

SARP Research Proceedings

Towards integration of simulation models in rice research

Selected papers presented at workshops on crop simulation of SARP network in 1995

**P.K. Aggarwal, F.P. Lansigan, T.M. Thiyagarajan & E.G. Rubia
(Editors)**

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Preface

Process-based crop simulation models together with other tools of systems research such as optimisation techniques, databases, and geographical information systems have provided us an opportunity to accelerate the use of interdisciplinary knowledge in agricultural planning and development. The Simulation and Systems Analysis in Rice Production (SARP) project involving the cooperation of almost 100 scientists in eight Asian national agricultural research systems, the Research Institute for Agrobiology and Soil Fertility, Wageningen, the Department of Theoretical Production Ecology, Wageningen Agricultural University, Wageningen, and the International Rice Research Institute has developed the capacity in systems analysis and crop simulation in Asian national agricultural research systems. Since the last few years, the project transformed into a collaborative research network focusing on applications of crop models for increasing the efficiency of crop breeding programmes, assessing the impact of climate change, optimising resource use in cropping systems, determining agroecological zones, and developing practices for integrated pest management. In the final year of the project, several workshops were organised to review the results achieved in the various application programmes. This book together with a special issue of the *Field Crops Research* journal documents the proceedings of these workshops.

The papers presented in this issue of the proceedings are grouped into categories by application programmes. The first section includes two papers on the use of simulation models in evaluating soil erosion risk in cropping systems and in the analysis of yield gaps. Another paper proposes an alternative method of conducting sensitivity analysis with simulation models.

The second section documents results of case studies for using crop models in plant type design for specific environments varying in nitrogen availability, drought and pest incidence, and for greater weed competitiveness. In addition, a framework on the possible use of systems approaches in increasing the efficiency of multi-environment trials and limitations in applications due to genotype by environment interactions on inputs of crop models are also described.

The next section deals with applications relating to use of models in optimising the N fertiliser applications. The various papers present results of experiments conducted in the People's Republic of China and India to compare nitrogen recommendations generated by the ORYZA_0 model with the local practices.

The last section describes the applications of simulation models in understanding host-pest interactions with an aim to develop integrated pest management strategies.

The editors wish to thank Perlita Villamayor, Anaida Ferrer, Cecilia Lopez and Benjamin Nuñez, Jr., SARP staff at IRRI, for their excellent support in organising the workshops and helping the participants in the simulation analyses and typing of papers.

Los Baños, Wageningen
January 1996

The Editors

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Simulation of soil erosion in rice-based cropping systems in sloping uplands

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Abstract

There is a high risk of massive soil erosion associated with upland rice cultivation in sloping fields that could rapidly deplete soil fertility and threaten the environment particularly in the humid tropics. To understand and predict soil erosion under sloping upland rice-based cropping system, a water balance subroutine called UPSWAT (Upland Soil Water Balance) and a soil erosion module were incorporated into ORYZA_W rice growth model. The modified ORYZA_W model simulated rice growth efficiently under upland soil conditions. Surface cover, which is a strong determinant of soil loss, was found to be highly correlated with weight of the aboveground dry matter which is an output variable of ORYZA_W and is an essential input to the soil erosion model. The modified ORYZA_W also gave a highly acceptable prediction of soil moisture content, runoff and soil loss. The model can be used to evaluate and design upland rice-based cropping systems that are environment-friendly and acceptable to upland farmers.

Introduction

Nearly a sixth of the world's riceland is planted to upland rice. In Indonesia, Bangladesh and the Philippines, about 20% of the total ricelands are grown to this system of rice culture (De Datta, 1975). Upland rice is commonly cultivated on a sloping field that is not banded. Land is prepared and seeded during the start of the rainy season and the crop depends entirely on rainfall and on what is stored in the soil for its water needs. Its cultivation is therefore limited to areas with abundant and well-distributed rainfall during the growing season.

Unlike in lowland rice where a large amount of water can be impounded during heavy rainfall, favourable soil moisture regime in sloping uplands is determined closely by the amount and distribution of daily rainfall. Soil water availability throughout the growing season could be the most important constraint to optimum rice production in rainfed uplands. Even in the humid tropics where annual rainfall is usually beyond 1500 mm, moisture stress can occasionally happen during drought periods between rains. A better understanding of soil moisture regime in sloping uplands is crucial to attaining the optimum upland rice production.

Another important constraint associated with upland rice cultivation on sloping land is too much rainfall during the wet season cropping that leads to high runoff and intense soil erosion. In the humid region in Asia, the physical environment is highly favourable to massive soil erosion particularly in cultivated sloping lands. In the Philippines, annual erosion rates were more than 100 t ha⁻¹ in several field sites conducted in the Southern Tagalog Region (Paningbatan, 1994). This is excessively more than the tolerable soil loss of less than 10 t ha⁻¹ yr⁻¹. Using the Universal Soil Loss Equation (USLE), El-Swaify (1993) reported that potential soil erosion in an Alfisol in Indonesia was 1840 t ha⁻¹ yr⁻¹ while it was 1625 t ha⁻¹ yr⁻¹ in an Andisol in the Philippines. These high values were primarily attributed to the very high rainfall erosivities in the region. Without effective soil conservation measures, there is the high risk of massive soil erosion that could rapidly deplete soil fertility and threaten the environment.

There is a need for a precise water balance subroutine for sloping upland conditions to predict soil moisture availability and other components of water balance like runoff, infiltration, drainage, capillary rise, surface evaporation and transpiration. Besides improving our capability to simulate growth and yield of upland rice, it will allow us to quantitatively predict soil erosion under various land management schemes. Also, this will help in designing appropriate soil conservation measures for sloping farmlands. This paper describes an alternate soil water balance and soil erosion subroutines suitable for upland rice-based cropping system in sloping lands.

Simulation model

The ORYZA_W model (Bouman et al., 1994) can simulate growth and development of rice crop under water-limited field condition. It uses SAHEL (Soils in semi-Arid Habitats that Easily Leach; van Keulen, 1975), a water balance module which is suitable for nonpuddled, freely draining, sandy and loamy upland soils with a deep groundwater table (Penning de Vries et al., 1989). This type of soil permits fast downward water movement when wet so that saturation of the soil surface layer does not occur. When used in clayey soils with impeded drainage, SAHEL poorly predicts soil moisture. Also, it does not simulate runoff and as such, cannot be used to predict soil erosion that considers runoff.

Hydrology and soil moisture prediction

As an alternative to SAHEL, a water balance module for ORYZA_W called UPSWAT (Upland Soil WATER balance) subroutine was developed. UPSWAT can be used to predict soil moisture regime for a wider range of upland soils. Precise prediction of runoff and infiltration was given emphasis in the new water balance module so that soil erosion could likewise be simulated and predicted. Fig. 1 illustrates the vertical soil

profile and the different water fluxes used in UPSWAT that determine the water balance. Volumetric moisture content of each soil layer is predicted using the mass balance equation (Eqn 1).

$$\frac{\Delta\theta}{\Delta t} = -\frac{\Delta F}{\Delta Z} - U(z,t) \quad (1)$$

where θ is volumetric soil moisture content (mm mm^{-1}), F is flux (vertical) of water (mm h^{-1}), Z is vertical distance (mm), U is a sink term representing water lost per unit time transpiration ($\text{mm mm}^{-1} \text{ h}^{-1}$) and t is time (h).

The flux (see Fig. 1) of infiltration (I) is determined by the antecedent moisture of the soil surface layer and the given rainfall rate (P). Runoff flux (R) is calculated using a simple hydrology equation $R = P - I$. The vertical redistribution flux (F_{Re}) at the boundary of two soil layers is calculated using Darcy's equation (Eqn 2) in which the moisture-dependent hydraulic conductivity $K(\theta)$ and matric potential $\Psi(\theta)$ of each soil layer are inputs in the calculation. Drainage is set to be highly dependent on saturated hydraulic conductivity of the bottom layer while capillary rise is considered negligible.

$$F = -K(\theta) \frac{\Delta[\Psi + Z]}{\Delta Z} \quad (2)$$

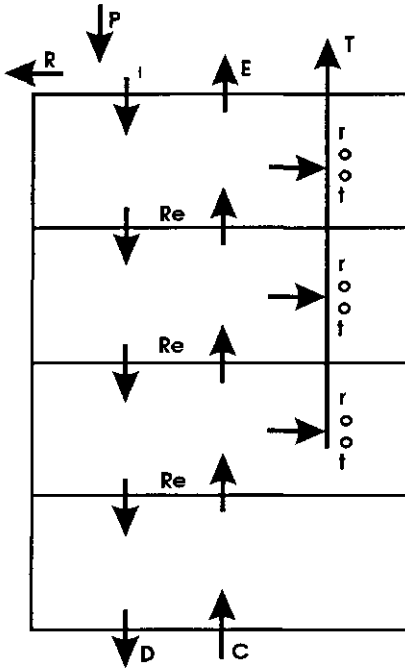


Figure 1. Vertical soil profile and fluxes of water in the UPSWAT (Upland Soil Water balance) subroutine for upland rice soils (P = precipitation, R = runoff, I = infiltration, Re = redistribution, D = drainage, C = capillary rise, E = surface evaporation, T = transpiration).

Soil loss prediction

A subroutine to predict soil erosion was incorporated to the current ORYZA_W. The theory of Rose (1985) provides the quantitative description of the subprocesses of erosion, such as rainfall detachment (r_i), entrainment (e_i), and deposition (d_i) occurring during an erosive rainfall event as illustrated in Fig. 2. The net sediment flux contribution of the subprocesses determines the average sediment concentration during a runoff producing rainfall event. Erosion is then calculated as the cross product of sediment concentration and runoff as presented in the simplified Eqn 3 derived by Rose (1985).

$$E = 2700S(1.0 - \text{cover})\lambda \frac{Q}{100} \quad (3)$$

where E is soil loss event (t ha^{-1}), S is sine of the slope angle, cover is fractional surface cover, λ is a factor approximating efficiency of entrainment, and Q is the amount of runoff.

Eqn 3 was successfully used by Littleboy et al. (1993) in their model PERFECT (Productivity Erosion Runoff Functions to Evaluate Conservation Techniques) wherein amount of erosion is estimated.

In the erosion model, the fractional surface cover (parameter cover in Eqn 3) is a strong determinant of soil loss (Paningbatan, 1994). It is not commonly measured in the field but is expected to be closely related to leaf area index (LAI) or the weight of the aboveground (WAG) parts and, hence, could be generated using crop growth simulation

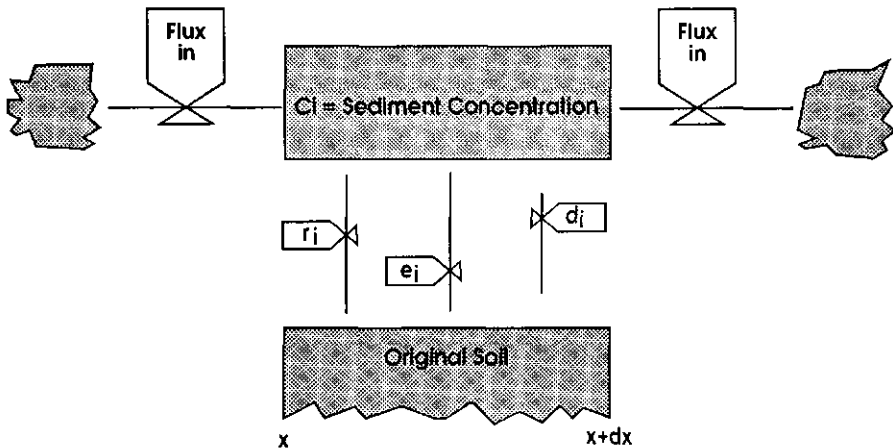


Figure 2. The subprocesses of soil erosion that determine sediment concentration (r_i = rate of rainfall detachment, e_i = rate of entrainment, d_i = rate of deposition) (Based on the theory of Rose, 1985).

model ORYZA_W. The functional relationship between LAI or WAG and surface cover is therefore needed to run erosion Eqn 3. The efficiency of entrainment is related to soil strength and the roughness of the soil surface, a soil erodibility parameter. It is best evaluated in the field using bare erosion plot data of soil loss and runoff.

The amount of soil loss calculated using Eqn 3 is also highly dependent on the amount of runoff. This could be generated by ORYZA_W with UPSWAT as the water balance subroutine.

Model validation

The simulation model was validated using data from erosion plots in a field experiment conducted at the Central Experiment Station of the University of the Philippines Los Baños (UPLB) located in Bay, Laguna, Philippines. The soil is Lipa clay loam, a Tropudalf, with field slope from 19 to 25%. Each erosion plot has 6 m width and 12 m slope length. Soil loss and runoff measuring devices (erosion trough, tipping bucket, event counter, magnetic switches, sediment sampling tubes) were connected at the lower end of each erosion plot. Mechanical counter and data loggers were installed to record runoff and rainfall. Rice was planted in the erosion plots on 13 Aug 1995. Measurements were made from July to November 1995.

To validate ORYZA_W and UPSWAT as the water balance module, soil moisture content was measured weekly at 0-20 cm and 20-50 cm soil depths. Biomass production of the rice was monitored periodically. Canopy and surface contact cover were estimated using a quadrant technique.

Results and discussion

There was good agreement between simulated and observed weight of the total aboveground dry matter (WAG) as presented in Fig. 3. The slight overestimation of WAG by ORYZA_W was attributed to slight N stress. ORYZA_W simulates rice growth under sufficient N. Rice was fertilised with a total of 90 kg N ha⁻¹ split three times but there were occasions when high amounts of erosion and runoff may have washed out the N fertiliser applied.

The measured surface cover, expressed in percent (%), was highly correlated to the observed and predicted WAG as shown in Fig. 4. It was also highly correlated to simulated LAI. The regression equation was $Y = 3.0 + 4.8 X$, where Y is the surface cover in % while X is the WAG in t ha⁻¹. It is a necessary equation in the erosion subroutine. The intercept may be adjusted depending on the initial surface cover condition of the soil. For example, if a crop residue is applied as mulch, the intercept

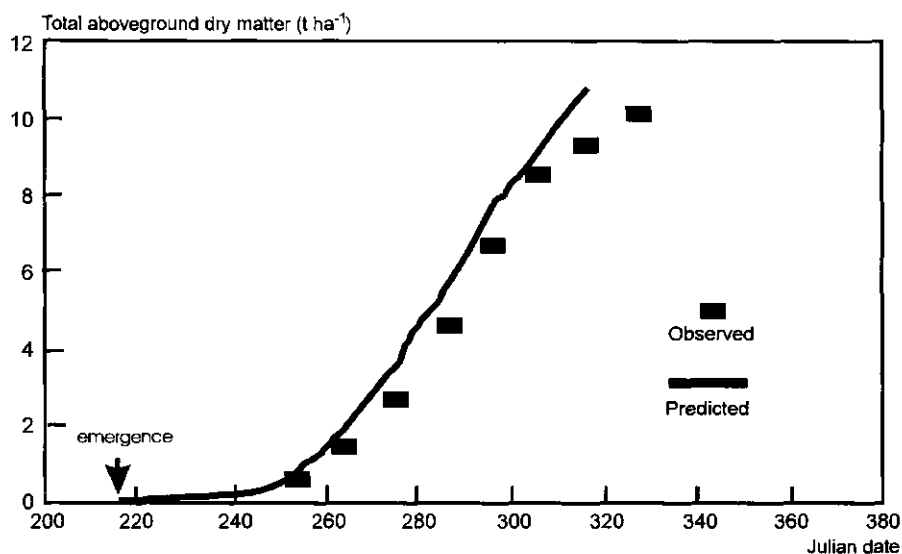


Figure 3. Predicted and observed weight of aboveground dry matter of rice (upland), UPLB, 1995 wet season.

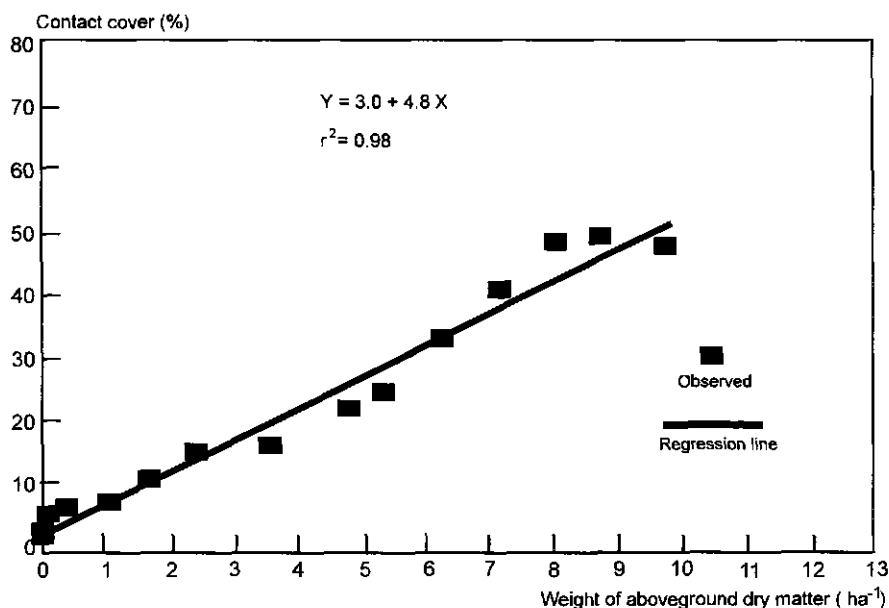


Figure 4. Contact cover as a function of aboveground dry matter of upland rice.

should be increased proportionately to the amount of mulch cover. Mulching is a soil conservation practice that could lead to a considerable reduction of soil erosion particularly if done during the crop establishment phase when the soil is highly vulnerable to the impact of runoff and erosion. The 4.8% slope of the line implies a considerable protection effect of crop vegetation against soil erosion particularly toward maturity when the amount of WAG is already high. This explained the observed small amount of soil loss (13 t ha^{-1}) in Julian date 173 in spite of a very heavy rainfall of 212 mm that generated runoff of 159 mm in 1 d (Fig. 5).

The good agreement between observed and simulated soil moisture content (Fig. 6) and runoff (Fig. 7) implies that the water balance subroutine UPSWAT is compatible with ORYZA_W. The modified simulation model is useful for upland rice-based cropping system. Besides soil moisture and runoff, it is also expected that the improved model will also give good prediction of the other water balance parameters for a wide variety of upland soils provided that the input data, namely, moisture-dependent hydraulic conductivity $K(\theta)$ and matric potential $\Psi(\theta)$ for each soil layer are available. Data base of these two hydraulic parameters and validation of UPSWAT for other soil types, however, is still necessary. The prediction of daily soil loss by the model was highly acceptable as shown in Fig. 8. It is important to mention, however, that the validation was done for an upland rice cultivation without any soil conservation measure. There is still a need for more model validation, calibration and further improvement for situations where soil conservation is practised.

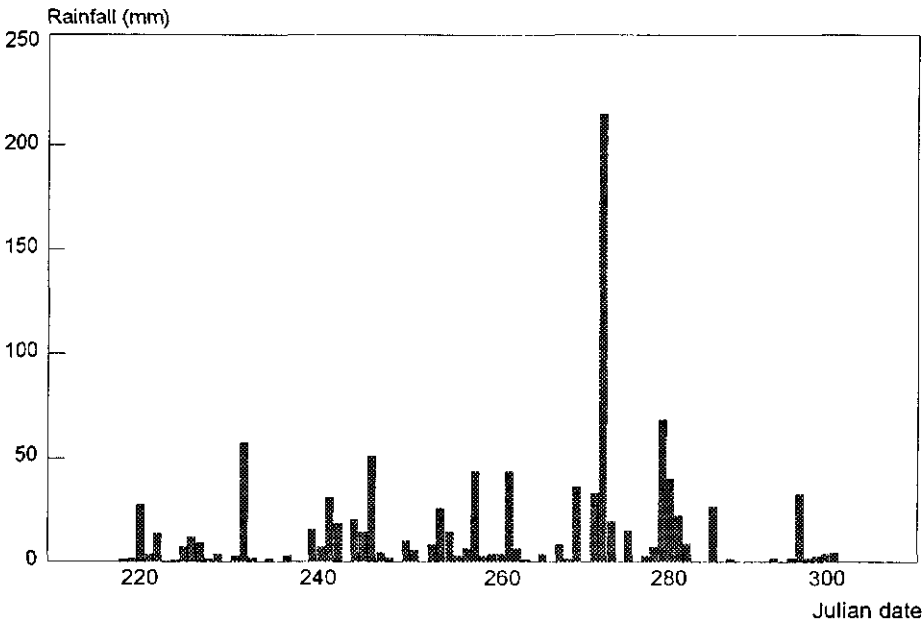


Figure 5. Amount of daily rainfall, 1995 wet season.

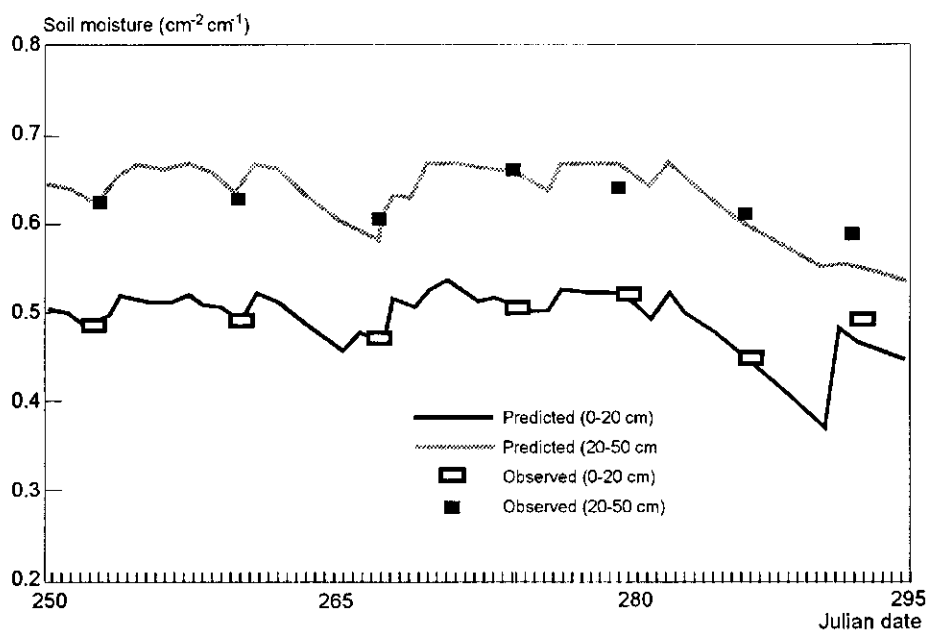


Figure 6. Observed and predicted soil moisture content at different soil depths (0-20 cm) and (20-50 cm).

