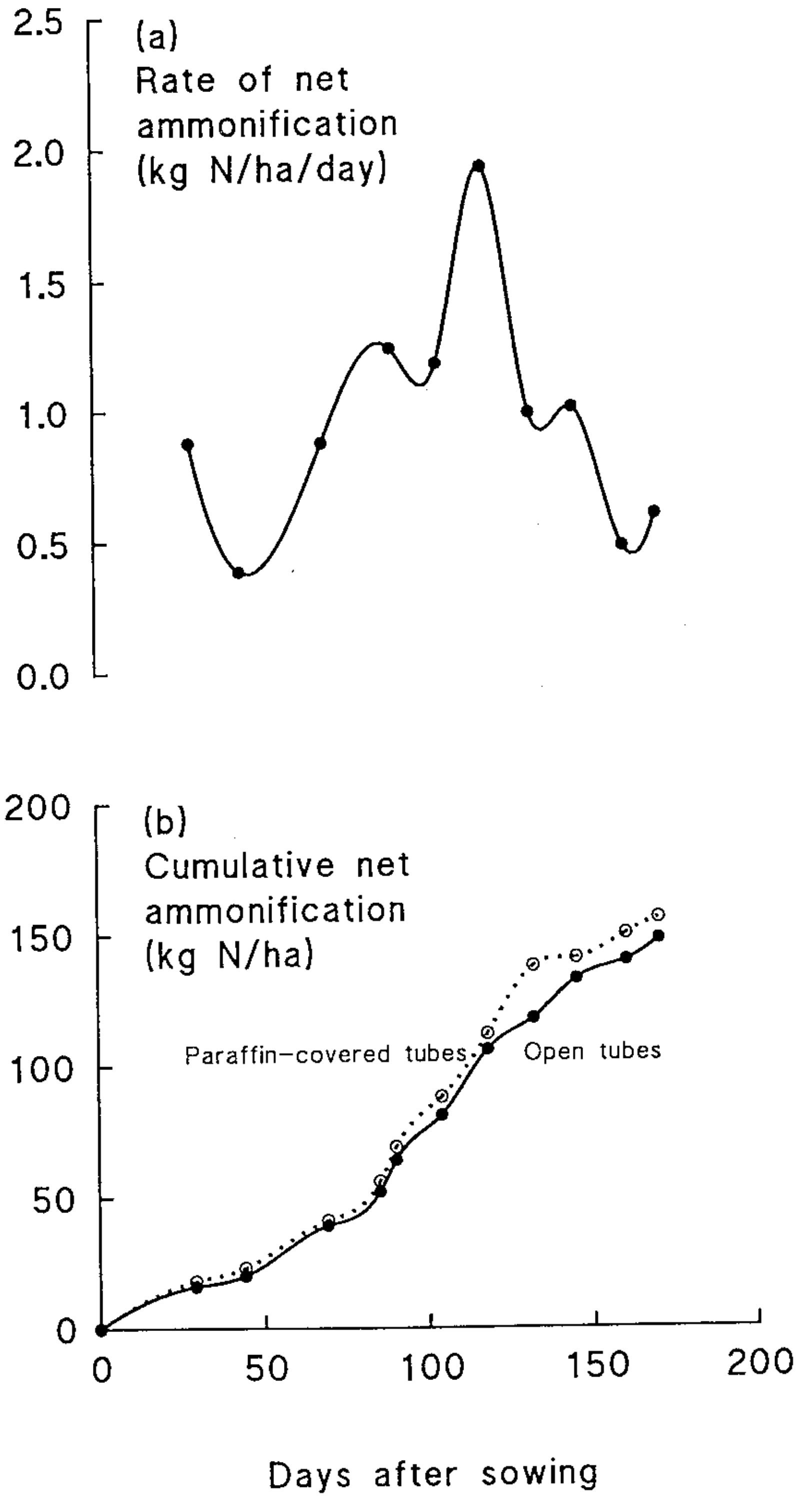

Fig 2 - Soil mineral-N relations of the zero-N treatment (a) the rate of net ammonification as determined by the method of Raison *et al* (1987). (b) Cumulative ammonification for an undisturbed soil and water and for a system in which O_2-access into the floodwater was restricted by means of a paraffin slick.