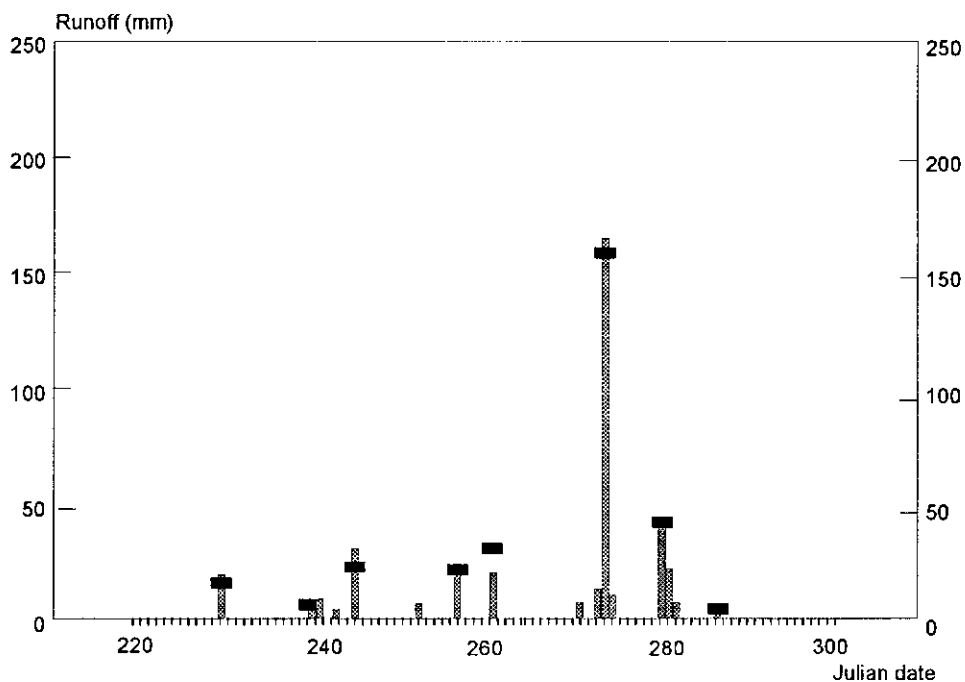


Figure 7. Observed (■) and predicted (▨) runoff.

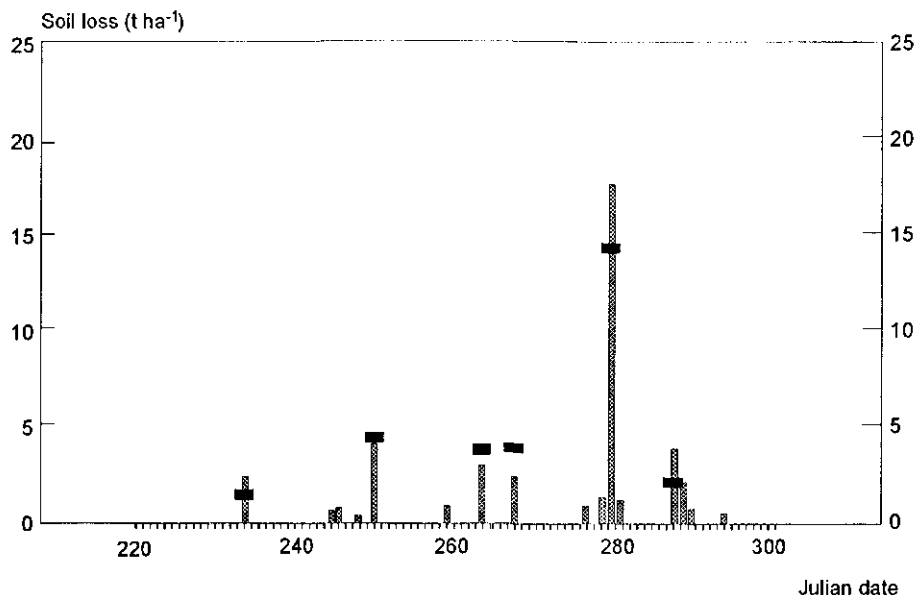


Figure 8. Observed (■) and predicted (bar) soil loss.

Concluding remarks

The new soil water balance module UPSWAT developed and incorporated in the ORYZA_W crop growth model enables the estimation of runoff and soil loss in rice-based cropping systems in sloping lands. The modified ORYZA_W model with a water balance module suitable for sloping uplands will facilitate the evaluation of soil erosion risk of rice-based cropping strategies in sloping uplands. The model can be used to design appropriate soil conservation strategies that can minimise soil erosion.

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Yield gaps in selected rice-producing areas in the Philippines

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Abstract

Analysis of yield gaps in selected rice-producing provinces in the Philippines was conducted with the use of a crop simulation model which provided estimates of potential and attainable yields. Simulated rice yields were compared with reported productivity statistics for each of the locations. Yield gaps based on potential yields in these areas vary from 5.6 to 8.2 t ha⁻¹ during the dry season and from 4.0 to 5.7 t ha⁻¹ during the wet season. Attainable yields estimated in these locations at the present level of fertiliser applications are lower than potential yields. The magnitude of yield gaps in these areas justifies the need to address the factors that limit and reduce rice yield to meet the increasing demand for the staple food.

Introduction

Rice production in the Philippines has increased tremendously from 5.3 million t in 1970 to 9.1 million t in 1992. The increase in rice production is attributed mainly to the increase in productivity from 1.71 t ha⁻¹ in 1970 to 2.85 t ha⁻¹ in 1992 (Fig. 1). Area planted to rice has remained relatively stable at around 3.1 million ha. Productive rice areas near urban centers are continuously being put to pressure by expanding industrial sites, residential complexes, increasing population and natural disasters such as lahar and earthquakes. The great pressure due to increasing population demands increasing rice production which can only be achieved by increasing productivity per unit area.

Crop growth and development are affected by several biotic and abiotic factors such as radiation, temperature (yield determinants), water and nutrients (yield limiters) and pest and diseases (yield reducers) (Rabbinge 1993). Moreover, yield is also determined by many factors such as varietal characteristics and cultural management practices. Yield gap analysis can be facilitated when different levels of crop production are distinguished

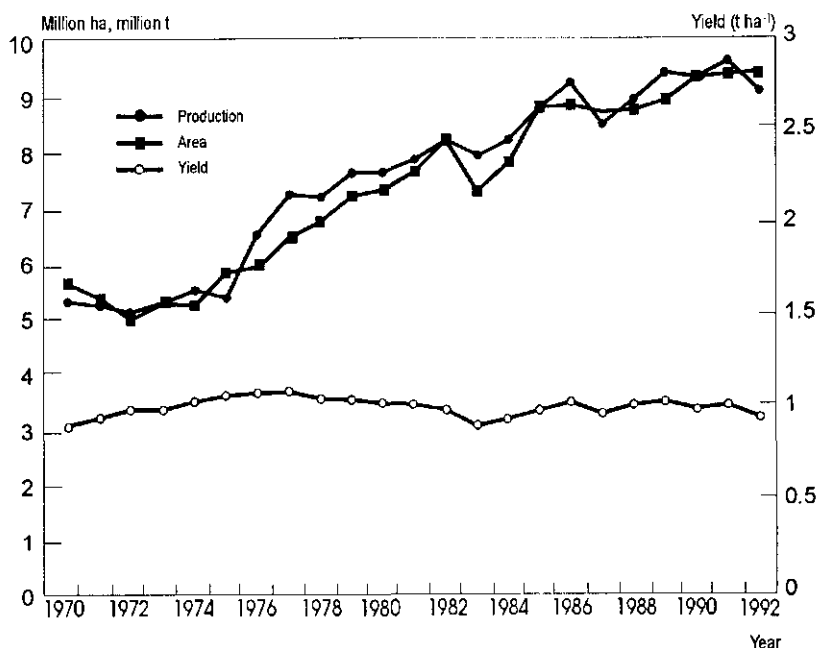


Figure 1. Area, production and productivity of rice in the Philippines, 1970-92 (PhilRice-BAS, 1994).

(Penning de Vries et al., 1989), allowing for the quantification of yields at optimum, water-limited, and N-limited conditions. Potential or theoretical rice yield is the productivity level determined solely by radiation and temperature in a given agroenvironment. This can be estimated using a crop growth simulation model that requires temperature and solar radiation data as well as crop/variety data as inputs. Attainable yield is the yield obtained under present management level.

Yield gap may be used as a criterion for quantitative land evaluation. This is useful in delineating hot spots or areas where research activities and extension support services to reduce yield losses can be concentrated or focused. Geographic information systems-generated maps of yield gaps and associated probabilities of occurrence and risks can be used in making recommendations by extension workers as well as development institutions (e.g., crop insurance companies) to determine the recommended production strategy with minimum risks (economic risk and environmental risk).

This paper presents the use of crop simulation modeling in the analysis of the productivity levels of selected rice-producing areas in the Philippines and the characterisation of these areas in terms of yield gaps.

Materials and methods

Selected rice-producing areas

The areas selected for the study are the major rice-producing provinces in the Philippines—Cagayan, Nueva Ecija, Tarlac and Laguna (Table 1). An important criterion in the selection of these provinces is the availability of necessary agrometeorological data for crop simulation such as maximum and minimum temperature, solar radiation, rainfall, vapor pressure and windspeed. Other major rice-producing provinces were excluded because the weather stations in these areas collect only rainfall and temperature data which are inadequate for quantitative evaluation of yield potentials using crop growth simulation model. Table 1 also shows the coordinates of the weather stations used including the relevant information on the weather data sets available.

Time series of reported rice yields from 1970 to 1993 in these areas were obtained from PhilRice-BAS (1994, 1995). Data on yields reported for each selected area were compared with the simulated yields to determine yield gaps. The actual yields already included the aggregated effects of all yield-limiting and yield-reducing factors.

Crop simulation model

The modified rice crop model (Aggarwal et al., 1996) based on ORYZA1 model (Kropff et al., 1994) is utilised to simulate attainable yield under the farmers' practice of N application and management. The crop simulation model has been calibrated and validated for different rice varieties and environmental conditions (Kropff et al., 1994). The model requires daily values of weather variables as input data. The model has also been calibrated and validated under the agroenvironmental conditions in the selected

Table 1. Locations and available weather data^a for the selected rice-producing areas in the Philippines.

Province	Weather station	Coordinates	Years available
Cagayan	Solana	17° 39' N 121° 41' E	14
Tarlac	Hacienda Luisita	15° 26' N 120° 36' E	14
Nueva Ecija	CLSU	15° 43' N 120° 54' E	17
Laguna	UPLB	14° 10' N 121° 41' E	35

^aWeather data in FSE format available at the IRRI Climate Unit.

rice-producing areas. Standard crop parameters for IR72 variety were used in the simulation.

The weather data in Fortran Simulation Environment (FSE) format (Kraalingen et al., 1990) used in the crop simulation were obtained from the IRRI Climate Unit. Maximum temperature in the selected locations varies from 26 °C to 34 °C while minimum temperature ranges from 19 °C to 25 °C in these areas. Solar radiation varies from 12 to 22 MJ m⁻² d⁻¹.

Results and discussion

Current rice productivity

Table 2 shows the reported rice area, rice production level and productivity statistics as well as fertiliser use in the selected major rice-producing areas in the Philippines. The province of Nueva Ecija has 80,000 ha planted to rice which contributes about 389,000 t of rice annually. Average farm productivity in this province is about 4.9 t ha⁻¹. It has the highest total fertiliser usage compared with other provinces. Almost all of the rice areas in these provinces are irrigated, and relative to other areas, average fertiliser application is also higher. Productivity in the other selected provinces ranges from 2.6 t ha⁻¹ (Cagayan) to 4.1 t ha⁻¹ (Laguna), relatively higher than in other areas.

Potential yields and yield gaps

Table 3 shows the average potential rice yields estimated for both dry season (DS) and wet season (WS) in selected provinces. The simulated potential yields for the location were assumed as the potential yields for the province. The average simulated potential grain yields varied between 9.4 t ha⁻¹ (in Laguna) and 10.5 t ha⁻¹ (in Tarlac) during DS and from 6.9 (in Laguna) to 8.8 t ha⁻¹ (Cagayan) during WS. Actual DS yields ranged from 2.4 t ha⁻¹ (in Tarlac) to 4.2 t ha⁻¹ (in Nueva Ecija), while actual WS yields varied from 2.4 t ha⁻¹ (Cagayan) to about 3.0 t ha⁻¹ in Laguna.

Table 2. Rice statistics for dry season (DS) cropping in the selected irrigated rice-producing areas in the Philippines (PhilRice-BAS 1995).

Province	Production ^a (1000 t)	Area (1000 ha)	Productivity (t ha ⁻¹)	Fertiliser use ^b	
				All (kg ha ⁻¹)	Urea (kg ha ⁻¹)
Cagayan	96.7	36.75	2.58	186	96
Tarlac	60.8	18.47	3.28	221	135
Nueva Ecija	389.6	80.88	4.89	282	136
Laguna	67.7	16.71	4.06	236	195

^aAverage for 1990-94 DS. ^bAverage for 1988-93.

Table 3. Average potential and actual irrigated rice yields (in t ha^{-1}) in the selected areas during the dry season (DS) and wet season (WS).

Province	DS			WS		
	Potential	Actual	Yield gap	Potential	Actual	Yield gap
Cagayan	9.75	2.44	7.31	8.10	2.44	5.66
Tarlac	10.53	2.38	8.15	8.00	2.80	5.20
Nueva Ecija	9.86	4.15	5.71	8.04	2.85	5.19
Laguna	9.41	3.85	5.56	6.94	2.99	3.95

The difference between potential yield and actual yield reported was considered as the yield gap. Based on the simulated and reported yields, yield gaps for the different locations were estimated. During DS, yield gap in Cagayan was about 7.3 t ha^{-1} and at least 8.0 t ha^{-1} in Tarlac. Yield gaps for Nueva Ecija and Laguna average about 5.6 t ha^{-1} . For WS cropping, yield gap in Laguna was about 4.0 t ha^{-1} , while in Nueva Ecija and Tarlac, yield difference was about 5.2 t ha^{-1} . Cagayan had the highest yield gap of 5.7 t ha^{-1} .

The time series of simulated and actual yields in Laguna for the period 1970-94 are shown in Fig. 2. The increase in reported actual yields even with the introduction of HYVs during the 1970s and beyond has not been very dramatic. This may be attributed to apparent increase in the effect of yield-reducing factors which may have also increased with these new introduced varieties. The increase in DS yields from 1973 to 1979 may be attributed to the extensive rice production enhancement programme implemented during that period where Laguna was one of the pilot areas.

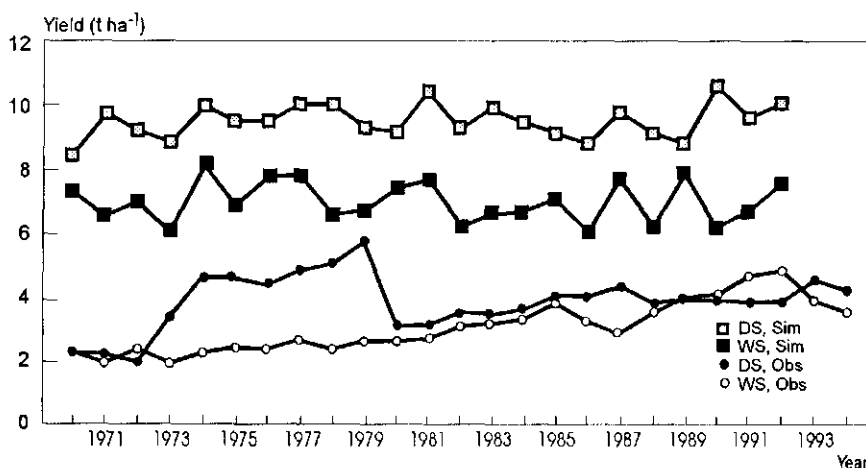


Figure 2. Actual yields and simulated potential yields during the dry season (DS) and wet season (WS) in irrigated rice areas in Laguna, Philippines.

The magnitude of yield gap determined based on potential yield is considerable because conditions are assumed to be optimal—i.e., no nutrient and water limitations and without pests and diseases and other yield-reducing factors. It is, however, unrealistic to assume that all environmental and management factors and inputs are optimal, and therefore, the large magnitude of yield gaps are expected. Thus, it is reasonable to compare reported actual yields with what can be achieved or attained under the best management strategy.

Attainable yield under adequately high N fertiliser application is expected to be lower than potential yield level. Fig. 3 shows the average simulated potential yield, attainable yield, and actual yield for Laguna for irrigated DS for the period 1970-94. Attainable yields for high fertiliser application average about 8.2 t ha⁻¹. For comparison, estimated attainable yields without additional application of fertiliser will give yields of about 3.9 t ha⁻¹, which is only slightly higher than the reported average actual yield of 3.85 t ha⁻¹. A similar analysis conducted for the other selected rice-producing provinces resulted in lower yield gaps based on what can be realised. For example, Fig. 4 shows the extent of yield gaps during the DS and WS for Tarlac Province.

Conclusions

There is considerable difference in yield potentials and actual yield levels in major rice-producing areas. The yield gaps are attributed to aggregated effect of several constraints

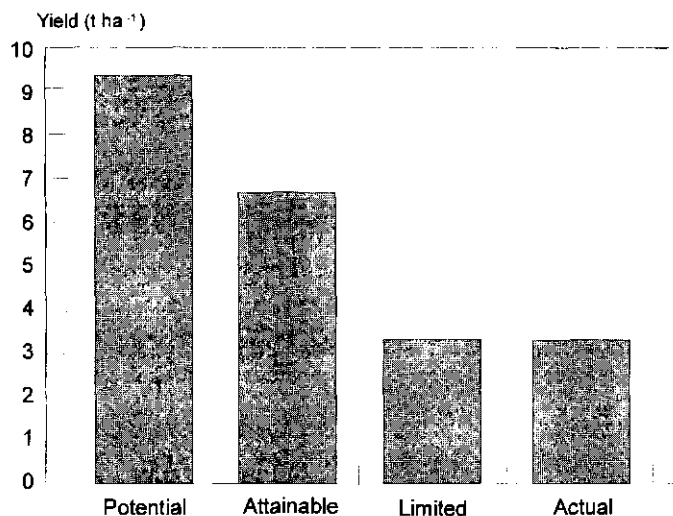


Figure 3. Average simulated and actual irrigated rice yields for dry season (DS) for the period 1970-94 in Laguna.

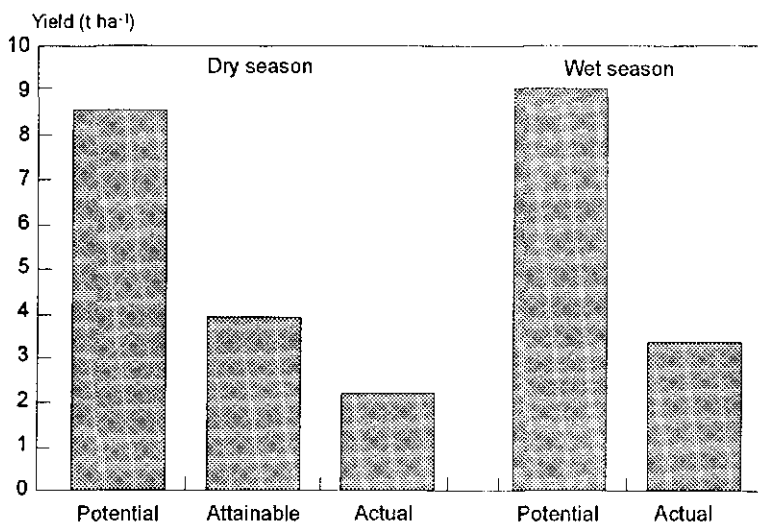


Figure 4. Average simulated and actual irrigated rice yields for dry season and wet season for the period 1970-90 in Tarlac.

that limit and reduce crop productivity such as soil nutrients, irrigation water, pests and diseases and weeds. Comparison of actual yields with attainable yields suggest that yield targets can be increased if limiting factors such as N fertiliser application can be maximised and yield-reducing factors can be controlled at a reasonable level.

Crop simulation modelling provides the methodology to analyse and quantify the yield potentials and attainable yield levels which will enable evaluation of the extent of the constraints to crop production in different agroenvironments. Quantification of magnitude and identification of causes of yield gaps can help define research priorities and extension support services in the rice-producing areas.

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Use of factorial experiment as a tool for sensitivity analysis of model outputs

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Abstract

An alternative method based on the use of the analysis of variance technique (ANOVA) for factorial experiments is proposed for sensitivity analysis of model outputs. The approach is illustrated with the simulated output (grain yield) of ORYZA1 model by varying the model parameters (DVRV, FLV and FSTR) by $\pm 15\%$ and $\pm 30\%$ for four generalized linear model structures with and without added noise assuming either fixed and random effects. It is noted that the F -test statistics for significance of main effects and first-order interactions via ANOVA is not valid, and can be misleading, for deterministic models when higher order effects are ignored.