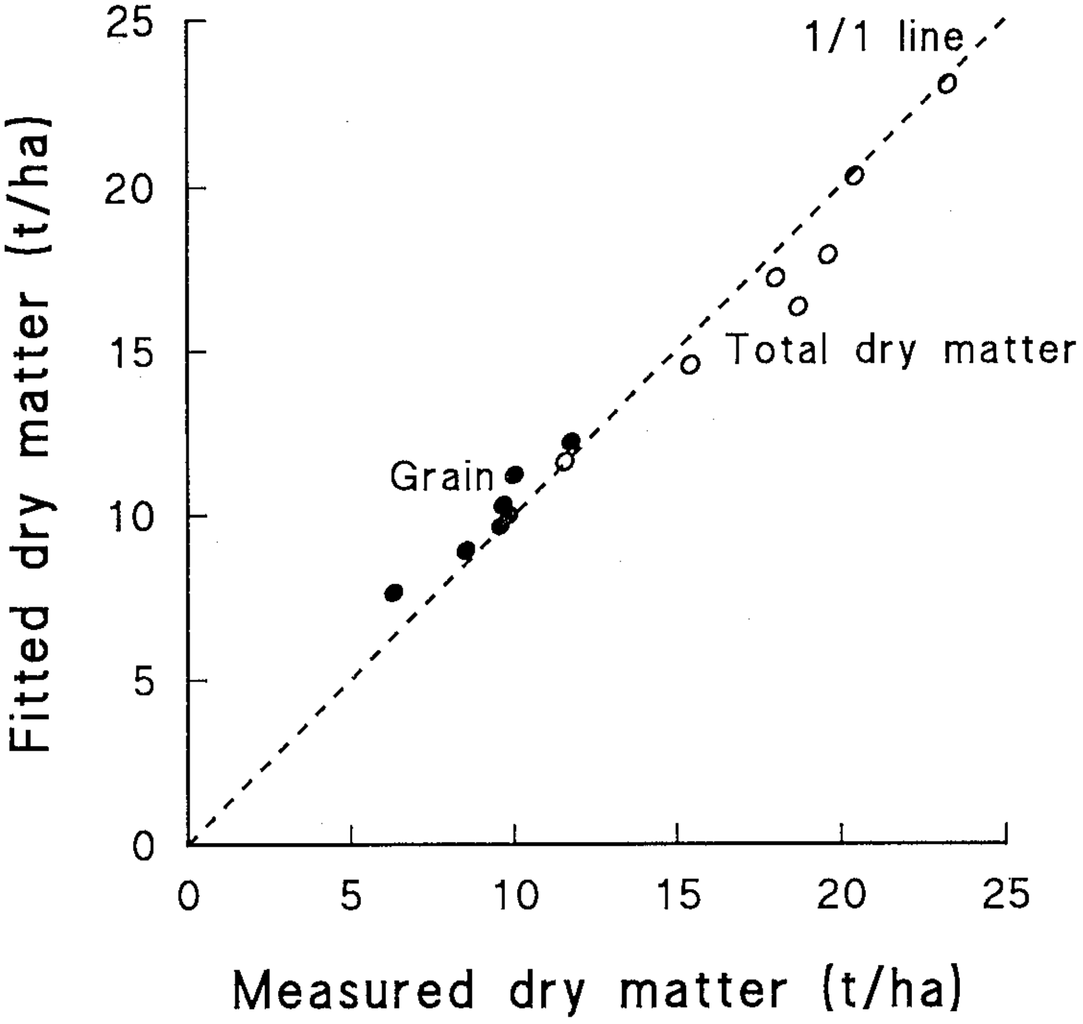

Fig 3 - Fit of the model to yield and final dry matter.