Introduction

Several methods of sensitivity analysis in modeling with widely differing conceptual approaches and computational efforts have been proposed (Steinhorst et al., 1978; Kohberger et al., 1978; Henderson-Sellers, 1992). But it is often difficult to decide which of these methods are appropriate for the problem at hand. For many models, the effect of one input may depend on the values of other inputs. Hence, there is a need to develop methods whereby possible parameter interactions and their effects on model outputs can be investigated. Steinhorst et al. (1978) applied the analysis of variance (ANOVA) technique to the values of the output variable from a fractional factorial design and used the F -test to provide a ranking of the parameter sensitivities based on mean squares. On the other hand, Kohberger et al. (1978) advocated the use of a linear regression model containing linear, quadratic and all two-parameter interaction terms over ANOVA. Rose (1983) noted, however, that the inclusion of all two-parameter

interactions restricts the regression model to designs of resolution greater than or equal to 5. A quarter factorial design was used by Henderson-Sellers (1992) for sensitivity testing assuming that higher order interactions are negligible.

This paper aims to demonstrate an alternative method for conducting sensitivity analysis based on the ANOVA using simulated results from an ecophysiological rice simulation model. The objectives of this study are (1) to examine the response of the model to simultaneous variation of selected model parameters on simulated grain yield; and (2) to demonstrate that interpreting the F -statistics as tests of significance for main effects and first-order interactions, assuming that higher order effects resulting from simultaneous errors in the parameters can be ignored, is not warranted for deterministic models.

Conceptually, the simplest method of sensitivity analysis is to take each input parameter, one at a time, and perturb its nominal value while all other inputs are left unperturbed. For a simple model, this is often not difficult to do, but for large and complex models, it can be extremely arduous since the number of simulations increases with more inputs. Furthermore, there is a potential weakness in perturbing a parameter singly since such a method assumes that interactions among parameters are nonexistent or negligible.

In a factorial experiment, however, all possible combinations of factors at different levels are used. This allows the estimation of not only the effects of each factor individually (called main effects), which can be assessed using the one-factor-at-a-time approach, but also the interactions between factors. The ability of this type of design to estimate interaction effects makes it more efficient and also more effective. The ANOVA is used to test for significance of main effects and interactions.

The use of a complete factorial design (with replication) permits evaluation of all interaction effects. However, if the model has many factors, using a full factorial design involves a large number of simulations. To reduce the number of simulations, a fractional factorial design is often used. However, with such fractional factorial designs, there is a loss of information about higher order interactions and the introduction of confounding patterns. That is, the inability to distinguish effects due to the particular parameter chosen (i.e., some effects are confounded or aliased). Thus, fractional factorials may give false conclusions if there are interactions.

In unreplicated experiments (such as simulation outputs of deterministic models), the problem lies in evaluating its variability. In a full (complete) or fractional factorial design in a usual biological experiment, this can be done by assuming that random experimental error gives rise to Gaussian noise. Interactions between a large number of variables are less likely to be important, and such high-order interactions can be safely ignored (Swartzman & Kaluzny, 1987; Henderson-Sellers, 1992); any significance being attached only to the lower order parameter effects. The analysis of results using full or fractional design can proceed using the ANOVA technique.

Theoretical considerations

The particular simulation experiment considered is a deterministic one in that every set of the same input parameters gives the same model outputs. Nevertheless, even though the model itself is deterministic, it is often assumed that the variability of the model output is the same as that of the data (Swartzman & Kaluzny, 1987). This is because the model can be viewed as a transformation between model inputs, having some underlying probability distributions, and model output. It can be assumed then that variability enters deterministic models via the estimation of input parameters. Thus, output in a simulation is composed of a deterministic term and a stochastic term.

There are two models that may be considered: fixed and random effects models. A fixed-effect factor model arises when the levels of a factor constitute the entire population of interest. On the other hand, an effect is classified as random when inference is made on an entire population of effects and the levels in the experiment constitute only a random sample from that population (Ott, 1988).

The linear model for ANOVA is the same for both models but the difference lies in the inferences made from the treatment effects. In a fixed effects model, each treatment or factor contributes a fixed amount to the expected values of the dependent variable. For a random effects model, the treatment effect is a sample from a population of normally distributed variables with mean 0 and variance σ^2_{α} . The computations for the sums of squares in the analysis of variance will be the same regardless of the model, though the choice of the error term and the type of inference may vary depending on the complexity of the model.

In deterministic simulation, the simulated responses for given values of parameters are completely fixed (not random). Consequently, the variance of a response for given model inputs is zero. Thus, if it is also assumed that the higher order interaction effects are negligible and they are pooled with the error variance, then an unreasonably small estimate of error could be obtained which may lead to an incorrect interpretation of results. It will be demonstrated that in sensitivity analysis for a deterministic model, the pooled interaction effects is not a useable estimate of error. Furthermore, applying the ANOVA technique to analyse the simulation results will provide test statistics for significance which are not appropriate because there is no random error component in the deterministic model.

If ANOVA is intended to be used as a technique to test the sensitivity of response to variations in the parameter (factor) levels, it is essential that some form of random error be applied to the model outputs (e.g., simulated yield from a crop model). To do this, it is proposed that a suitable normally and independently distributed (NID) error with zero mean and certain finite variance be generated and added to the output from the deterministic model. The variance can be parameterised using variance estimates from data obtained from field experiments used in the validation procedure.

Sensitivity analysis methods

The ORYZA1 model (Kropff et al., 1994) was used to investigate the applicability of four basic models in examining possible interaction effects between three parameters. Generally, it is sensible to select only a few parameters of special interest for examination. For the ORYZA1 model, these parameters were

- a) development rate constant during the vegetative phase (DVRV),
- b) fraction of shoot dry matter allocated to leaves (FLV) and
- c) fraction of carbohydrates allocated to the stems stored as reserves (FSTR).

The development rate during grain filling (DVRR) was not considered because the values of DVRR measured from a number of experiments in a range of environments showed that these values were relatively constant, suggesting that there is not much genetic variation available for selection (Dionora et al., 1995). For this study, four models were considered and are described as follows:

Model 1. Deterministic model with fixed effects.

This model is an extension of the one-parameter-at-a-time approach. It assumes the highest order (i.e., three-way) interaction as the estimate of error.

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + (\alpha\beta)_{ij} + (\alpha\gamma)_{ik} + (\beta\gamma)_{jk} + (\alpha\beta\gamma)_{ijk}$$

where Y_{ijk} is the response variable model output, μ is the overall mean, α_i is the DVRV parameter at the i^{th} level, β_j is the FLV parameter at the j^{th} level, γ_k is the FSTR parameter at the k^{th} level and interaction effects are defined accordingly.

Model 2. The same form as in Model 1 but with an added normally and independently distributed error ε_{ijk} which is NID ($0, \sigma^2$).

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + (\alpha\beta)_{ij} + (\alpha\gamma)_{ik} + (\beta\gamma)_{jk} + (\alpha\beta\gamma)_{ijk} + \varepsilon_{ijk}$$

Model 3. Deterministic model with random factor levels.

It has been suggested by Rose (1981), as cited by Swartzman and Kaluzny (1987), that information on the variability associated with parameter estimates must be included, thus generating factor levels as random samples from populations of sets of factors would introduce a suitable experimental error. The values for each factor level can be varied so that the model can be written as

$$Y_{ijk} = \mu + \alpha'_i + \beta'_j + \gamma'_k + (\alpha'\beta')_{ij} + (\alpha'\gamma')_{ik} + (\beta'\gamma')_{jk} + (\alpha'\beta'\gamma')_{ijk} + \varepsilon_{ijk}$$

where α'_i , β'_j , γ'_k , $(\alpha'\beta')_{ij}$, $(\alpha'\gamma')_{ik}$, $(\beta'\gamma')_{jk}$, and $(\alpha'\beta'\gamma')_{ijk}$ are random samples generated

from normal populations, each with a particular mean and a particular variance. Thus, effectively, a random effect is added over and above the fixed effect for each level of a particular factor.

Model 4. The same form as in Model 3 but with an added normally and independently distributed error with mean 0 and variance σ^2_e .

The main objective of the simulations using the four models is to demonstrate that the ANOVA procedure is not valid statistically when the higher order interactions are used to estimate error in a deterministic model which has no random error (Models 1 and 3). An alternative method (using Models 2 and 4) where random error is incorporated (based on field experimental mean square error [MSE] as an estimate of the variance σ^2_e) is proposed and investigated.

Application

There are five levels for each parameter including the nominal (standard) value used in the model making a total of 125 combinations. The ranges of the factor levels are given in Table 1. It was not obvious in advance which of the parameters and first-order interactions would have important effects on the model's output, i.e., grain yield. The four models described earlier were used to generate data. As in field experiments, the simulated data were used to test the existence of interaction.

First, a 5³ complete factorial design with levels of factors specified in Table 1 was performed using the ORYZA1 model. The 125 data points were analysed with Model 1 using the GLM (Generalized Linear Model) procedure in SAS (Statistical Analysis System) version 6.03 with the highest order interactions as the estimate of experimental error.

Table 1. Parameters and the range of values used for simulations.

Parameter	Range				
	-30%(a)	-15%(a)	(a)	+15%(a)	+30%(a)
DVRV (°Cd) ⁻¹	0.000526	0.000638	0.000751	0.000864	0.000976
FLV (-)	0.42	0.51	0.60	0.69	0.78
FSTR (-)	0.14	0.17	0.20	0.23	0.26

(a) - refers to the nominal value.

Second, the data from the above simulation were provided with a properly parameterised normally and independently distributed error with zero mean and variance s^2 . This was done by generating 125 NID (0,1) values and multiplying these by the standard deviation, s , estimated from the field data used in the validation of the simulation model. The MSE for grain yield obtained from field data was 445,926 and a standard deviation of 668. The generated random errors using this standard deviation were then added to each of the 125 values derived from the deterministic model.

Third, the random effects model requires the levels of the factors to be random samples from the population for each factor. A coefficient of variation of 3% for DVRV, 5% for FLV and 10% for FSTR were assumed. The random level of any factor (F_{ij}) was generated as

$$F_{ij} = m_{ij} + (s_i * z)$$

where m_{ij} is the value for the j^{th} level of the i^{th} factor, s_i is the computed standard deviation of the nominal value of the i^{th} factor, and z is a random variable distributed $N(0,1)$. The values of s_i were computed from the relationship

$$s_i = cv_i * m_i$$

The 125 factor-level (5^3) combinations were then used to simulate 125 new output values. Finally, the data generated using Model 3 was modified by adding random error as in Model 2.

Results and discussion

Each data set generated according to the approaches detailed above was analysed using ANOVA to test the applicability of the four models. Examination of the results for Model 1 from the calculated ANOVA (Table 2) showed that the highest order interaction (DVRV*FLV*FSTR) that was addressed by the design and subsequently used as an estimate of error had a very small mean square (MS) value of 278. Every factor and their interactions are shown to be significant. Perhaps there may be an overestimation of the significance of the main effects due to the small error. The profile plots in Figs. 1a-c showed no apparent parameter interactions which contradict the analysis. Therefore, results for Model 1 can be regarded as anomalous. It is most likely that the significant interactions shown in the analysis were due to the very small MS value of the three-factor interaction. Thus, it is clear that Model 1 does not provide the data capable of testing interaction effects in the simulation outputs.

Table 2. Analysis of variance of simulated yields for Model 1.

Source	Degrees of freedom (df)	Mean square	F value
DVRV	4	14526855	52240**
FLV	4	4869179	17510**
FSTR	4	1140350	4100**
DVRV*FLV	16	276721	995**
DVRV*FSTR	16	18337	65.9**
FLV*FSTR	16	1712	6.2**
DVRV*FLV*FSTR	64	278	
Total	124		

**Significant at $p < 0.01$.

Analysis of simulated yields for Model 2 is presented in Table 3. The results showed significant main effects whereas interactions were not significant. The MSE of the simulated data is 429,487, which is close to experimental error equal to 445,926 obtained from the field data, and which was used to generate random errors in the simulation. In practice, there is no need to plot interaction effects if the *F*-test is not significant. However, it was deemed useful to plot the interaction effects in this case to check the response pattern of the model with the addition of random errors (Figs. 2a-c).

The simulated yields for Model 3 were analysed in two ways: (1) as a fixed effects model and (2) as a random effects model. The reason why this was done was because

Table 3. Analysis of variance of simulated yields for Model 2.

Source	df	Mean square	F value
DVRV	4	19884207	46.3**
FLV	4	5741048	13.4**
FSTR	4	2927526	6.8**
DVRV*FLV	16	708857	1.6ns
DVRV*FSTR	16	451790	1.0ns
FLV*FSTR	16	343961	<1ns
DVRV*FLV*FSTR	64	429487	
Total	124		

**Significant at $p < 0.01$, ns - not significant.

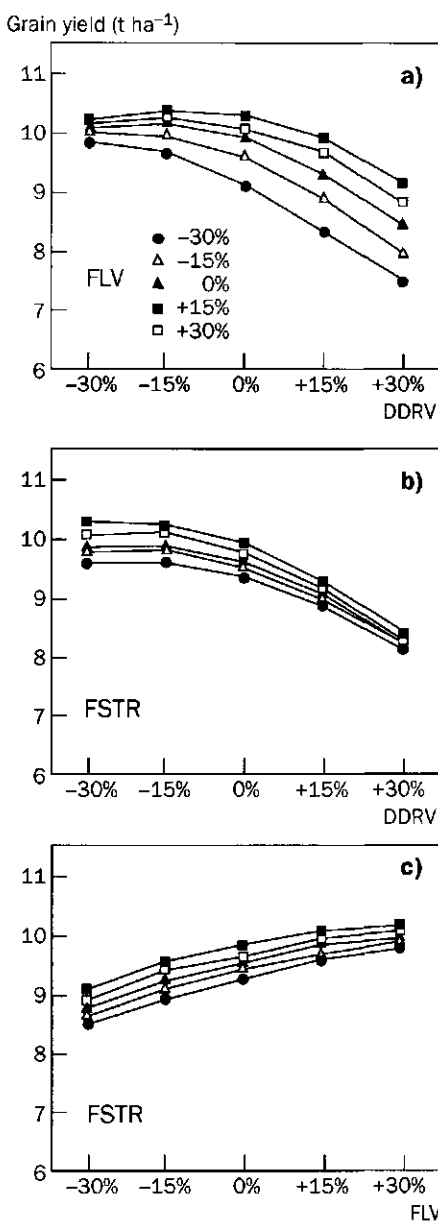


Figure 1a-c. Profile plots of interaction effects for Model 1. The levels of the two factors are the percentage change in the parameter value from standard and the response is in grain yield (t ha^{-1}).

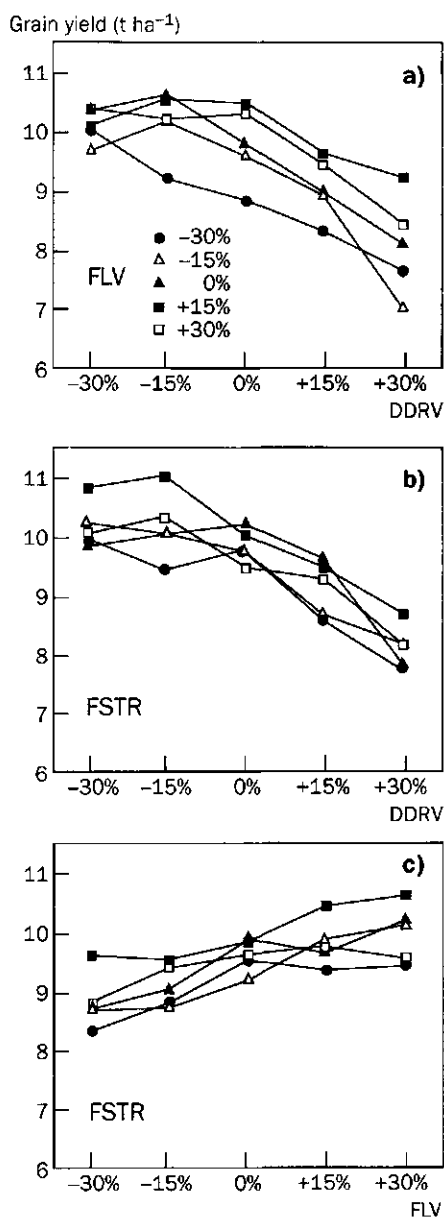


Figure 2a-c. Profile plots of interaction effects for Model 2. The levels of the two factors are the percentage change in the parameter value from standard and the response is in grain yield (t ha^{-1}).

Model 3 is neither a fixed effects model nor is it the usual random effects model. The results of the analyses (Table 4) are similar to those of Model 1. The results indicated that this model would still be deterministic in nature since the random part is only in the level of the effects applied to the model. Hence, whether the simulated data is analysed as fixed or random does not really matter since there is no interaction exhibited. The analysis of yields for Model 4 (Table 5) gave the same results as Model 2, that is, only the main effects were statistically significant with an MSE of 416,327.

The test of contrasts for Model 1 showed that DVRV, FLV and FSTR all had significant linear and quadratic effects. This appears to result from the unreasonably small error estimate. For Model 2, however, only DVRV had both significant linear and quadratic effects. The graph of means of grain yield for each model (Fig. 3) and for each parameter (Fig. 4) illustrates the response pattern of the models to changes in parameter values.

Table 4. Analysis of variance of simulated yields for Model 3.

Source	df	Mean square	F value	
			Random	Fixed
DVRV	4	23865360	82**	43661**
FLV	4	5906668	23**	10806**
FSTR	4	1982339	47**	3626**
DVRV*FLV	16	250795	458**	458**
DVRV*FSTR	16	39042	71.4**	71.4**
FSTR*FLV	16	3503	6.4**	6.4**
Error	64	546		
Total	124			

**Significant at $p < 0.01$.

Table 5. Analysis of variance of simulated yields for Model 4.

Source	df	Mean square	F value	
			Random	Fixed
DVRV	4	22754969	39.8**	54.6**
FLV	4	3789101	17**	9.1**
FSTR	4	2296273	9**	5.5**
DVRV*FLV	16	477384	1.1ns	1.1ns
DVRV*FSTR	16	525944	1.3ns	1.3ns
FLV*FSTR	16	155492	<1ns	<1ns
Error	64	416327		
Total	124			

**Significant at $p < 0.01$, ns - not significant.

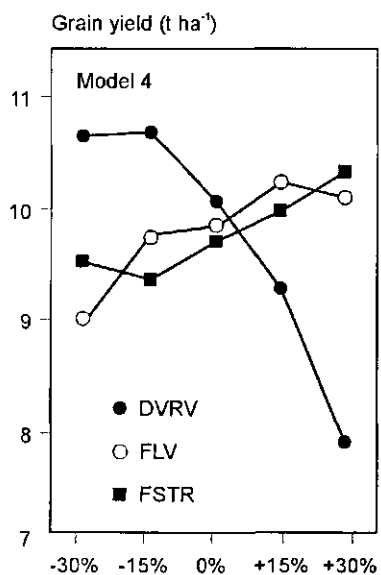
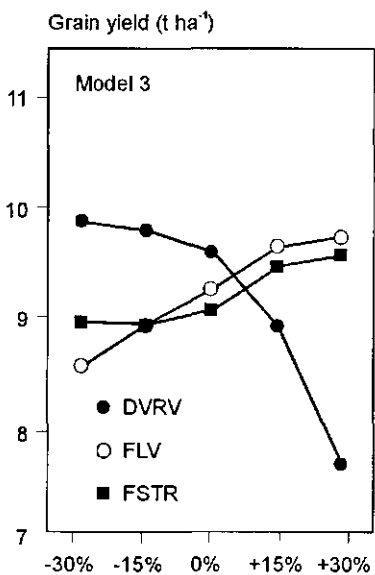
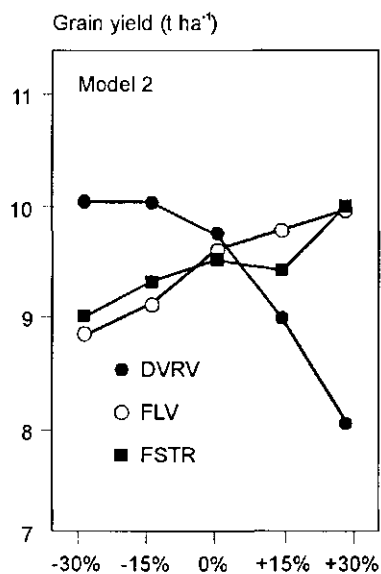
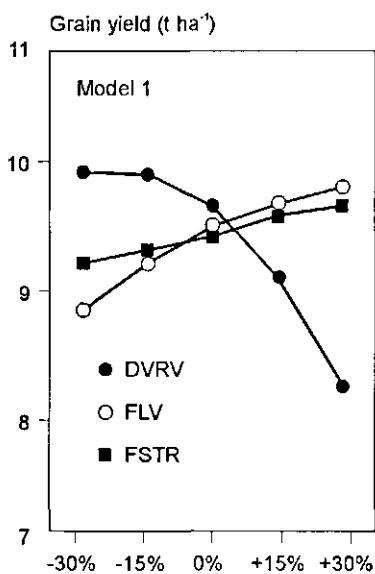


Figure 3a-c. Response pattern of the factors on grain yield for the four models. The levels of each factor are the percentage change in the parameter value from standard.