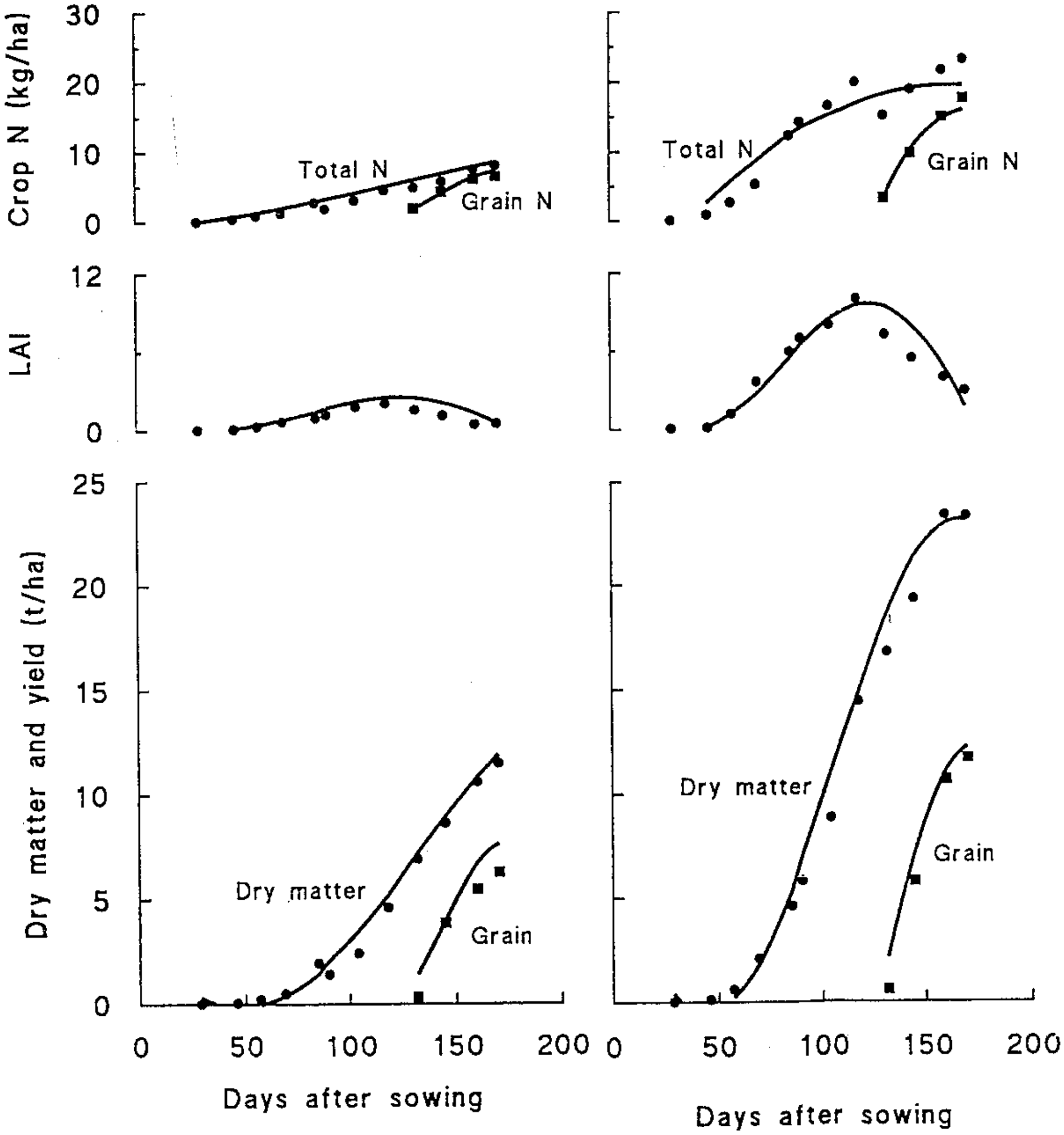

Fig 4 - Fit of the model to growth, grain growth, leaf area index and the uptake of N into the above-ground parts of the plant and to the grain.