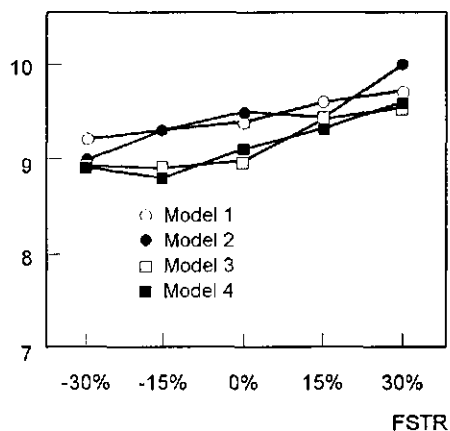
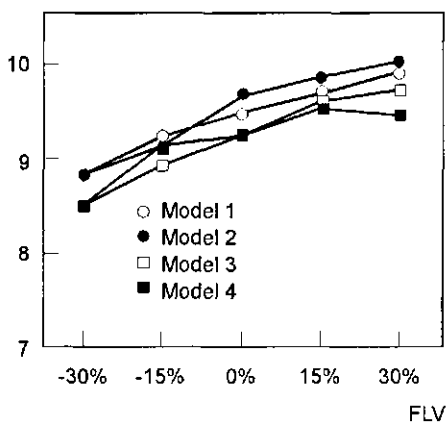
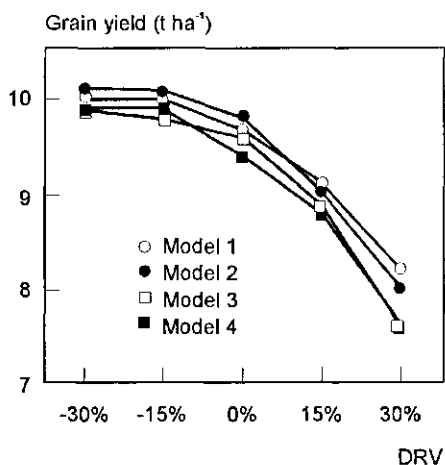


Figure 4. Response pattern of grain yield (t ha^{-1}) for the four models. The levels of each factor are the percentage change in the parameter value from standard.

FLV and FSTR appear linear while DVRV appears to have both linear and quadratic components. There was no test on contrasts for Models 3 and 4 because the factor levels were random samples from specified values and therefore were not equally spaced as required by the orthogonal polynomials used in the analysis of Models 1 and 2. However, it is assumed that the random levels are close to the fixed levels, thus, for simplicity, equal spacing has been used on the horizontal axis in the graphical displays.

Conclusions

The simulation experiments based on the four models demonstrated that in unreplicated experiments such as simulations generated from deterministic model, there is no error

component. Thus, the use of higher order interactions as an estimate of variability for deterministic models is not valid. This is because, in reality, the mean square values of higher order interactions are so small that significance of the factors (and their interactions) indicated from the *F*-tests can be misleading.

Alternatively, simulation results obtained by using Models 2 and 4 gave more convincing results for sensitivity analysis. As it turned out for Model 3, the addition of random effects on top of fixed effects does not alter the interpretation of results of the analysis.

If conditions can be identified under which the assumptions of sensitivity analysis are reasonably valid, the ANOVA technique would still be effective in screening the sensitivity of outputs to parameter interactions. The question arises as to which model to choose between Models 2 and 4. Although both models gave appropriate analysis of simulation results, the use of Model 2 is more advantageous because it is much simpler and easier to apply. It is worth mentioning that although the model output has been changed from deterministic to stochastic by the addition of random error, the basic shape of the curves remained the same.

The major deficiency in using a factorial design is that the number of simulations increases exponentially with the number of inputs. However, this problem can be approached by conducting a systematic sensitivity analysis to identify which inputs may have significant effect on the results. Then, only sensitive parameters are used in a joint parametric sensitivity analysis using the ANOVA technique.

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Role of varietal characteristics in optimising nitrogen management for irrigated rice

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Abstract

A sensitivity analysis was done with crop parameters like fraction of N allocated to leaves (FNCLV), time course of maximum crop N concentration (FNMAX) and site-variety interaction factor during postflowering (FSV2) which are used in the simulation model ORYZA_0 (in a shell package, MANAGE-N). The analysis showed that increasing N partitioning to leaves, increasing N uptake efficiency at active tillering, and increasing the efficiency of utilisation of radiation and N during postflowering are some of the breeding options that may be taken to increase N use efficiency in irrigated rice.

Introduction

Grain yield is closely related with total N accumulation in aboveground biomass and high yields are possible only when plant N uptake is sufficient (Cassman et al., 1994). Kropff et al. (1994) predicted that 200 kg of N must be taken up by a crop yielding 10 t ha⁻¹ and 300 kg of N is required for 15 t ha⁻¹ yield. To facilitate this, a large amount of fertiliser N has to be applied. Cassman et al. (1994) emphasised that even with large number of split applications, breeders must select their germplasm in an appropriate N supply environment. The increasing costs of fertilisers demand an efficient, optimum and timely use of fertilisers for maximum benefit particularly in rice where N use efficiency is low. In determining optimum fertiliser recommendations, weight is given to soil N-supplying capacity and the nutrient requirement of the crop but varietal characteristics (except duration) are rarely emphasised. The relationship between grain yield and growth duration varies due to different N absorption abilities of the cultivars. Most of the latest IRRI lines have early vigour and higher N uptake at early stages (Akita, 1989). Evaluating different rice genotypes for N uptake and utilisation efficiency, Kesava Reddy (1994) found that total N uptake was largely governed by root area and leaf area indices.

He also observed that genotypic differences in N uptake efficiency were least when climatic, phenological, morphological and physiological differences were eliminated and N utilisation efficiency for biological yield was largely dependent on N absorbed than on dry matter. Thiyagarajan et al. (1994a) proposed a specific time course of leaf N concentrations required for achieving a yield target of 8 t ha⁻¹ and Cassman et al. (1994) specified that a minimum N uptake requirement at each growth stage was needed for obtaining targeted yields. Thiyagarajan et al. (1994b) also observed the phenomenon of maintaining leaf N concentration within a certain range, irrespective of N supply, through increased number of leaves per unit area with increased N supply. Sinclair and Horie (1989) found that for each rate of N supply to leaves, an optimum leaf N content existed to maximise crop biomass accumulation. These findings emphasise the importance of maintaining N in crop at some adequate levels throughout crop growth for achieving higher yields.

A systems approach is necessary to handle the dynamic nature of the rice-N relationships for developing optimal fertiliser N recommendations. The ORYZA_0 model (ten Berge et al., 1994) together with an optimisation algorithm (wrapped in a 'shell' named MANAGE-N, Riethoven et al., 1995) is a recent model for generating site-tailored fertiliser N recommendations for irrigated rice based on the characteristics of soil, cultivar and climate. The main objective of this study is to use sensitivity analysis of the crop parameters used in the model to determine the critical factors affecting N use efficiency.

Materials and methods

The MANAGE-N package calculates, for each user-defined N input level, the maximum attainable yield for a given soil, cultivar and weather (solar radiation) conditions. The physiological processes of rice crop related to N demand, uptake and utilisation are the main considerations in the model. The crop parameters mostly represent physiological limitations for N uptake (N demand parameters). The exponential growth equation used in the model calculates daily crop growth from the current total amount of N contained in the leaf canopy (per ha of ground surface) and daily incident global radiation. The crop parameters (see ten Berge et al., 1994, for description) used in the model are presented in Table 1.

Crop parameters

The crop parameters used in the model could be a result of the net interaction between variety, environment (soil and climate) and management. However, some of them may be variety-dependent especially when maximum limits are considered. The parameters FNCLV, FNMAX and FSV are considered to be variety-specific in this study.

Table 1. Description of crop parameters used in the model ORYZA_0.

Acronym	Description	Unit
ANLVMX	Maximum amount of N in leaves	kg ha ⁻¹
FNCLV	Fraction of absorbed N allocated to leaf biomass	g ⁻¹ g ⁻¹
FNMAX	Maximum overall N concentration in the total crop biomass	kg ⁻¹ kg ⁻¹
FNSO	Fraction of N in storage organs (panicles)	-
FSV	Site-variety match factor	-
HI	Harvest index (ratio of rough rice [moisture free] to total biomass including roots)	kg ⁻¹ kg ⁻¹
MAXUP1	Maximum daily N uptake rate	kg ha ⁻¹ d ⁻¹
NUPCO	Ratio of daily N uptake to daily biomass production	kg ⁻¹ kg ⁻¹
RUR	Relative uptake coefficient during the exponential phase	d ⁻¹

FNCLV (the fraction of total crop N allocated to leaves)

FNCLV is the parameter that ultimately decides the amount of N in the crop. This in turn, determines the potential dry matter production for a given radiation level. This partitioning of N to the leaves is stable up to the first flowering (FF) stage (ten Berge et al., 1994) but its level varies with variety. A review of literature indicates that the values for different cultivars range from 0.40 to 0.55 (Table 2).

In the present study, we considered the data set for IR64, obtained at Paiyur and Tirur in Tamil Nadu, India (Thiyagarajan et al., 1995) where mean FNCLV over four locations and three treatments was found to be 0.5. To examine the effect of increased FNCLV values on grain yield, we used higher values of 0.6 and 0.7 (other crop and soil parameters remained constant).

Table 2. Fraction of crop N allocated to leaves up to first flowering in different rice cultivars under different environments.

Cultivar	Location	FNCLV	Source
CR1009	Thanjavur, India	0.40	Sivasamy et al., 1994
IR72	Los Baños, Philippines	0.55	Wopereis et al., 1994
IR72	Los Baños, Philippines	0.50	Kropff et al., 1993
BR3	Joydebpur, Bangladesh	0.45	Sattar et al., 1995
IR36	Cuttack, India	0.55	Rao et al., 1995
IR64	Tamil Nadu, India	0.47-0.54	Thiyagarajan et al., 1995
IR64	Thanjavur, India	0.55	Sivasamy et al., 1994
Xieyou 46	Jinhua, People's Rep. of China	0.47	Zheng Zhiming et al., 1995
Sanyou 63	Nanchang, People's Rep. of China	0.65	Shi et al., 1995

FNMAX (time course of maximum crop N concentration)

Plant shoots contain nutrients at a certain concentration, so high dry matter accumulation must be associated with higher nutrient uptake (Yamauchi, 1994). The maximum overall (including roots) crop N concentration usually has a peak at around active tillering and declines toward maturity and this pattern has been found to be consistent in all varieties. But the values vary with variety though there could be some errors due to suboptimal N supply in some environments. A multilocation experiment conducted simultaneously in nine sites with IR64 revealed site effects on values although a general pattern is discernible (Fig. 1). The values observed for IR36 at Cuttack, India, exhibit higher concentration in the wet season than in the dry season. It is to be determined whether the crop tends to accumulate N in the wet season as dry matter production is limited by lower radiation. Fig. 1 also shows the different patterns of time course of FNMAX observed for different cultivars in different seasons and locations grown with different levels of N application. A general pattern that could be observed is that the FNMAX values vary widely among cultivars before FF, thereafter there is considerable uniformity. Using the envelope curve obtained by pooling all cultivars (Fig. 2), we examined the effect of different levels of FNMAX (Fig. 3) on grain yield. To ensure that FNMAX was the only demand limitation, N supply and ANLVMX were removed as limiting factors. The grain yields were simulated with observed radiation regimes at Aduthurai (ADT), Ambasamudram (ASD), Coimbatore (CBE), Madurai (MDU), Paiyur (PYR) and Tirur (TKM) with each set of FNMAX. In all, six FNMAX sets (artificial FNMAX curves, except FNMAXT-3) were used as follows:

FNMAXT-1 : The overall maximum concentrations (upper limits) observed at important growth stages like transplanting (TP:0 DAT), active tillering (AT:21 DAT), panicle initiation (PI:42 DAT), first flowering (FF:60 DAT) and harvest (HT:100 DAT) for several cultivars.

FNMAXT-2 : The overall minimum concentrations (lower limits) observed at important growth stages like transplanting (TP:0 DAT), active tillering (AT:21 DAT), panicle initiation (PI:42 DAT), first flowering (FF:60 DAT) and harvest (HT:100 DAT) for several cultivars.

FNMAXT-3 : The overall maximum concentrations observed for cultivar IR64 in Tamil Nadu.

FNMAXT-4 : Same as in FNMAXT-3 but the value at active tillering (AT) is increased to 0.49, the highest value observed for this stage (as in FNMAXT-1) to mimic a boosted crop N concentration around AT.

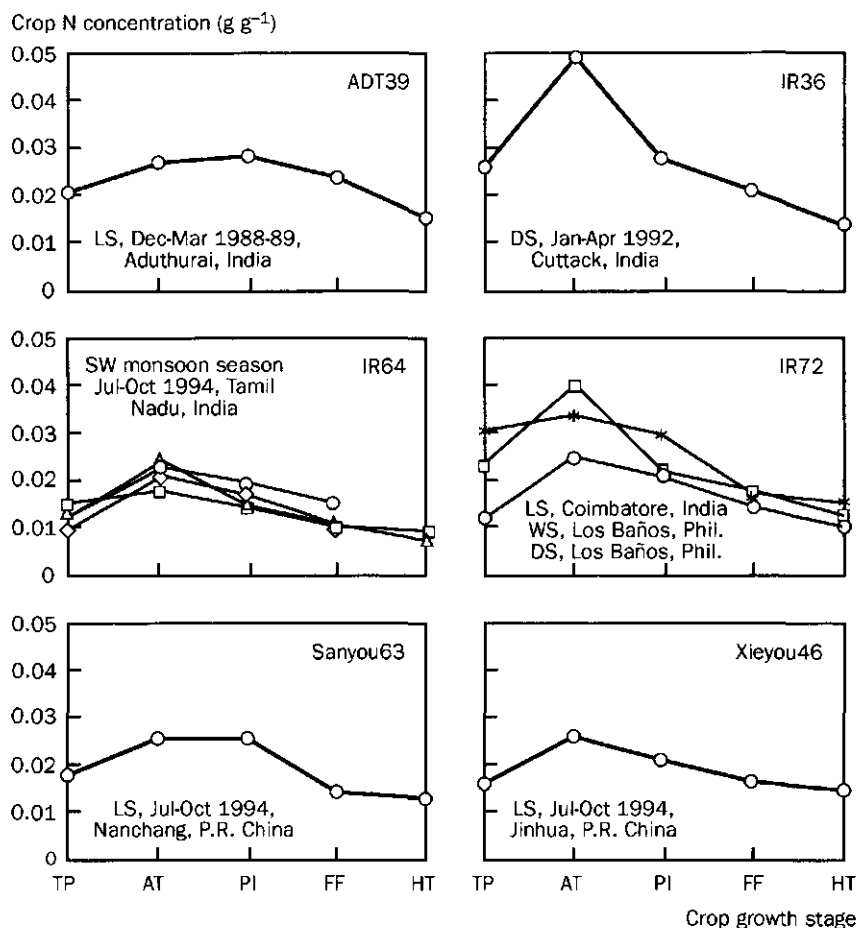


Figure 1. Maximum crop N concentrations observed at important growth stages in different cultivars at different seasons and locations (DS = dry season, LS = late season, WS = wet season).

FNMAXT-5 : Same as in FNMAXT-3 but the value at panicle initiation (PI) is increased to 0.30, the highest value observed for this stage (as in FNMAXT-1) to mimic a boosted crop N concentration around PI.

FNMAXT-6: Same as in FNMAXT-3 but the value at first flowering (FF) is increased to 0.26, the highest value observed for this stage (as in FNMAXT-1) to mimic a boosted crop N concentration around FF.

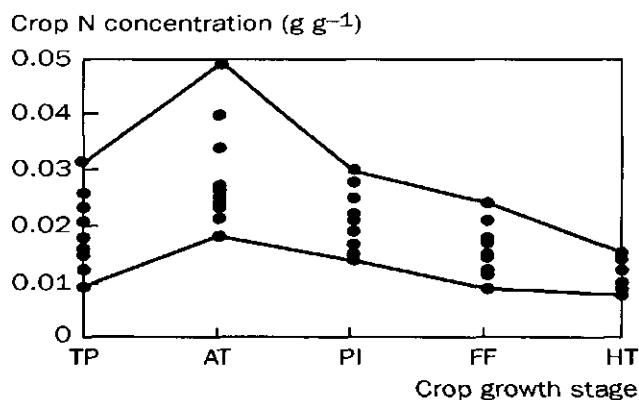


Figure 2. Overall maximum crop N concentrations observed at different crop growth stages in different cultivars shown in Figure 1.

FSV (site-variety interaction factor)

The model ORYZA_0 calculates crop growth rate from daily incident global radiation and the amount of N contained in the leaf canopy. The efficiencies with which radiation (initial global radiation use coefficient, p) and leaf N (initial leaf N use coefficient, e) are utilised to produce dry matter are interdependent and affected by site-variety interactions. This site-variety interaction effect usually exhibits a drastic reduction in dry matter production efficiency especially after FF and has been termed as FSV. To account for the effect after FF, preflowering and postflowering values are used in combination with p and e and these values are obtained by calibration using observed crop biomass data in comparison with simulated ones. The observations made in the Tamil Nadu experiments with IR64 had shown that the FSV1 values range from 0.8 to 1.2 and the FSV2 values range from 0.3 to 0.9. Thus, IR64 has a potential FSV1 of 1.2 and FSV2 of 0.9; the lower FSV values signify the interactions between variety and local conditions which lead to reduced dry matter production efficiencies. The site depression effect is strong after FF. Cultivars that are less sensitive to this site depression are needed. To focus on increased dry matter production efficiency of a genotype, higher FSV2 values were tried for Paiyur (0.5, 0.6, 0.7, 0.8, 0.9) and Tirur (0.7, 0.8, 0.9).

Results and discussion

Effect of increased allocation of N to leaves

The simulated grain yields for Paiyur and Tirur were different due to the differences in demand limitations (Fig. 4). The results showed that the yield obtained with FNCLV of

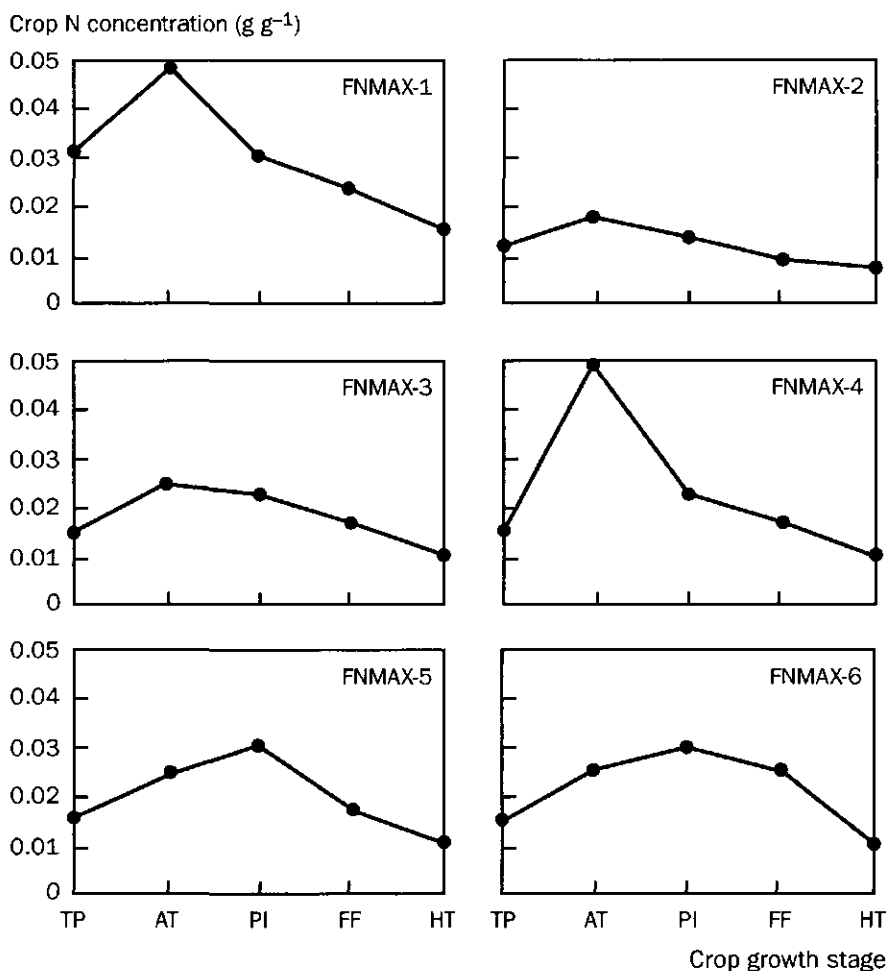


Figure 3. Different time courses of FNMAX used in the sensitivity study.

0.5 at 200 kg N ha^{-1} could be achieved with 150 kg N ha^{-1} at both Paiyur and Tirur and if the FNCLV is increased to 0.6, the same yield could be obtained with 120 kg N ha^{-1} at Paiyur and with 100 kg N ha^{-1} at Tirur, if the FNCLV could be increased to 0.7. Increasing the FNCLV from 0.5 to 0.6 increased the yield by 9.0 to 12.9% for N levels ranging from 0 to 200 kg N ha^{-1} at Tirur and by 8.6 to 14.6% at Paiyur. Similarly by increasing the FNCLV to 0.7, the yield increases were 17.9 to 24.3% at Tirur and 16.5 to 27.8% at Paiyur. The yield increases decreased with increased N levels. Thus, one of the breeding options to increase N use efficiency is to increase partitioning of N to the leaves.

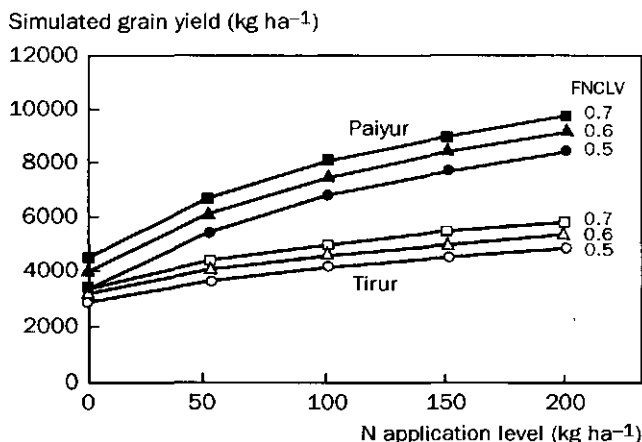


Figure 4. Simulated grain yields for different N application levels at Paiyur (filled markers) and Tirur (unfilled markers) with different FNCLV values.