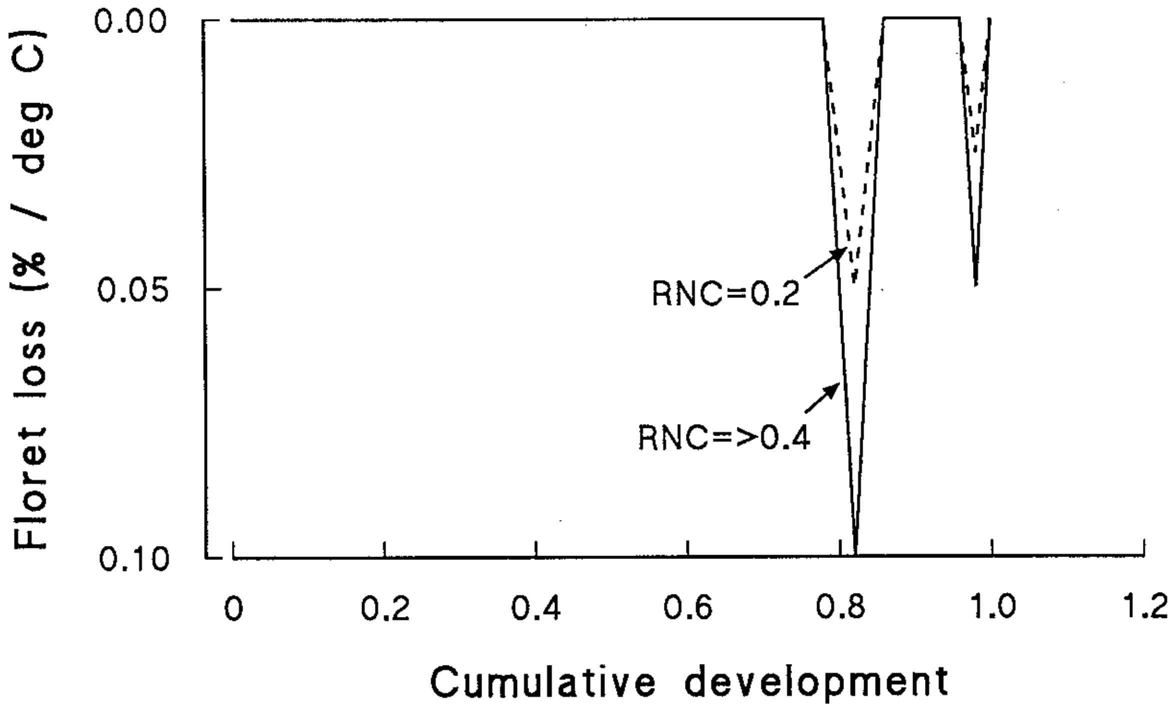

Fig 5 - Loss of florets in relation to Relative Nitrogen Concentration and to the timing and severity of cold injury.