Effect of maximum crop N concentration

If no demand limitation exists other than the time course of maximum crop N concentration for the FNMAXT-1 (highest values observed for different cultivars), the simulated yields obtained for the weather conditions at the locations in Tamil Nadu ranged from 11.2 t ha⁻¹ (Ambasamudram) to 14.1 t ha⁻¹ (Paiyur). For FNMAXT-2 (lowest values observed for different cultivars), the yields ranged from 8.1 to 9.8 t ha⁻¹. These results showed the lower and upper limits of maximum yields possible if only FNMAX were the only demand limitation and thus reflect the importance of varietal character in this aspect. The simulated yields with FNMAXT-3 (observed FNMAX values for IR64 in Tamil Nadu) ranged from 9.9 to 12.2 t ha⁻¹ in different locations (Fig. 5). With increased FNMAX at AT, the yields could be increased by 8.1 to 9.9% in the different locations. When the FNMAX values were increased either at PI or FF, the yield increases were similar and ranged from 3.0 to 3.7% only. These results showed that the N uptake efficiency of the cultivar should be increased around AT to increase the yield potential.

Effect of increased FSV2

The FSV2 values observed at Paiyur and Tirur were 0.5 and 0.7, respectively. Increasing this value to 0.9 increased the yields (Table 3). The impact of increased FSV2 on increased yield was higher at Paiyur than at Tirur due probably to the higher radiation regime and better N recovery. At Paiyur, the yield could be increased by 24% with 200 kg N when the FSV2 is 0.9.

The results showed that by increasing the genotypic efficiency of postflowering dry matter production, the site-variety interaction effect in reducing yield could be overcome.

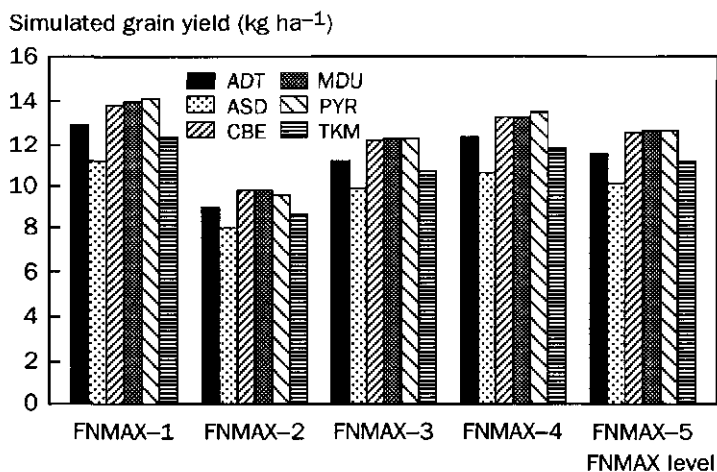


Figure 5. Simulated grain yields for different FNMAX levels at Aduthurai (ADT), Ambasamudram (ASD), Coimbatore (CBE), Madurai (MDU), Paiyur (PYR) and Tirur (TKM) in Tamil Nadu, India.

Table 3. Increase in grain yields at Paiyur and Tirur for different FSV2 values at different N application levels.

N level (kg ha ⁻¹)	FSV2 values					
	Paiyur				Tirur	
	0.6	0.7	0.8	0.9	0.8	0.9
0	4.8	8.8	12.1	14.8	3.2	5.8
50	5.5	9.7	13.4	16.3	4.3	7.6
100	5.2	10.6	14.4	19.3	5.0	9.7
150	6.0	12.6	17.3	22.2	5.4	11.1
200	6.7	12.9	18.0	23.7	5.0	10.1

Conclusions

This study emphasises the importance of various crop parameters in determining the utilisation of radiation and N in dry matter production. The sensitivity analysis study showed that increasing the N partitioning to leaves, N uptake efficiency at active tillering and efficiency of utilisation of radiation and N during postflowering are some of the breeding options for increased N use efficiency in irrigated rice. However, it should be

noted that the potential of a cultivar is depressed by site factors and cultivars insensitive to these site factors are also an essential part of exploiting the potential.

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Ideotyping: matching the length of growing season with that of growth cycle

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Abstract

Annual crops are usually only grown during part of the year when environmental conditions are favourable. The factors that limit the length of the available growing season for a crop are discussed from the points of view of meteorology, crop physiology and crop management. Crop yields that may be expected depend on the length of the growing season, how well the available season is used by a growing crop and on environmental factors that determine, limit or reduce yields. Designing genotypes for such environments requires quantitative knowledge of the influence of environmental factors on the length of the season and on dry matter accumulation and partitioning. This approach is discussed and the potato crop is used as example.

Introduction

The objective of breeding programmes is to create and introduce genotypes with the highest economical yield of a specific product, with a specific quality for a specific environment. The specific product of the potato crop is the potato tuber. The main determinants of quality are dry matter content (the higher the dry matter content, the better its storability and processing characteristics) and tuber size (distribution). The specific environment is mainly determined by temperature. In environments with mean monthly temperatures below 5 °C or above 25 °C, potato is not grown. Optimal temperatures for rice growth are higher than those for potato as is schematically represented in Fig. 1. In subtropical regions of Madagascar, for instance, potato is grown in the same field as rice, with potato grown during the coolest part of the year and rice during the warmest part of the year. In this particular situation, interruption of monocropping of potato by a crop that needs flooding (rice) is beneficial as flooding controls certain devastating soil-borne diseases such as bacterial wilt caused by *Pseudomonas solanacearum*.

Besides temperature, other factors may determine available length of the growing season (Haverkort, 1990). In the Central African highlands, for instance, temperatures

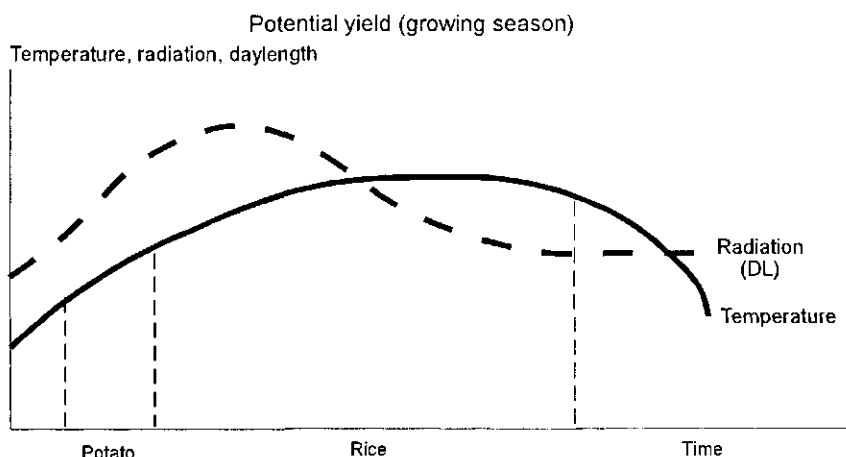


Figure 1. Schematic representation of the growing periods of potato and rice as related to temperature and radiation regimes in a subtropical area.

are suited for potato production throughout the year. Rainfall at the equator, however, occurs in two main rainy seasons 6 mo apart, necessitating two crops per year. Theoretically this would restrict the length of the growing season to 6 mo for ware potato crops as part of this crop is used as seed for the next crop because no separate seed potato production system exists at the farmers' level. But practically this period has to be reduced by 2-3 mo because the tubers that are harvested only sprout again after 2-3 mo. So, although temperaturewise, potato can be grown throughout the year (length of the growing season = 365 d), environmental and physiological reasons make 100 d the ideal length of the growing season. Ideal genotype (ideotypes) should then have a growing cycle of 100 d. Longer cycles would lead to an imbalance of the growing and seed rest period. Also, from the point of view of disease control, longer cycles are not desired as part of the cycle would then fall within periods of most intensive rain and consequently expose the crop to damage by potato late blight (*Phytophthora infestans*). In the Mediterranean area, the growing season is limited in spring by low temperatures at planting and by high temperatures at harvest. In northern Europe, low temperatures limit the length of the growing season in spring (late frosts in March, April and May) but at the end of the season, temperatures are low again (early frosts in September and October).

Another important factor that may limit the length of the growing season and consequently the length of the growth cycle is related to market prices. Prices are often higher at the beginning of the harvest period of crops that are harvested fresh, necessitating a reduction in the length of the season.

Ideotypes have a length of the growth cycle characterised by a green leaf area intercepting solar radiation for as long as possible during the available growing season to accumulate as much dry matter as possible. Earlier genotypes divert dry matter to harvestable parts (grains, tubers) so that insufficient assimilates are available for the foliage that then senesces and dies. Genotypes that are too late still have full ground cover with green leaves at the end of the available growing season indicative of an unfavourable distribution of dry matter to the foliage and to the harvestable parts of the crop. Fig. 2 schematically represents the three situations of a potato crop under northern European conditions.

To describe ideotypes with the desired length of the growth cycle, one needs to first determine the length of the available growing season as it is delimited by growing conditions or market demands. Second, an assessment is needed of the yield-determining factors (temperature, radiation, daylength) that cannot be changed or influenced by the farmer once the crop is planted, with emphasis on the influence of such factors on the length of the growth cycle. Third, the presence of yield-limiting factors such as water and nutrients needs to be studied. What is the influence of drought and lack of nutrients

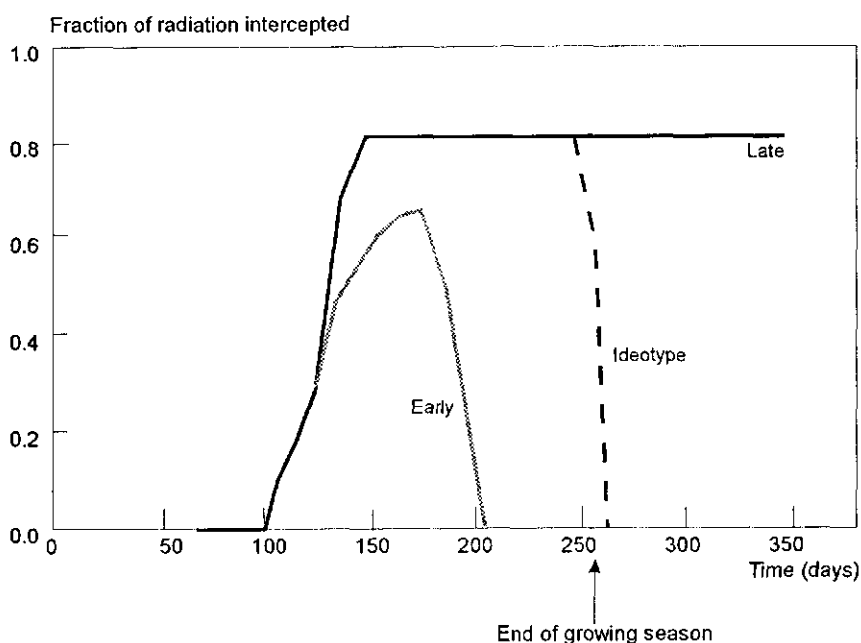
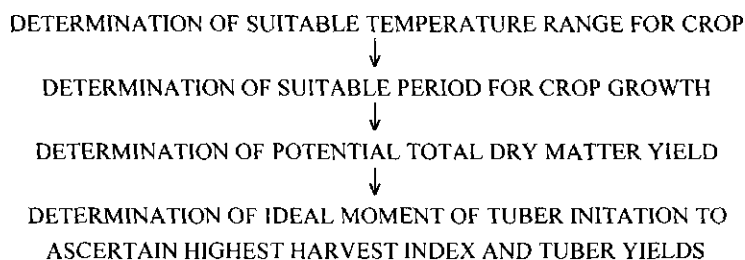


Figure 2. Schematic representation of the course of light interception by green crop foliage of ideotypes versus early and late genotypes. Planting is on day 75, emergence on day 100 and harvest on day 260.

on the length of the growth cycle? Finally, the risk of crop yield-reducing factors such as pests, diseases and weeds should be evaluated and quantified.

The objective of this paper is to determine the influence of yield-defining, -limiting and -reducing factors on crop growth parameters and their repercussions on the length of the growth cycle and to establish a framework that can help to match the length of the cycle with that of the season. To that end, we will first discuss an appropriate model of potato growth and development with temperature and daylength as 'length of growth cycle-influencing' factors and in subsequent paragraphs will discuss the influence of a yield-limiting factor (drought) and of a yield-reducing factor (potato cyst nematodes) on the length of the growth cycle, total dry matter accumulation and dry matter distribution to the harvestable part. The principles explained here largely apply to any field-grown crop, including rice.

The approach followed can be represented schematically as follows:



The model

A simple model describing growth and development of crops is based on light interception, utilisation of light to produce dry matter, allocation of dry matter to harvestable parts and the percentage of water in the harvestable parts. Schematically this is represented in Fig. 3. The growth cycle is shown in the graph (Fig. 3); the abscissa (thermal time) starts at planting. The course of light interception or ground cover from planting until crop senescence is shown. Cumulation of the amount of daily intercepted radiation over time versus total and tuber dry matter yields the efficiency coefficients for total and tuber dry matter production. The simplest potato growth model that can be derived from the observation of light interception and dry matter accumulation over time is

$$Y = R E H / D$$

where Y = tuber fresh yield, R = the amount of intercepted radiation, E = conversion efficiency, H = the harvest index and D = the dry matter concentration of the freshly harvested tubers.

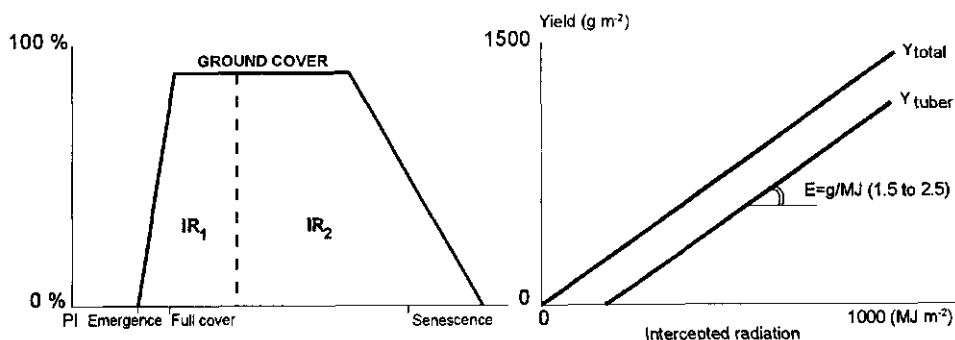


Fig. 3. Schematic representation of tuber production in potato based on ground cover (and) light interception and conversion of intercepted light into total and tuber dry matter.

These parameters can easily be derived from potato experiments in which periodic harvests are taken and fresh and dry matter of haulms and tubers are determined, where the percentage ground cover is measured weekly and where daily solar radiation is recorded. Van Keulen and Stol (1995) used this model approach to calculate potential yields at about 1000 meteorological sites worldwide. They assumed that potato cannot grow below 5 °C or above 28 °C and that the conversion rate is 2.5 g MJ⁻¹. They also assumed that each site is planted to a cultivar with appropriate length of the cycle fitting the length of the season. This means that for each site, a harvest index of 0.75 at crop senescence was assumed. Thus they calculated potential yields as shown in Fig. 4. Around the equator at sea level, potato production does not take place because it is too warm year-round. At latitudes higher than 55 °C, no potatoes are grown because insufficient thermal time is accumulated to allow one growth cycle. Yields are highest in the tropical highlands where potato production is feasible year-round, followed by Mediterranean climates where two cropping seasons are possible and then by temperate areas with one long growth cycle.

Matching under varying temperature and daylength conditions

In Fig. 5, potential yields are shown globally assuming that cultivars exist that fit the local conditions in terms of temperature and daylength responses exist. Potato is known to react to shorter days and lower temperatures: such conditions hasten tuber formation and favour tuber growth at the expense of haulm growth. LINTUL-POTATO (Kooman and Haverkort, 1995) was developed to quantify the effect of temperature and daylength

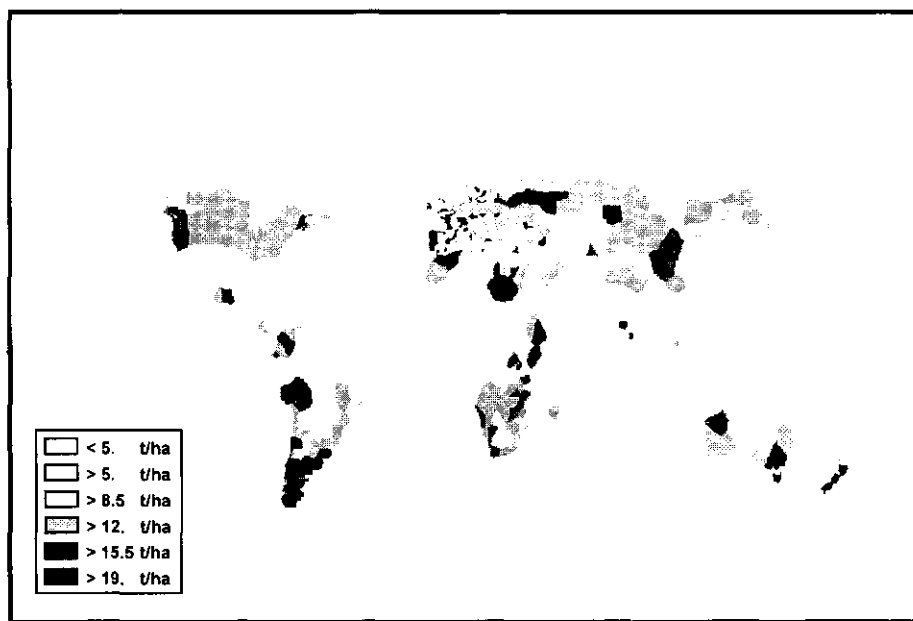


Figure 4. Calculated potential potato dry matter yields (Van Keulen and Stol, 1995).

on tuber initiation and subsequent dry matter partitioning over tubers and haulms. The main features of the LINTUL-POTATO model are shown in Fig. 5.

The model starts with a routine describing Phase 0 between planting and emergence (also described by MacKerron and Waister (1985), assuming a sprout growth rate of 1 mm per day degree (base temperature 2 °C). This means that a tuber planted at 12 cm depth with a sprout length of 2 cm will emerge after 10 d when the average soil temperature is 10 °C. Once emerged (defined when the leaf area per plant is 0.0155 m² m⁻² × the number of stems per plant per m²), the relative leaf extension rate is 0.012 m² m⁻² per day degree and the leaf area is formed to build up the leaf area index (LAI). Light is extinguished by the canopy according to Beer's Law with an extinction coefficient of 1. Thus initial growth (until LAI = 1.5) is sink-limited and thereafter growth is source (light)-limited. Leaf classes that are formed have a temperature-dependent longevity. Other temperature-dependent rates, but with an optimum around 20 °C are sprout growth rate, light use efficiency (see Fig. 4, optimally 2.5 g MJ⁻¹) and, most importantly, tuber initiation and tuber growth rates. The latter optimally is assumed to be 0.37 g g⁻¹ d⁻¹. The most crucial in this model approach is the moment of tuber initiation and subsequent tuber growth rate. The tuber initiation rate (inverse of number of days between emergence and tuber initiation, defined as the presence of 1 g of tuber

dry matter per m²) also depends on daylength: longer days reduce the relative effect of optimal temperatures so plants continue to grow for a longer period.

When tubers are initiated early (with an early cultivar) and when conditions for tuber growth are optimal, soon all daily accumulated assimilates will be allocated to the tubers and the crop will die early. Fig. 6 shows the different phases of a crop: 0 is between

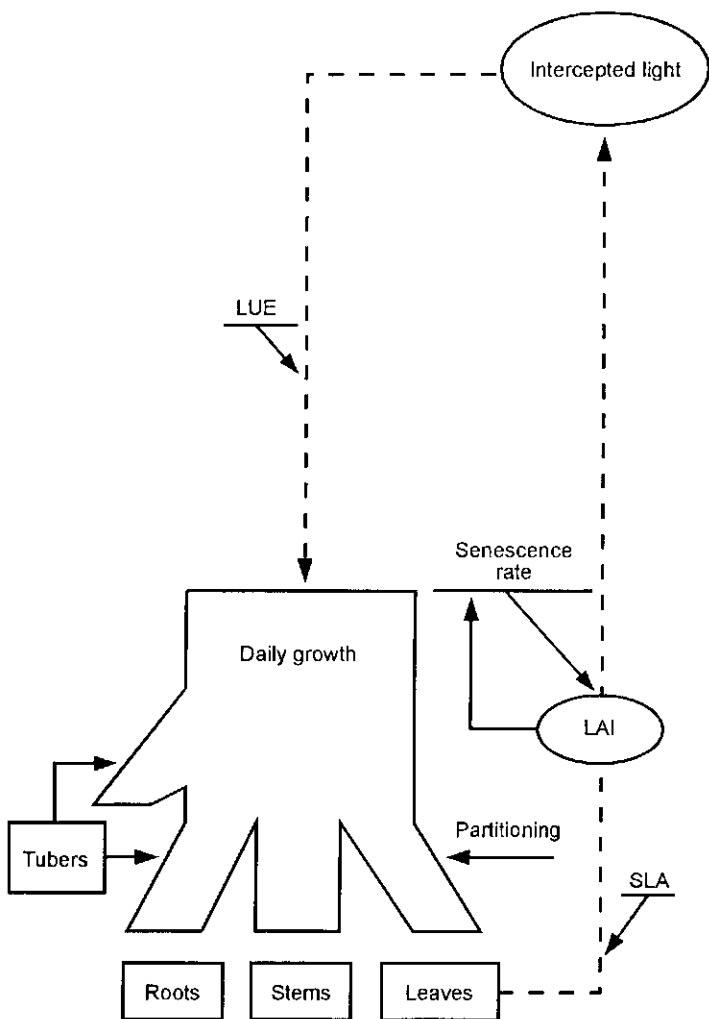


Figure 5. Schematic representation of the LINTUL-POTATO model.

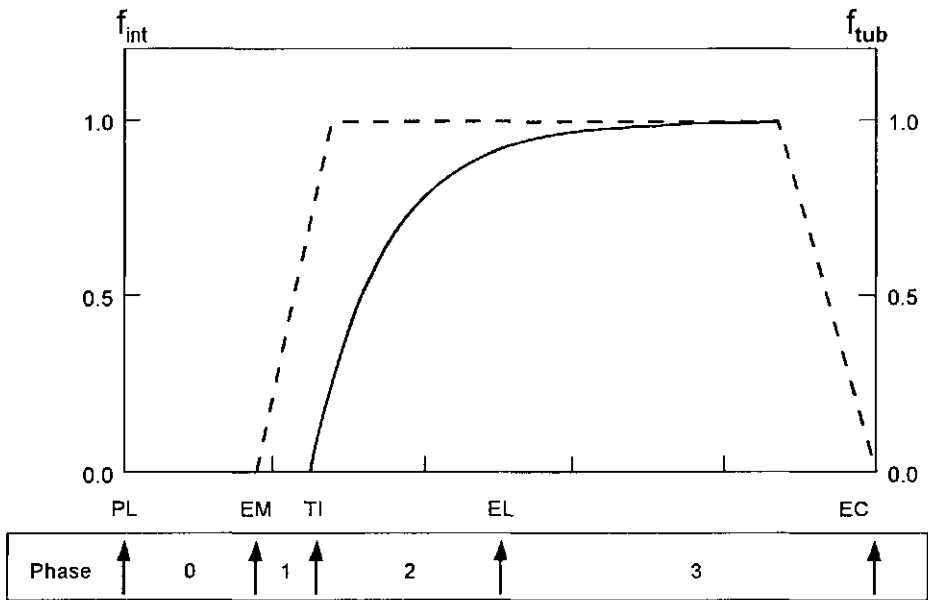


Figure 6. The phases of crop growth and development of potato (PL = planting, EM = emergence, TI = tuber initiation, EL = end of leaf growth, EC = end of crop growth, f_{int} = fraction of incoming solar radiation intercepted by the crop [solid line] and f_{tub} = fraction of daily accumulated dry matter allocated to the tubers [unbroken line]).

planting and emergence (the sprout growth rate is temperature-dependent), 1 is between emergence and tuber initiation (the tuber initiation rate is temperature- and daylength-dependent), phase 2 is between tuber initiation and the moment when 90% of all daily produced assimilates are partitioned to the tubers (the tuber growth rate is temperature- and daylength-dependent) and phase 3 is between the moment when 90% of the assimilates are partitioned to the tubers and crop senescence (the leaf senescence rate is temperature-dependent).

With LINTUL-POTATO, it is possible to explore what happens to a standard cultivar when grown under different temperature and daylength conditions but under a standard radiation regime. For model parameterisation, experimental results were obtained of eight cultivars varying in lateness from very early to very late were grown under various temperature and daylength conditions in Rwanda (two altitudes), Tunisia (spring, autumn and winter seasons) and in The Netherlands (summer season). Fig. 7 shows the expected tuber yields of a standard genotype of medium lateness with average temperature and daylength effects on tuber initiation rate. Potato crops have a considerably broader optimal temperature range at longer days. This phenomenon may explain the wide adaptability of the crop which is grown in a wide range of environments.

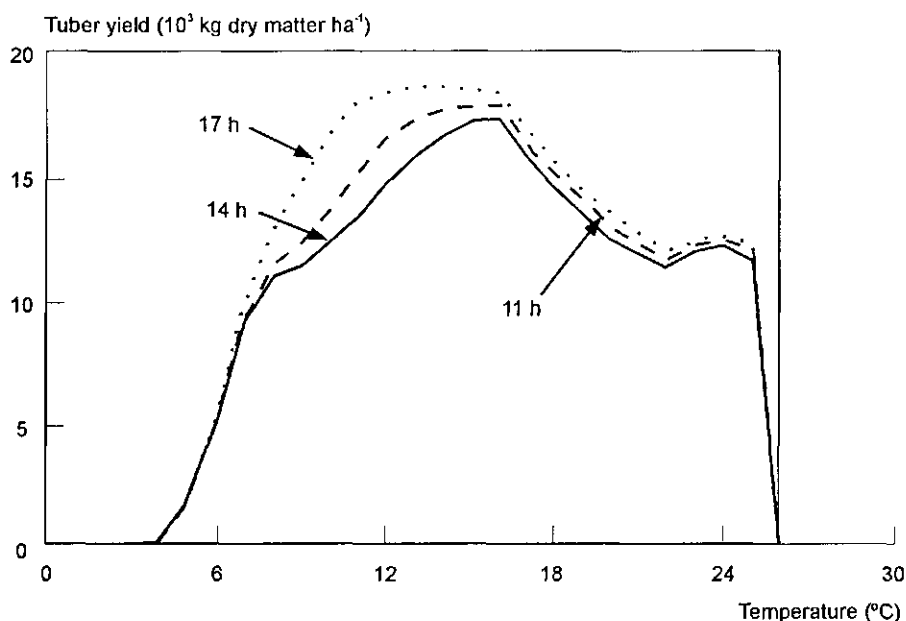


Figure 7. Tuber yields of a standard genotype of potato grown at different temperature and daylength combinations.

A second application of LINTUL-POTATO is to identify genotypes adapted to the climatic conditions at any site in the world. Fig. 4 showed the potential yields of 1000 meteorological sites. To find out how late a cultivar should be so that the length of the growth cycle matches the length of the growing season, LINTUL-POTATO is able to calculate the ideal moment of tuber initiation for each site. If, for a particular site, tuber initiation takes place before the optimal moment, plants are still too small and all assimilates will be allocated too early to the tubers leaving none to the foliage that will die too early to match the length of the potential growing season (when temperatures are between 5 ° and 25 °C). When tuber initiation takes place too late, much foliage is formed and the allocation pattern is unfavourable for tuber growth, resulting in too low harvest indices. This is shown in Fig. 8 for two sites: a spring and an autumn season in Tunisia and a single summer season in The Netherlands.

Matching under water-limiting conditions

Water probably is the most yield-limiting factor for most crops. Effects of drought on crop growth processes may be short-term effects and long-term effects. Short-term effects show within a few days after plants have been withheld water. Stomates close and

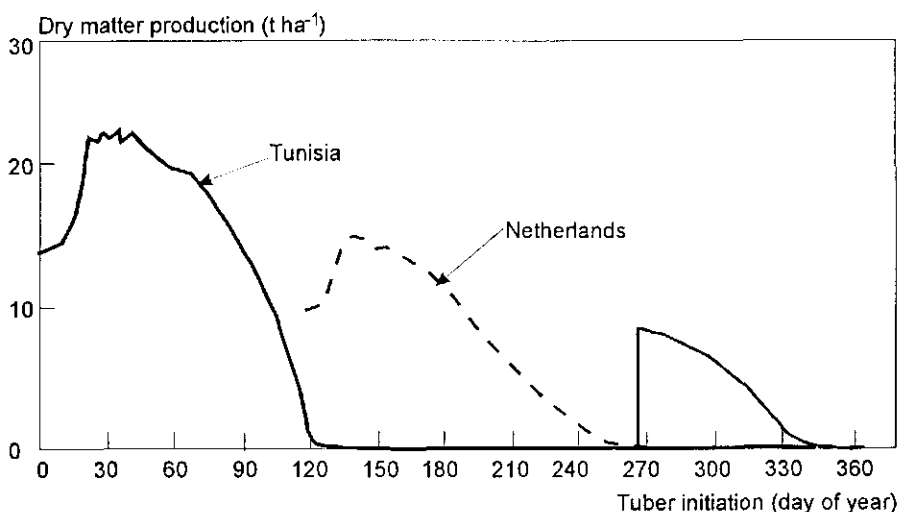


Figure 8. Expected potential dry matter production (30-yr average temperature data) at varying moments of tuber initiation) in three varying seasons, calculated with LINTUL-POTATO.

the resistance to flows of water (strong effect) and carbon dioxide (weaker effect) increases, leading to an increased transpiration efficiency. The plant water potential decreases (measured by a pressure chamber) and the cellular osmotic potential increases (measured osmotically) and chlorophyll fluorescence increases. Following stomatal closure, ^{13}C discrimination decreases as may be observed from stable isotope analysis with mass spectrometry. Plant physiologists, for a long time, have successfully determined such short-term effects of drought. They give insight into the degree of drought stress a plant is (or has been) subjected to. However, each of these methods on its own cannot be considered as a suitable instrument to predict the degree of tolerance of genotypes. A small reaction to drought may be indicative of a luxurious use of water and a strong reaction, on the other hand, may point to an insufficient ability of the roots for water uptake. The use of crop growth models may improve the search for drought-tolerant genotypes.

The kind of drought which is expected is crucial in the strategy to increase the efficient use of water. Three drought types are distinguished: a dry spell at the beginning of the growing season leading to a delay of emergence and to reduced early growth; a short transient drought period in the course of the growing season, only slightly reducing growth but potentially strongly affecting crop development and quality of the produce; and a drought which intensifies in the course of the growing season leading to premature

senescence of the crop. These different types of drought have different effects on crop growth and on the development and quality of the product. Crops may react in different ways (and so do their producers) to limit the extent of damage. Long-term effects become visible when growth is retarded. Fewer leaves are formed which are thicker (higher specific leaf weight), plants remain shorter, and root growth is favoured over haulm growth resulting in reduced shoot-root ratios (Fasan & Haverkort, 1991). Again, as for the short-term effects, no strategy based on crop morphological observations can be developed that shows whether a genotype is tolerant or not.

Yield analysis following the basic principles of LINTUL-POTATO (periodic observation of fresh and dry total and tuber mass and cumulative intercepted radiation by the crop) showed that yield losses are mainly due to reduced amounts of intercepted radiation by the crop and for less than 10% due to reduced conversion efficiencies or to reduced harvest indices (Haverkort et al., 1992). Leaf shedding following drought is the main factor responsible for reduced radiation interception and dry matter accumulation. Haverkort and Goudriaan (1994) simulated the long-term effects of drought on crop growth. They chose a potato crop which was made to emerge on day of year 130, grown in the climatic conditions of de Bilt (centre of The Netherlands) averaged over the period between 1960 and 1990. There were three treatments of water supply: ample supply, no rain until day 170, and a late drought from day 170 onward. They used the crop growth model SUCROS92 (van Laar et al., 1992) with dry matter distribution, developmental and leaf senescence rates after Spitters and Schapendonk (1990) and Bessembinder (1991). Modifications involve switching of leaf expansion from exponential sink-limited growth to source-limited growth and crop earliness depending on maturity class as defined by the temperature sum at which leaf senescence starts. This temperature sum decreases when the ratio of actual to potential transpiration is less than 1 (Bessembinder, 1991). Table 1 shows the results of the simulation runs.

The influence of increased leaf death was small for the late drought but much larger for the early drought period. When subjected to drought, leaf senescence was advanced by 30 d in the late cultivar and by about 20 d in the early cultivar which prevented

Table 1. Simulated results of a SUCROS potato model (after Haverkort and Goudriaan, 1994).

Parameter	Irrigated cultivar		Early drought cultivar		Late drought cultivar	
	Late	Early	Late	Early	Late	Early
Tuber dry matter (t ha ⁻¹)	22.4	13.2	10.2	3.7	7.4	6.0
Harvest index	0.78	0.81	0.75	0.76	0.55	0.65
Transpiration efficiency (g l ⁻¹)	6.33	5.99	5.92	5.52	5.95	5.85

recovery in the second half of the growing season. An early dry spell affected the tuber yield of an early cultivar more than that of a late cultivar, whereas a late dry spell affected the tuber yield of a late cultivar more than that of an early cultivar as they could not escape the drought and especially a reduced harvest index contributed to tuber yield reduction of the late cultivar subjected to the late drought.

This exercise shows how type of drought and type of cultivar (its lateness which depends, as LINTUL-POTATO showed, on the moment of tuber initiation) should be considered when screening for drought tolerance. With regard to adaptation to dry spells (as previously with adaptation to temperature and daylengths), it has been shown how important it is to match length of growing season (as determined by availability of water) with that of growth cycle of the genotype (as determined by its earliness or lateness).

Matching under nematode-infected conditions

Potato cyst nematodes (*Globodera rostochiensis* and *G. pallida*) are a major yield-reducing factor in potato production. Short- and long-term effects (Fasan & Haverkort, 1991, Haverkort & Fasan, 1991) of drought and potato cyst nematodes are similar: both reduce plant water potential, stomatal aperture, shoot-root ratio, specific leaf area, stem length, number of leaves and increase tuber dry matter content. Also, the long-term effects of potato cyst nematodes are similar to those of drought: both mainly reduce yields through reduced light interception by green foliage (37-52%) whereas the conversion efficiency of intercepted radiation into crop dry matter is only reduced by about 10%. As with drought, the harvest index is decreased only slightly and tuber dry matter is increased by a few percent. Cultivar Elles was the most tolerant of both drought and of potato cyst nematodes. This is not surprising inasmuch as it was the latest cultivar tested, and when subjected to a yield-limiting or a yield-reducing factor, it made best use of the available growing season. Elles is a cultivar that initiates its tubers late, allowing the plant to allocate much dry matter to the foliage. When subjected to stress, such a genotype makes better use of the available growing season because its growth cycle length better matches the growing season length than does an earlier genotype.

Unlike drought, potato cyst nematodes cannot be avoided and the higher the nematode population, the later a genotype should be in order to still be able to match the length of the cycle and the season. Another important yield-reducing factor in potato is late blight caused by the fungus *Phytophthora infestans*. Here, however, interaction between genotype and timing of the disease incidence exists. Haverkort and Bicomumpaka (1986) demonstrated that in an area where farmers have the possibility of avoiding the highest peak of the rainy season (by either harvesting just before this peak or by planting just after the peak), their crops may be confronted with either a relatively late or a relatively early incidence of the disease. To best match the length of the cycle

and the season (season length is limited by severe incidence of potato late blight), an early cultivar (early initiation of tubers and early tuber growth at the expense of haulm growth) is most appropriate because as soon as the disease strikes and foliage is removed, at least a favourable proportion of the dry matter produced is allocated to the tubers. When late blight strikes late, a late cultivar is most appropriate since it will have produced much foliage (high leaf area index) that takes more time to be destroyed by blight and thus will continue to intercept more light compared with an early cultivar.

Conclusions

Typically, a potato breeding programme, from crossing parental lines to final selection of a new cultivar, will take 10-15 growth cycles (Caligari, 1992). In areas with temperate climates, this means that it takes 10-15 yr, and in areas where two cycles can be completed within a year, breeding a new cultivar takes at least 5 yr. We showed here how using a simple model of crop growth and development based on dry matter accumulation and partitioning helps to identify genotypes with a length of the growth cycle matching the length of the available growing season. We showed how crop yield-defining, -limiting and -reducing factors each influence the length of the season and cycle and how modelling helps to quantify the effects. Other modelling approaches may be valid when breeding-related aspects other than matching the length of the cycle and the season have to be tackled. Elliseche and Hoogendoorn (1995) reviewed the use of models in plant breeding and included resistance mechanisms to potato late blight caused by *Phytophthora infestans* (van Oijen, 1992) and to potato cyst nematodes (*Globodera* spp., Spitters and Ward, 1988). Future emphasis of modelling and breeding, besides resistance, will be on genotypical influences on the relation between biotic and abiotic factors and quality parameters such as size distribution, dry matter content and contents of desired (starch) and undesired (nitrate, glycoalkaloids) compounds in the harvested produce.

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Simulating critical plant traits in rice for increased weed competitiveness

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Abstract

The use of a dynamic simulation model species was investigated using available experimental data for identifying and quantifying parameters that significantly influence competitive ability of direct seeded rice. Early height increment, higher relative growth rate in leaf area development during the juvenile phase and lower relative growth rates at both the vegetative and reproductive stages were quantifiable characters that strongly influenced competitiveness. For a 10-20% change in all of the above traits, the model predicted very high yield increases for the crop in mixtures (111-228%) compared with the monocrop (7.6-12%). A major portion of the yield increases is attributed to the increased growth duration.

Introduction

Weeds are a major limiting factor in rice production, particularly in Asia. The literature on yield losses due to weeds and the high cost of weed management is numerous and includes a wide range of ecosystems, weed species and management scenarios.

High cost of labour coupled with the shortage of on-farm labour has resulted in a rapid shift to direct seeding practices in Southeast Asia (De Datta, 1986; Erguiza et al., 1990). Currently, farmers have no alternative but to use traditional varieties which were selected for transplanted cultures. Thus, there is an urgent need for new varieties suitable for these target areas. From a global perspective, high yields are also essential to justify increasing labour costs or the adoption of cost-intensive production practices.

In recognition of the need for high-yielding varieties in various ecosystems, there has been considerable emphasis on efforts to develop new plant types (Vergara, 1988; Janoria, 1989; Khush, 1990; Dingkuhn et al., 1993). The major essential attributes considered by breeders were the following: low tillering with 3-4 panicles per plant, no unproductive tillers, 200-250 grains per panicle, 90-100 cm tall, very sturdy stems, vigorous root system, multiple disease and insect resistance, 100-130-d growth duration, harvest index of 0.6, and a yield potential of 13-15 t ha⁻¹. Much research has also been

conducted to determine effects of different traits including leaf area index, canopy structure and leaf N on yield potential (Tanaka et al., 1966; Akita, 1989; Dingkuhn et al., 1993).

While selection for suitable height, canopy structure, vigorous root system and improvements in influx (photosynthetic efficiency) and efflux (maintenance respiration) parameters may offer varying degrees of competitive ability to the new plant type, evaluation for competitiveness has not been given importance as a significant criterion in breeding programmes. This is mainly due to 1) the expression of competitiveness being strongly dependent on cultural and management practices that influence emergence time and establishment rate of the crop relative to weeds, 2) technological advances in weed management that have overshadowed the contribution by the plants' potential competitive ability, and 3) the laborious and complex experimentation required. Hence, the contributions of these desirable traits toward the competitive ability of a new plant type are rarely, if ever, quantified. The current demand for pest management strategies with reduced pesticide input now places greater emphasis on the need to develop more competitive cultivars for efficient weed management.

In view of the above, ecophysiological competition models may be useful tools in quantifying and predicting performance of a given cultivar in a hypothetical environment and the performance of hypothetical plant types in specific environments. Identification of parameters that significantly influence competitive ability of species could provide useful information to rice breeders in their search for more efficient plant types. In this paper, we present results of simulation analysis using a validated competition model, with the objective to identify traits for improving competitiveness in rice cultivars. The performance of the theoretical plant types was evaluated using weather data from two rice-producing regions in Malaysia (Location 1 - Tanjong Karang, Selangor 03° 30' N, 101° 12' E and Location 2 - Kota Baru, Kelantan, 05° 56' N, 102° 20' E).

Materials and methods

The validated INTERCOM model (Rajan et al., 1995) was used to evaluate competitiveness of hypothetical new plant types against barnyardgrass (*Echinochloa crus-galli* L.) for a direct-seeded irrigated environment, where nutrients and water are nonlimiting. The plant parameter inputs that were changed to adapt the original model parameters for the local rice cultivar (MR84) and ecotype characteristics of the weed were as previously described (Rajan, 1991; Rajan et al., 1995). A rice density of 270 plants m⁻² (equivalent to 50 kg seed ha⁻¹) and an initial weed density of 130 plants m⁻² were used. All other initial parameter inputs were as previously incorporated in the model based on competition experiments between rice (cultivar IR64) and barnyardgrass at IRRI (Kropff and van Laar, 1993).

The traits evaluated in this study were plant development rates during vegetative (DVRV) and reproductive (DVRR) phases, improved seedling vigour as measured by relative growth rate in leaf area (RGRL) and early height increment rate (HS) and plant height. Growth was simulated in both monocultures and mixtures for each of the respective traits, individually and in combination, with increments of 5% to a maximum of 20%.

Results and discussion

Reducing the development rates during the vegetative phase (DVRV) gave the highest yield increase for the crop in mixtures compared with improvements in other traits investigated in isolation (Figs. 1-4). Yield increases in mixtures were between 30 and 116% for a 5-20% reduction in DVRV. The resulting extended vegetative growth phase increased crop growth duration by about 5-22 d, depending on location and growing season, while flowering was delayed by up to 21 d for a 20% reduction in DVRV. Crop growth duration was extended from 118 to 140 d.

A corresponding reduction in the reproductive development rate (DVRR) also indicated a competitive advantage for the crop in mixtures, giving yield increases of 15-39% and an increase in reproductive growth duration of about 2-8 d (Fig. 2). Increasing the grain-filling period was also beneficial to grain yield in the monoculture, with a 5-20% yield increase.

Tanaka et al. (1966) and Tanaka and Vergara (1967) reported that the optimal growth duration for maximum rice yield in the tropics was 120 d. The simulation results are in agreement with the above reports for rice in monoculture. In mixtures, on the other hand, the simulation results suggest that an increase in growth duration is favourable to the crop under competition due to the added advantage of a higher maximum LAI and a slightly longer period of grain filling. This plant type is desirable in situations where the standard of weed management after crop emergence is inadequate. For practical considerations, however, a medium duration of 110-120 d is desirable so that intensive double-crop production systems can be adopted (Khush, 1990).

Plant height increases of 5, 10, and 15% gave 15, 31, and 43% yield advantages to the crop in mixtures. However, increase in plant height above the current value of 110 cm is undesirable as lodging would present major problems, unless the new plant type is also selected for sturdier stems.

Relative growth rate in leaf area development (RGRL), which reflects seedling vigour or early maximum carbon assimilation, was found to be an important character that gave a significant competitive advantage to the crop in mixtures (Fig. 3). A 5, 10, 15 and 20% increase in vigour, which favoured earlier canopy development, resulted in a competitive advantage in the mixtures with yield increases of 14, 25, 38 and 48%,

respectively. The increase in seedling vigour did not influence yield of the crop in monoculture. A 5-20% increase in the height increment (HS) parameter resulted in a 9-31% increase in yield in the mixture, but it did not influence yield in the monoculture (Fig. 4).