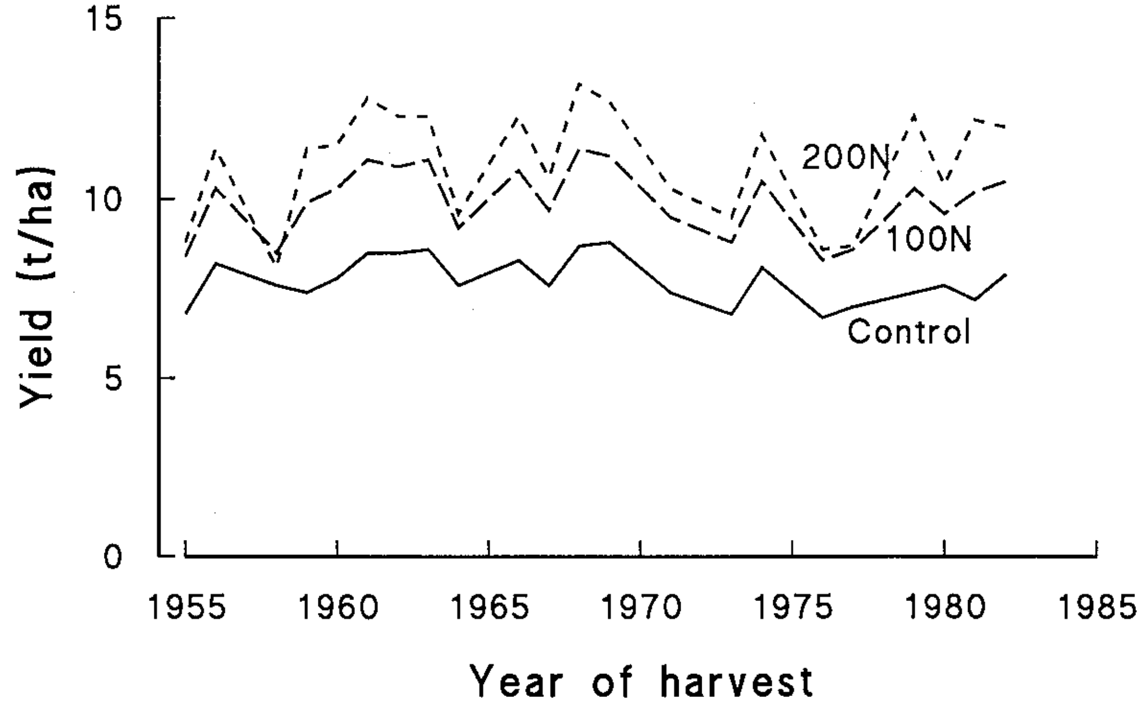

Fig 6 - Simulated N response for 1954-55 to 1980-81, based on daily temperature and radiation at Griffith using the relative nitrogen concentration, RNC as an indicator of N-status.

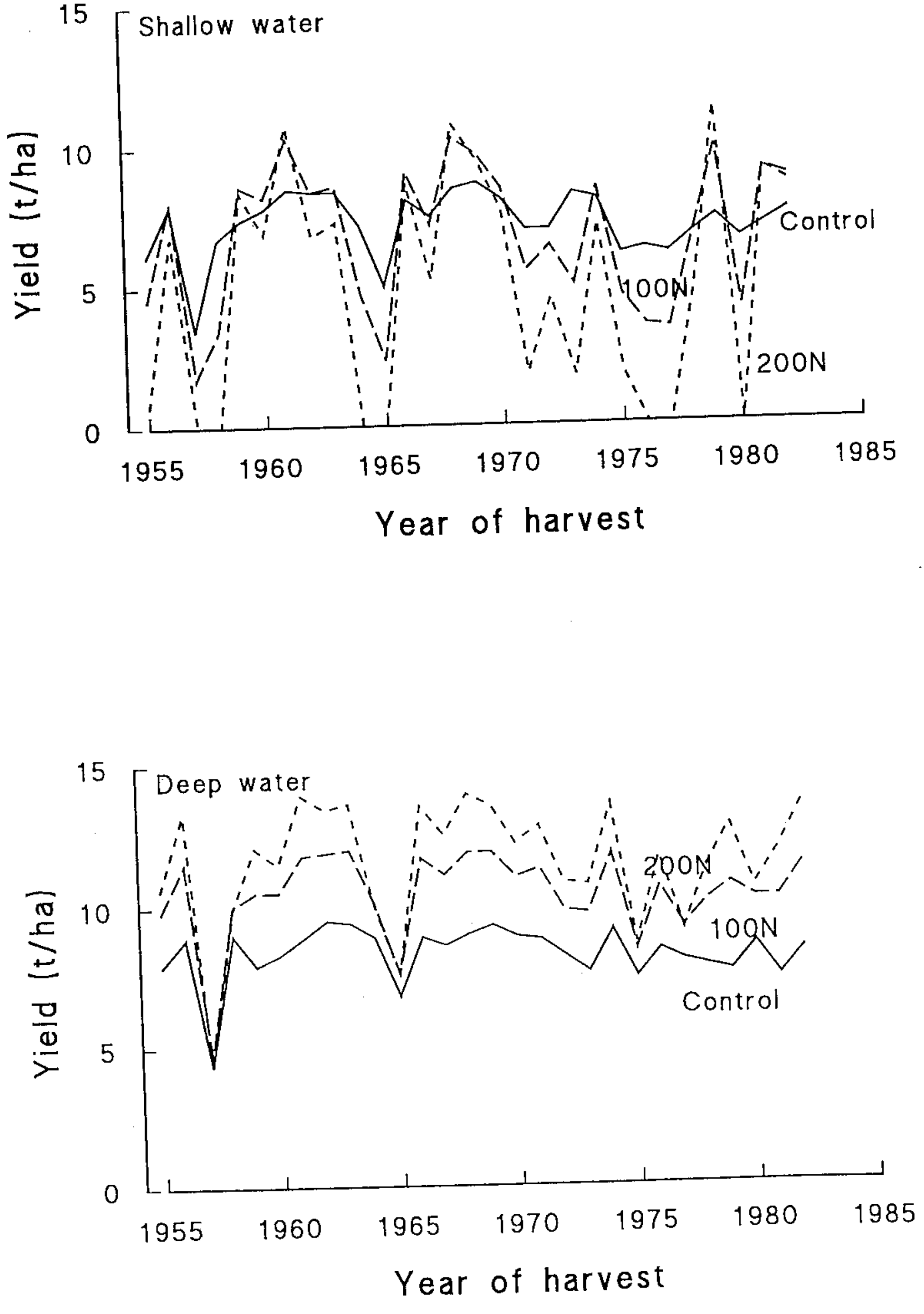

Fig. 7 Simulated N responses for the same environment, using the mass of above-ground N, CROPN, as an indicator of N-status (a) using observed minimum air temperatures (b) using minimum temperatures 5°C above air temparature to represent water temperature.

Table 1. Time and amount of applied N

Treatment	Amount of N (kg ha^{-1}) applied at the stages of: permanent flooding	panicle initiation
1	0	0
2	100	0
3	200	0
4	0	100
5	0	200
6	100	100
7	50	50

Table 2. Model of growth and development of rice in relation to temperature, radiation and N-supply.

Growth		
Dry matter growth	$\Delta W = \varepsilon\, R\, \mathrm{TI}\, \mathrm{NI} - \chi\, Q_{10}\, W$	[1]
Grain growth	$\Delta G = \Delta W + \delta\, \Delta D_g\, W_{anth}$	[2]
Intercepted radiation	$R_P = Q\ (G/600),\ R_P < Q$ $R_I = R_P[1 - \exp(-kL)]$	[3]
Veg. leaf growth Reprod. leaf growth	$\Delta L = \Delta W\, \alpha\, [0.70 - 1.076(D_v - 0.25)]$ $\Delta L = -0.02L\, D_g$	[4]
Temperature index	$\mathrm{TI} = 1/[1 + \exp(-\tau(T - T_{mid})]$	[5]
Temperature effect on respiration	$Q_{10} = 2^{[(T-20)/10]}$	[6]
Nitrogen index	$\mathrm{NI} = [1 - \exp(\eta \mathrm{RNC}]/[1 - \exp\eta]$	[7]
Relative N concentration	$\mathrm{RNC} = [(N-GN)/(W-WG) - N_{min}]/[N_{max} - N_{min}]$	[8]
N-uptake	$\mathrm{NUPT} = \text{minimum} \begin{array}{l} NH4 \\ W[N_{max} - (N-GN)/(W-GW)] \end{array}$	[9]
Development		
Emergence	$\Delta D_e = \alpha_e(T - T_{base})$	
Vegetative	$\Delta D_v = \alpha_v[1 - \exp(-\beta_v(T - T_{base}))]\ [1 + (16-P)/16)]$	
Grain-filling	$\Delta D_g = \alpha_g[1 - \exp(-\beta_g(T - T_{base}))]$	
Soil N		
Net ammonification	$\mathrm{MIN} = \o\ (T - 5)$ $\mathrm{MIN}_{lab} = \o_{lab}\ \mathrm{TI}\ N_{lab}$	
Mineral-N balance	$NH4_i = NH4_{i-1} + \phi(\mathrm{MIN} + \mathrm{FERT}) - \mathrm{NUPT}$	