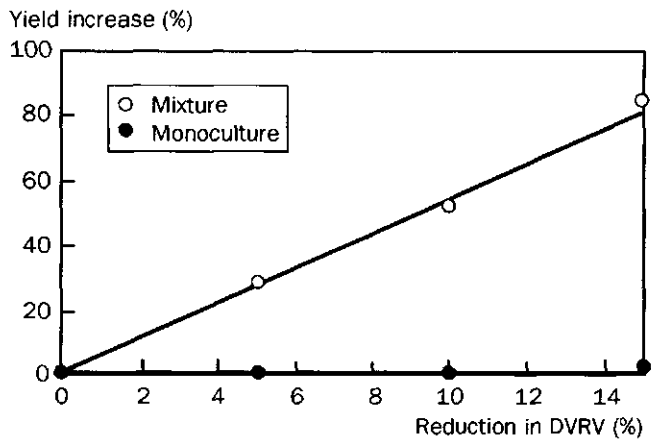


Figure 1. Potential yield increases in rice cultivar MR84 in response to reduction in vegetative development rate (DVRV) prior to flowering. (Competing weed: *E. crus-galli*; days to DS1=92-109, days to DS2=118-141; Station-Tanjong Karang.)

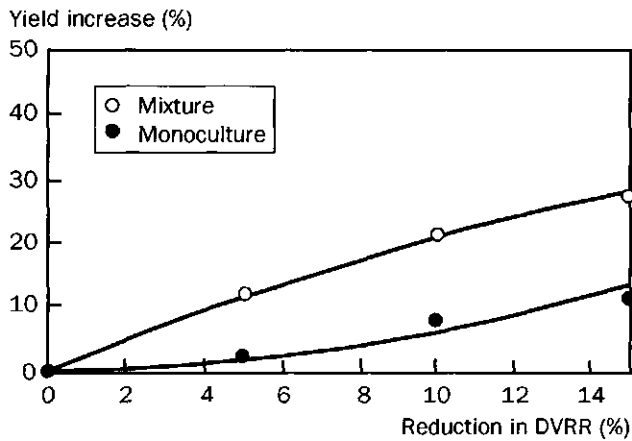


Figure 2. Potential yield increases in rice cultivar MR84 in response to reduction in reproductive development rate (DVRR) after flowering. (Competing weed: *E. crus-galli*; days to DS1=88, days to DS2=118-126; Station-Tanjong Karang.)

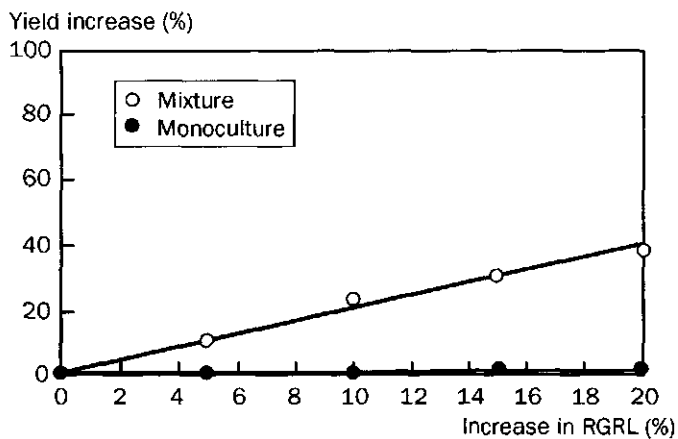


Figure 3. Potential yield increases in rice cultivar MR84 in response to increases in seedling vigour (RGRL). (Competing weed: *E. crus-galli*; days to DS1=88, days to DS2=118; Station-T. Karang.)

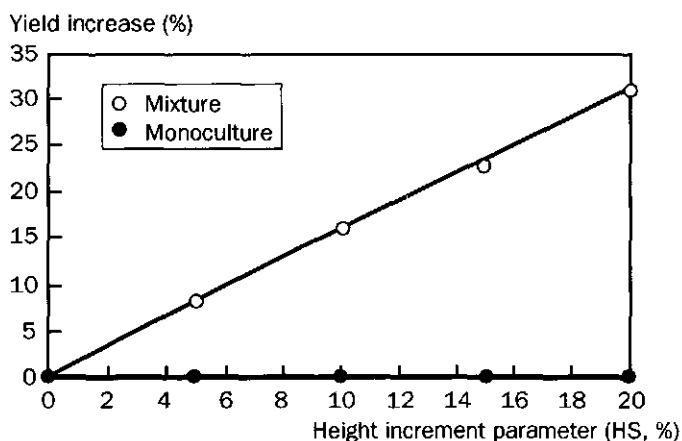


Figure 4. Potential yield increases in rice cultivar MR84 in response to increased height increment rate. (Competing weed: *E. crus-galli*; days to DS1=88, days to DS2=118).

Conclusion

The results of this study indicate the potential application of the INTERCOM model to evaluate quantitatively the relative importance of traits that enhance competitive ability

in a new plant type. It can be a useful tool for predicting the performance of diverse germplasm and for testing improved plant types for adaption to different environments.

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Relative influence of genotype, environment and their interaction on crop input parameters of ORYZA1

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Abstract

Greater use of crop simulation models is being suggested to increase the efficiency of multi-environment trials. An irrigated lowland field experiment with seven genotypes was conducted at three locations to examine the relative influence of genotype (G), environment (E), and G \times E interaction on crop input parameters of ORYZA1. The crop parameters were DVRJ (development rate constant for basic vegetative phase), DVRP (development rate constant for panicle formation phase), DVRR (development rate constant for grain-filling phase), SPGF (spikelet formation factor), and WGRMX (maximum weight for grain). Genotypic and G \times E interaction effects were significant for all parameters. The size of G \times E interaction varied among parameters. The environmental influence on development rate constants was greater than that of genotypic and G \times E interaction. More than 50% of variation in SPGF was due to genotypic effects. WGRMX was influenced more or less equally by genotype and environment. G \times E interaction accounted for about one-fourth of total variation for SPGF and one-fifth for WGRMX. The large environmental and G \times E interaction influences on development rates suggest that the model needs to be refined further to accurately determine development rate constants. The relatively negligible influence of environment on SPGF shows that this parameter can be used to understand and predict the determination of spikelet number in irrigated, well-fertilised rice crops.

Introduction

In multilocation trials, crop growth and yield characters are influenced by interaction between genotype (G) and environment (E). Knowledge on relative influence of G and G \times E components is needed by plant breeders for achieving genetic advance by manipulating these components (Lawn et al., 1995). Simulation models can be used for analysing and extrapolating G \times E interaction (Aggarwal et al., 1995; Hammer and Vanderlip, 1989), thus increasing the efficiency of plant breeding programmes.

Crop models use several coefficients to characterise a crop or a variety. In general, these inputs are assumed to be 'genetic'. Sutoro and Makarim (1995) showed large variation in plant traits among rice varieties. In this paper, we report the results of a multilocation trial conducted to study the relative influence of G, E and G \times E interaction on ORYZA1 (Kropff et al., 1994) input parameters relating to phenology and sink capacity.

Materials and methods

A field experiment arranged in a randomised complete block design with three replications and seven genotypes was conducted at three environments (locations) in 1994 season (June-October) under lowland irrigated condition. The genotypes were IET13231, IET13232, IET13238, IET13239, IET13245, Ratna and Vikas. The locations were Aduthurai (11°00' N, 79°30' E, 20 m MSL), Hyderabad (17°25' N, 78°26' E, 545 m MSL) and New Delhi (28°35' N, 77°12' E, 216 m MSL). Recommended agronomic practices were followed and the crop was maintained free from abiotic and biotic stresses.

Data were collected on days to panicle initiation, flowering and physiological maturity; dry matter accumulation in plant parts at panicle initiation, flowering and maturity; spikelet number per unit area; and maximum weight per grain. Panicle initiation was observed through a magnifying glass after peeling off the shoot daily around the expected period. Maximum grain weight was recorded from grains borne on matured panicles from which 70-90% of spikelets had been artificially removed at the flowering stage.

Using the experimental data, the following ORYZA1 model parameters were derived for each replication:

- DVRJ, development rate constant ($^{\circ}\text{Cd}^{-1}$) for basic vegetative phase from sowing to start of photoperiod-sensitive phase
- DVRR, development rate constant ($^{\circ}\text{Cd}^{-1}$) for panicle formation phase from panicle initiation to first flowering
- DVRR, development rate constant ($^{\circ}\text{Cd}^{-1}$) for grain-filling phase from first flowering to physiological maturity
- SPGF, spikelet growth formation factor (number of spikelets $\text{kg dry matter}^{-1}$)
- WGRMX, maximum weight per grain (kg grain^{-1})

Combining the data from the three environments, analysis of variance was performed to apportion the source of variation and to find out the statistical significance of effects of G, E and G \times E interaction on each parameter.

Results and discussion

The means of seven genotypes (G) and the corresponding coefficients of variation for the ORYZA1 model parameters at three environments (E) are presented in Table 1. Variations in DVRJ and DVRP were relatively more than that in DVRR among environments. The efficiency in spikelet production (SPGF) was not significantly influenced by the environment, though DVRP (regulating the period of spikelet differentiation and formation) varied by more than 60% between environments.

The environment influenced the potential weight of grain. WGRMX was more at Hyderabad than at the other two locations. A negative association between DVRR and WGRMX is apparent. It is understandable that the longer grain-filling phase ensures greater assimilate translocation for grain growth.

The coefficient of variation was relatively high for DVRP at Hyderabad and New Delhi. It is likely that the method of observation for determining the onset of panicle initiation contributed to the high coefficient of variation.

Table 1. Values of input parameters (mean of seven genotypes) and coefficients of variation at three locations in India.^a

Input parameter ^b	Aduthurai		Hyderabad		New Delhi		LSD (5%)
	Mean	CV(%)	Mean	CV(%)	Mean	CV(%)	
DVRJ (°Cd) ⁻¹	1.003	0	0.557	0	0.626	3	0.0060
DVRP (°Cd) ⁻¹	0.772	1	1.256	11	1.106	15	0.0767
DVRR (°Cd) ⁻¹	1.958	0	1.330	4	1.762	4	0.0313
SPGF (no. kg ⁻¹)	65.750	1	64.909	14	62.498	4	3.2731
WGRMX (kg grain ⁻¹)	20.529	2	24.752	2	21.524	3	0.3366

^aDifferences among G and G × E interactions are highly significant for all parameters.

^bFor actual values of DVRJ, DVRP, and DVRR, multiply by 10⁻³; for SPGF, by 10³, and for WGRMX, by 10⁻⁶.

Statistically, the differences among G and G \times E interactions were highly significant for all parameters. The sums of squares have been partitioned into G, E G \times E interactions and residuals and presented as percentages in Table 2.

The environmental influence on development rate constants was greater than that of genotypes and of G \times E interaction. Nearly 80% of the variation in DVRR and 87% in DVRJ were due to environment. Relatively, the genotypic and G \times E interaction influences on DVRP were more than those on DVRJ and DVRR and the environmental influence on DVRP was far less than that on DVRJ and DVRR. The large environmental and G \times E interaction influences on development rates suggest that the model needs to be refined further to determine the development rate constant. Imprecise measurements and absence of stress effects on crop development could also be partially responsible for the large G \times E effects.

More than 50% of variation in SPGF was due to genotypic effects. Moreover, the environmental influence was least on SPGF. Sutoro and Makarim (1995) found considerable varietal difference in SPGF in a field experiment with 17 varieties. The high genotypic variation and the negligible influence of environment on SPGF add strength to the model because efficient breeding lines can be identified with confidence, although G \times E interaction accounted for about one-fourth of the total variation. These

Table 2. Partitioning of sums of squares (SS) into genotype (G), environment (E), G \times E interaction and residual for input parameters.

Model parameter		Genotype (df ^a =6)	Environment (df=2)	G \times E interaction (df=12)	Residual (df=40)
DVRJ	SS	0.132	2.425	0.224	0.004
	%	4.7	87.1	8.0	0.1
DVRP	SS	1.018	2.576	2.317	0.605
	%	15.5	39.3	35.4	9.2
DVRR	SS	0.457	4.344	0.553	0.101
	%	8.4	79.6	10.4	1.8
SPGF	SS	3032.98	119.62	1319.15	1101.70
	%	54.2	2.1	23.6	19.7
WGRMX	SS	224.48	204.78	101.71	11.65
	%	41.4	37.7	18.7	2.1

^adf = degrees of freedom.

lines may or may not be high-yielding but the most efficient ones will be useful parents in breeding programmes to increase spikelet number. WGRMX was more or less equally influenced by G and E. The G \times E interaction constituted about one-fifth of the total variation. Differences in soil fertility, crop management practises and source-sink interactions would have contributed to the G \times E interaction effects on SPGF and WGRMX.

A relatively high proportion of residual sums of squares for SPGF and DVRP warrant accurate measurement of crop characters from which these model parameters are derived. The present study showed that G \times E interaction significantly influenced model parameters and that size of interaction varied among parameters. We need to know the causes for the G \times E interaction on model parameters so that we can minimise them to improve the reliability of the predictions of crop simulation models.

Acknowledgments

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Agroenvironment characterisation for crop improvement programmes

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Abstract

Characterisation of agroenvironment for crop improvement programmes using spatial databases on biophysical properties and management inputs and systems tools can help identify and delineate genotype adaptation domains and better define breeding targets. In this paper, a framework for agroenvironment characterisation for plant breeding to determine suitable adaptation environments and to define environmental challenges to germplasm improvement is presented.

Introduction

The rate of growth of the rice-eating population is increasing faster than that of the rest of the world while the rate of increase of rice production is slowing down. IFPRI (1977) predicts that the demand for rice will exceed rice production by the turn of the century. As the land area devoted to rice remains the same, or even decreases in some rice-producing countries due to population pressure, the increasing demand for more rice will have to be met by increasing the yield potential of rice (Khush, 1995). It is estimated that by 2025, rice yields need to be doubled (Hossain & Fischer, 1995).

The traits required in new plant types for increased yield potential can be determined by applying crop simulation models where a range of parameters can be defined to determine the differences between genotypes in terms of their contribution to grain yield increase. This requires evaluation of the range of variability and the sensitivity of grain yield to changes associated with each of these parameters. The relative importance of traits may vary with location, crop season and crop management. It is now feasible to use systems tools such as simulation models and historical weather data to conduct a conventional risk analysis to determine optimal plant traits for a given agroenvironment.

A major activity in plant breeding research is the identification of genotype-specific adaptation domain. This involves multilocation and multiseason crop performance evaluation of plant breeding lines. Every year in international, national and regional

germplasm evaluation programmes, hundreds of experiments are conducted for this purpose. This involves huge investment of time, money, manpower and other resources. It will be ideal to characterise testing sites into homogeneous zones based on their biological and physical characteristics. On the other hand, limited multilocation breeding trials will require extrapolation from key sites to a large number of locations or to a larger domain of production area or agroecological zone.

This paper presents the use of systems approach in agroenvironment characterisation to determine suitable adaptation domains for genotypes and to identify breeding targets for germplasm improvement. A framework is described for this purpose which entails the application of systems tools, the spatial databases on biophysical properties and management inputs in crop production.

Framework for agroenvironment characterisation in plant breeding research

Agroenvironment characterisation involves the use of existing databases on biophysical characteristics (e.g., climate, soil) and on management inputs (e.g., labour, planting density, irrigation), and the application of systems tools such as crop simulation models, geographic information systems (GIS and weather data generators to determine the adaptation environments or recommendation domains for breeding lines or genotypes (Fig. 1).

Stepwise, the framework consists of the following activities:

1. Delineation of agroecological zones or agroenvironments based on databases on biophysical variables and management inputs. This is facilitated by the use of GIS and systems tools including weather generators.
2. Evaluation and screening of breeding lines and genotypes using crop simulation and field experiments. Preliminary screening of genotypes can be done via crop simulation to determine genotypic groups with similar crop performance. Field experiments can be conducted to evaluate further the performance of the selected genotypes.
3. Multienvironment evaluation of crop performance across different locations and several seasons or years such as in multilocation trials (MLTs) or crop improvement testing sites.
4. Determination of adaptation domains and breeding targets by extrapolation using GIS for delineating the recommendation domains and crop models for designing new plant types for increased yield, drought resistance or resistance to pests and diseases.

Several examples are now available where this framework has been illustrated. Aggarwal (1993) proposed ten zones for wheat in India based on the biophysical characterisation of the environment. This classification is very different from the existing wheat zones recognised by the variety evaluation programme of the Indian Council for Agricultural Research. It would be worthwhile to determine if the systems analysis-based classification can increase the efficiency of the breeding programme by reducing the number of sites within a zone. Chapman and Bareto (1994) recently conducted a detailed study using crop models, weather databases, and GIS to determine adaptation domains for maize in Latin America and southern Africa. They used phenology and drought resistance to cluster sites. The simulated midseason drought in southern Africa indicated that there are large areas where drought-tolerant germplasm should be advantageous. These examples illustrate the power of systems approach to better define the crop- and variety-specific environment. There is a need for a critical review of agroecological zones used in germplasm evaluation programmes.

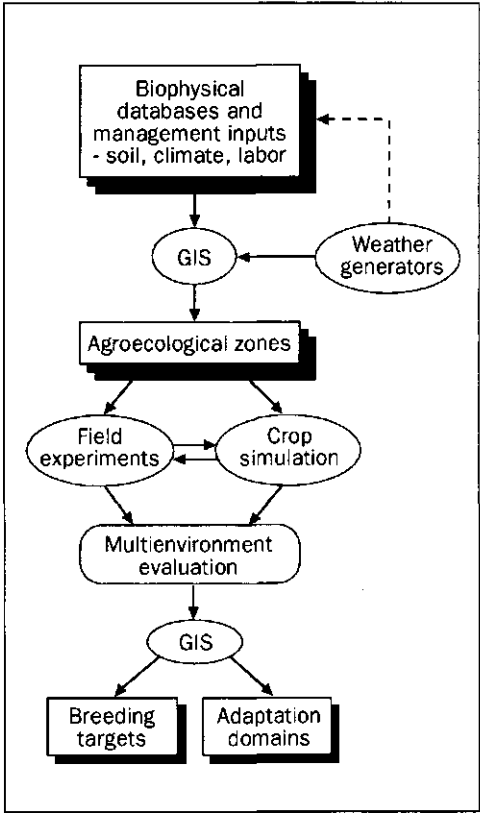


Figure 1. Framework for agroenvironment characterisation for plant breeding.

Concluding remarks

The research framework for agroenvironment characterisation in plant breeding presented in this paper provides a strategy to identify and delineate the genotypic adaptation environment and to define the breeding goals targeted for specific agroecological zones. The framework can assist in designing and testing improved plant types suited to regional agroenvironments and in increasing the efficiency of multilocation trials by this approach.

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Predicting yields of new varieties in different test environments in the Philippines

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Abstract

Field experiments were conducted in irrigated lowland conditions at PhilRice in Nueva Ecija, Philippines, to evaluate the model ORYZA1 and use the input parameters from the Philippine Seed Board (PSB) variety in predicting yields in the different NCT I test environments. Results for PSB Rc2 and PSB Rc14 showed a good correlation between simulated and observed yields. Yield predictions in most of the NCT I environments tested (Nueva Ecija, Iloilo, Agusan del Norte, Ilocos Norte and Laguna) showed that yields were 7-8 t ha⁻¹ when sown in January, 5 t ha⁻¹ in September and 8 t ha⁻¹ in December. In Cagayan, yields were stable at 7 t ha⁻¹ until September and 9 t ha⁻¹ from October to December due to relatively stable solar radiation and lower temperatures. In Nueva Ecija, Iloilo, Ilocos Norte and Laguna, simulated yields of PSB Rc14 and IR72 were higher than the observed yields of check variety IR72 and four breeding lines (PR23391-1, PR24291-2, PR21209-389 and PR23117-1072) during the dry and wet seasons. Yield differences were partly attributed to lower N fertiliser application rates used in the NCT I sites. Further model evaluation using crop input parameters from breeding lines in NCT test environments will have to be done to strengthen future simulation studies.

Introduction

Before recommending new rice varieties to the Philippine Seed Board (PSB), the National Cooperative Rice Performance Test (NCT) evaluates promising breeding lines in many testing sites in the Philippines for several seasons. Tests involve evaluation of yield performance, pest resistance, and grain quality. The yield performance test evaluates traits such as crop maturity, height, productive tillers and grain yield. Because yield is the result of the interplay of variety, management and environment (Yoshida, 1981), quantitative assessment of crop performance in a given environment may facilitate the evaluation process (Hunt, 1993). Ecophysiological models (Penning de Vries et al., 1989; Kropff et al., 1994) can be used to quantitatively assess crop growth and yield. In the present study, we report results of evaluation of the ORYZA1 model (Kropff et al., 1994) using data from field-grown PSB varieties and predicted yields in the different

NCT sites in the Philippines.

Materials and methods

Field experiments and model inputs

Varieties PSB Rc2 (120 d duration) and PSB Rc14 (110 d) were grown at the PhilRice experimental farm (Maligaya clay soil) in Muñoz, Nueva Ecija, Philippines, during the 1994 cropping seasons. Seedlings were grown in the seedbed for 21 d prior to transplanting in the experimental field. Seedlings were transplanted at 2-3 seedlings/hill and 20 cm x 20 cm distance between hills. Treatments had four replications and were laid out in a split-plot design with nitrogen (N) levels as the main plots and varieties as subplots. In the wet season, NPK rates were 0-40-40, 90-40-40 and 135-40-40 kg ha⁻¹. In the dry season, NPK rates were 0-40-40, 90-40-40 and 180-40-40 kg ha⁻¹. In both experiments, N was applied in three splits: 1/2 basal, 1/3 at panicle initiation and 1/6 at flowering and physiological maturity; 8-10 hills were sampled and analysed for leaf area index (LAI), dry matter and N concentration (Kjeldahl method). Planting dates, weather data, leaf N concentration at particular growth stage and crop development rate coefficients for each variety were used as inputs to the model ORYZA1. Plant parameters were obtained from N treatment of 180 kg ha⁻¹. For each of the six sites, 5-10 yr of weather data were used. Observed and predicted yields of PSB Rc2 and PSB Rc14 under PhilRice conditions were compared. Yields of PSB Rc14 as a function of weekly sowing dates were predicted in six NCT I test sites (see NCT Test). Yields of PSB Rc14 and IR72 were predicted in four NCT I test sites and compared with observed yields of IR72 and four breeding lines (see NCT Tests).