Table 3. Growth parameters

Symbol	Description	Value	Units	Source
ε	Radiation-use efficiency	3.4	g MJ^{-1}	Optimiser
χ	Maintainance respiration	0.005	g g^{-1}	Amthor (1984)
k	Light extinction co-eff.	0.5	d'less	Fixed
σ	Specific leaf weight	0.018	m^{-2} g^{-1}	Optimiser
η	N-response curvature	3.5	d'less	Optimiser
δ	Translocation reserves	0.41	g g^{-1}	Optimiser
τ	Curvature of temp sigmoid	0.79	d'less	Fixed
T_{mid}	Temp. for half max growth	16	°C	Fixed
Φ_{PF}	Efficiency of N recovery	0.57	g g^{-1}	Optimiser
$\o$	Ammonification	0.064	kgN ha^{-1} d^{-1} TI^{-1}	Optimiser

Development parameters

Symbol	Description	Value	Units	Source
α_e	Sowing-emergence development	0.02	d^{-1}	Fixed
α_v	Emergence-anthesis development	0.0015	d^{-1}	Fixed
α_g	Anthesis-maturity development	0.0026	d^{-1}	Fixed
T_{base}	Threshold temp. for development	15	°C	Fixed

State variables

Symbol	Meaning	Units
W	Crop biomass	g m^{-2}
G	Grain biomass	g m^{-2}
N	Crop nitrogen	g m^{-2}
GN	Grain nitrogen	g m^{-2}
TI	Temperature index	dimensionless
NI	Nitrogen index	dimensionless
RNC	Relative nitrogen concentration	dimensionless
N_{max}	Maximum nitrogen concentration	g g^{-1}
N_{min}	Minimum nitrogen concentration	g g^{-1}
W_{anth}	Cop biomass at anthesis	g m^{-2}
R_I	Intercepted radiation	MJ m^{-2} d^{-1}
R_P	Radiation beneath the panicle	MJ m^{-2} d^{-1}
L	Leaf area index	m^2 m^{-2}
S	Specific leaf weight	m^{-2} g^{-1}
NH4	Soil ammonium-N	g m^{-2}
MIN	Rate of ammonifiaction	g m^{-2} d^{-1}

Driving inputs

Symbol	Meaning	Units
Q	Intercepted radiation	MJ m^{-2} d^{-1}
T	Daily mean air temperature	°C
P	Daily photoperiod	h
FERT	Applied N fertilizer	g N m^{-2}

Table 4. Root mean square (RMS) error for calculated attributes.

Attribute	Number of observations	*RMS	units
Dry matter	64	1.3	$t\ ha^{-1}$
Grain dry matter	28	1.0	$t\ ha^{-1}$
Above-ground N	64	1.7	$g\ m^{-2}$
Grain N	28	1.2	$g\ m^{-2}$
LAI	64	0.8	$m^2\ m^{-2}$
Cumulative soil mineral N	12	0.8	$g\ m^{-2}$

*RMS = $(1/n)\ \Sigma_i(\text{Observed}_i - \text{Calculated}_i)^2$