NCT test

After going through hybridisation, field observation nursery and preliminary yield trials, the entries are tested in NCT sites I and II (Fig. 1). There are 9 sites in NCT I and 15 sites in NCT II. Entries are assessed for pest resistance in other sites usually considered 'hot spots' or where pests are more prevalent. The outstanding entries are presented to the Philippine Seed Board (PSB), now called National Seed Industry Council (NSIC), prior to approval and release of entries as varieties.

Yields as a function of different sowing dates were predicted for six sites of NCT I—1) Muñoz, Nueva Ecija; 2) Jaro, Iloilo; 3) Iguig, Cagayan; 4) Butuan, Agusan del Norte; 5) Dingras, Ilocos Norte; and 6) Los Baños, Laguna. Predicted grain yields of PSB Rc14 and IR72 and observed yields of PSB Rc14 (only in Muñoz), check variety IR72 and four breeding lines (PR233399-1, PR24291-2, PR 21209-389 and PR23117-1072) were obtained from 4 NCT test sites—Muñoz, Jaro, Dingras and Los Baños.

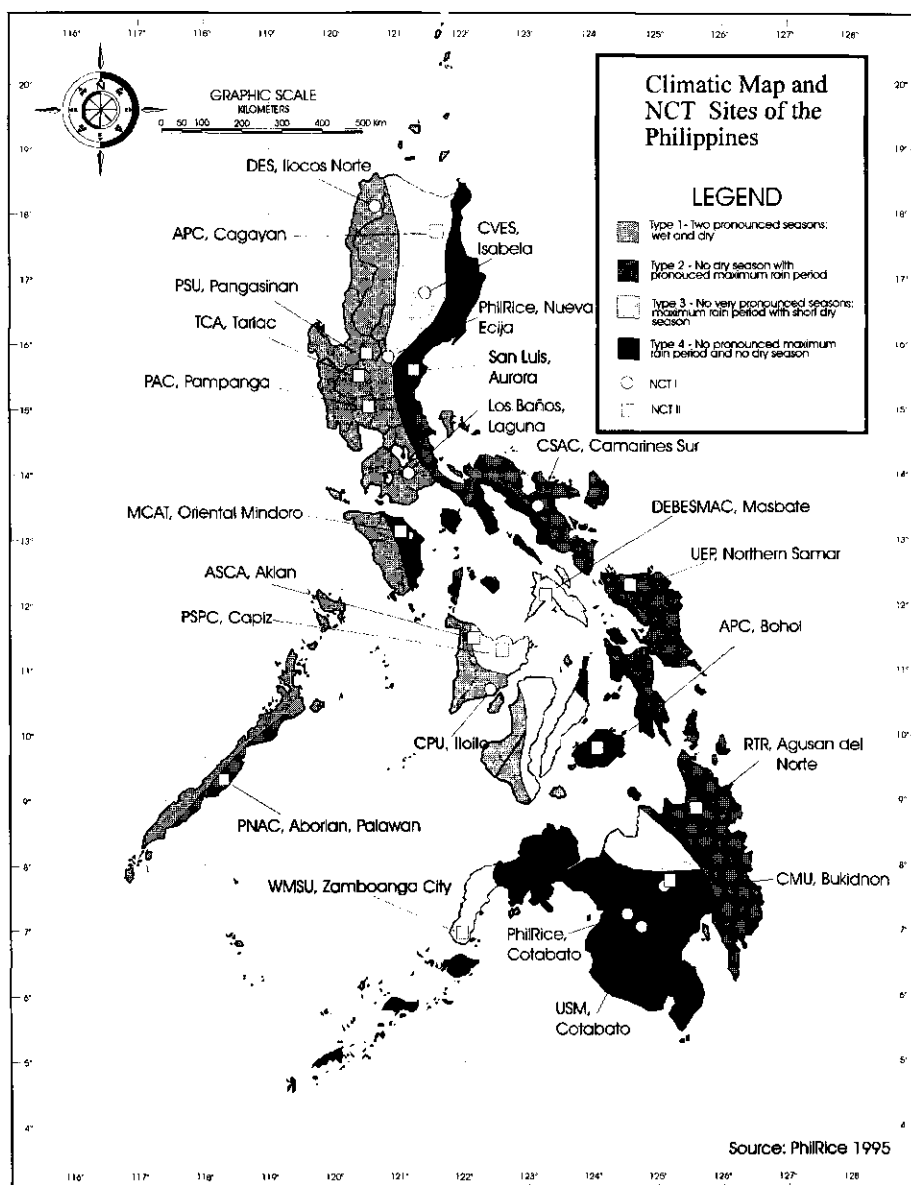


Figure 1. Climatic map and the National Cooperative Rice Performance Test (NCT) sites I and II of the Philippines. NCT tests are coordinated by PhilRice. Institutions (acronyms) and municipalities are followed by their provinces.

Results and discussion

Evaluation of the crop model

When grain yields were simulated with inputs of solar radiation temperature, crop specific development rates and leaf N, the relationship between observed and simulated yields for PSB Rc 14 and PSB Rc2 was very close ($r^2 = 0.86$, Fig. 2), indicating that the model can be used for predicting grain yields in Philippine environments.

Yields at weekly sowing dates

The model was run with crop inputs from PSB Rc14 (at 180 N kg ha⁻¹) and site weather data to predict grain yields in six NCT I sites. In Nueva Ecija, Iloilo, Agusan del Norte, Ilocos Norte and Laguna, average yields decreased from 7 to 5 t ha⁻¹ during January-September sowing dates (Fig. 3) due to lower solar radiation (Fig. 4). Then yields increased to 8 t ha⁻¹ during December due to exposure of the later growth stage to higher solar radiation. Average solar radiation was 20 MJ m⁻² in March and 18 MJ m⁻² in September. In Iguig, Cagayan, however, average yields were relatively stable at 7 t ha⁻¹ until September and 9 t ha⁻¹ during the October-December sowing dates (Fig. 3). Average solar radiation at Iguig was relatively stable at 20 MJ m⁻² and average minimum (20 °C) and maximum (28 °C) temperatures were lower than those in the other NCT sites

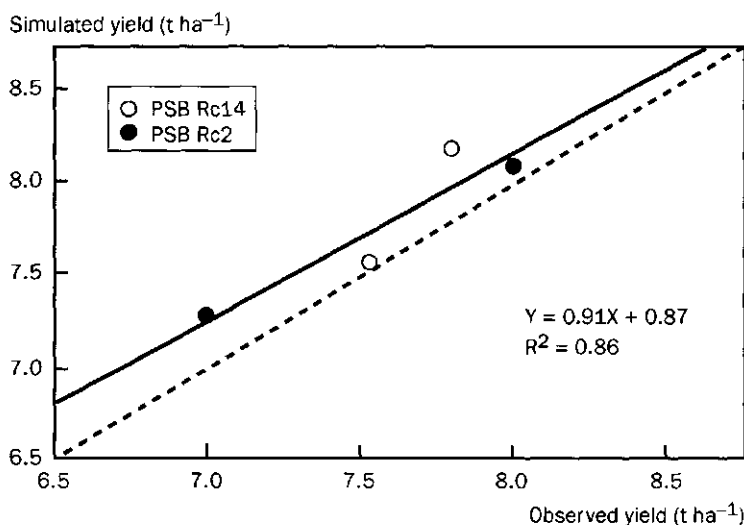


Figure 2. Relationship between observed and simulated yields of rice and its deviation from the 1:1 line. Data were obtained from 1994 field experiments at PhilRice, Muñoz, Nueva Ecija, Philippines.

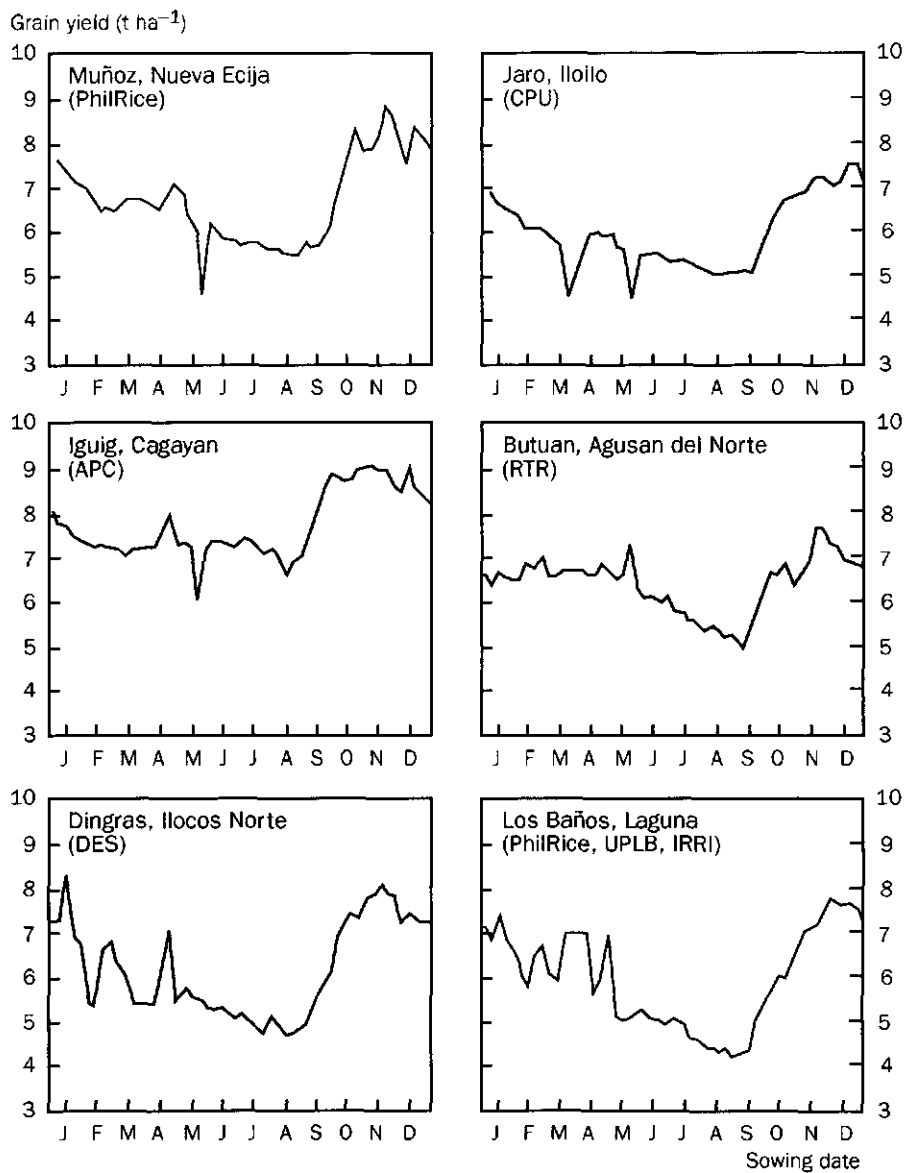


Figure 3. Weekly predictions of yields of PSB Rc14 in selected NCT I test sites in the Philippines (coordinating institutions in parenthesis). Five-year weather data for Nueva Ecija and Agusan del Norte, 9-year weather data for Cagayan and Ilocos Norte, and 13-14-year weather data for Iloilo and Laguna were used.

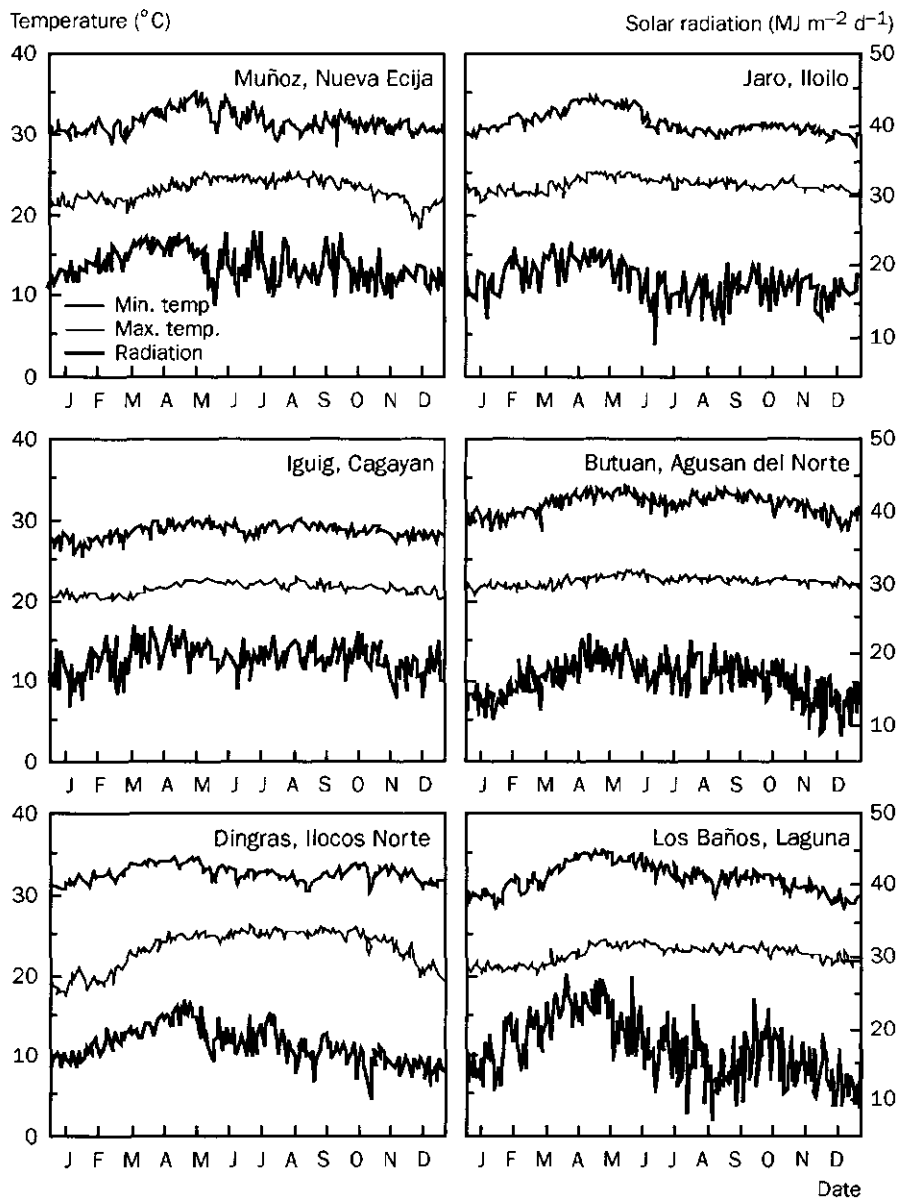


Figure 4. Daily temperature and solar radiation data (5-year average) for the selected NCT I test sites.

(Fig. 4). Based on regression analysis of 2-yr crop yield-weather data from long-term soil fertility studies, the high yields observed especially during the dry season was due to higher solar radiation and lower minimum and maximum temperatures (Pamplona et al., 1995). A combination of temperature and radiation can explain the differences in yield potential (Kropff et al., 1994). In Yanco, Australia, for variety YRL39, low temperature (21-23°C) results in a long grain-filling duration and the high radiation level (23 MJ m⁻²) results in high growth rate per day and thus high yields (close to 15 t ha⁻¹). In the tropics, temperature is high and growth duration is short, and high radiation in the dry season (usually January-May in the Philippines) helps attain higher yield than the wet season.

Yields at NCT I sites

In NCT I sites in Nueva Ecija, Iloilo, Ilocos Norte and Laguna, average observed yields of the four breeding lines (PR23399-1, PR24291-2, PR21209-389 and PR23117-1072) and check variety IR72 were close to 6.0 t ha⁻¹ in the dry season and 4.3 t ha⁻¹ in the wet season (Fig. 5). However, across the four sites during the dry season, observed yields of PR23399-1 ranged from 4.8 to 6.1 t ha⁻¹; PR24291-2 from 4.9 to 6.7 t ha⁻¹; PR21209-389 from 5.4 to 6.5 t ha⁻¹; and PR23117-1072 from 5.0 to 7.0 t ha⁻¹. In wet season, observed yields of the 4 breeding lines were lower and yield differences across sites were greater than in the dry season (Fig. 5). At Nueva Ecija (close to an NCT site), average observed yields of PSB Rc14 were 7.5 t ha⁻¹ in the dry season and 5.4 t ha⁻¹ at 90 kg N ha⁻¹ in the wet season. In the 4 NCT I sites mentioned, simulated yields of PSB Rc14 ranged from 6.9 to 7.7 t ha⁻¹ in the dry season and 4.9 to 5.7 t ha⁻¹ in the wet season, indicating closeness to the observed yields. For IR72, simulated yields ranged from 8.7 to 9.5 t ha⁻¹ in the dry season and from 6.5 to 7.0 t ha⁻¹ in the wet season. Simulated yields of PSB Rc14 were higher than the observed yields of the breeding lines and check variety IR72 by about 1 t ha⁻¹. Simulated yields of IR72 were higher by about 3 t ha⁻¹. That observed yields in experimental plots (PSB Rc14 at 180 kg N ha⁻¹ in Muñoz) and simulated yields were higher than yields obtained in NCT sites suggest that N applied in NCT sites could be lower. Most NCT sites have been farmed for a number of years and hence, will require higher fertiliser inputs due to nutrient depletion. In multilocation trials similar to those in NCT, Palanisamy et al. (1995) suggested that the higher yields obtained in simulation studies could be attributed to the standard leaf N content input of completely IR72 obtained from well-fertilised experiments. Furthermore, the NCT sites may not be completely free from biotic and abiotic stresses. Thus, these sites will have to be managed as in experimental plots. Detailed genotypic/phenotypic characteristics of breeding lines in NCT test environments and characteristics of sites will be needed for greater use of this approach in multienvironment testing.

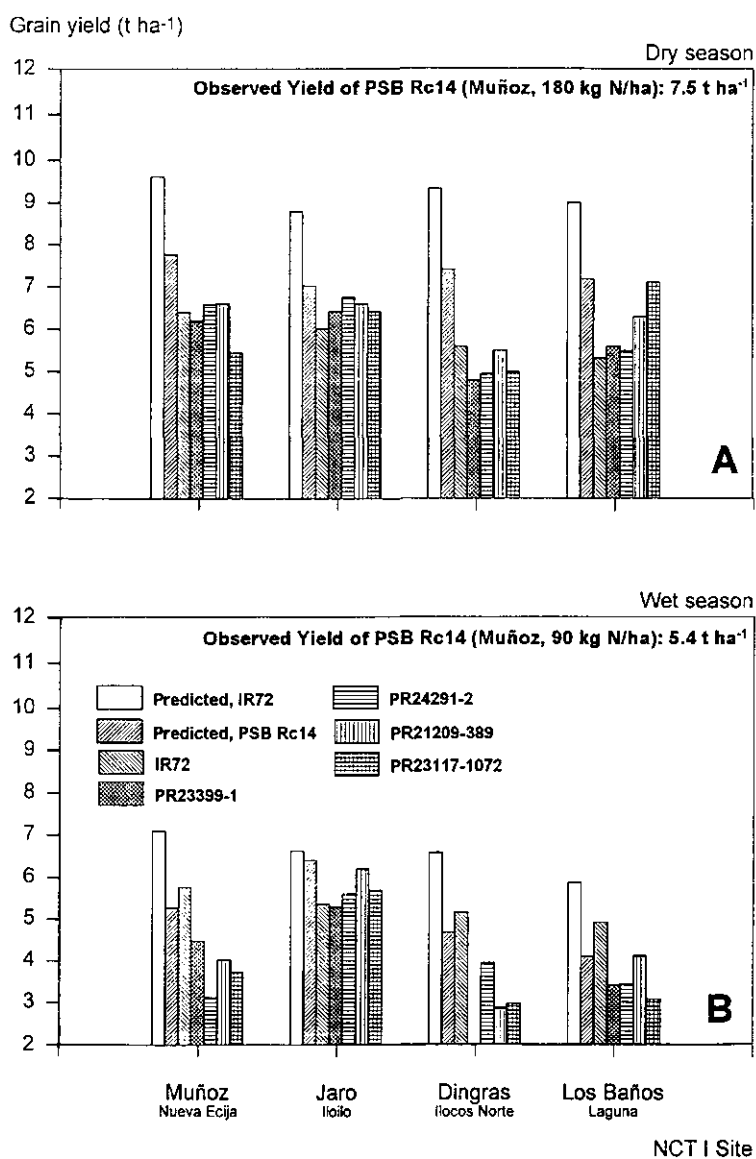


Figure 5. Predicted yields of IR72 and PSB Rc14 and observed yields of check variety IR72 and four breeding lines in 4 sites of NCT 1 during the dry (A) and wet (B) seasons. Nitrogen rates were 60-90 kg ha⁻¹ during the wet season and 100-120 kg ha⁻¹ during the dry season.

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Nitrogen recommendation for irrigated rice in Jiangxi Province of South China

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Abstract

This paper describes the issues related to the method of determining the amount of N to be applied to irrigated rice in Jiangxi Province, People's Republic of China. The results of using the recommendation generated by the simulation tool MANAGE-N showed the advantage of late N application in increasing the grain yields. The model recommendation has been included in the crop cultivation chart used by farmers.

Introduction

Nitrogen is one of the main nutrients for rice growth. In the last forty years, the application of chemical N fertiliser has increased rapidly in ricefields in China. Although the amount of total N application increased grain yield, economic efficiency had not increased proportionately. Most of the N application methods used by farmers followed recommendations from early research (Zhang, 1987). Since 1985, scientists have started introducing the concept of applying fertiliser according to soil fertility measurement in south China (Ding et al., 1987). The amount of N application could be determined based on soil fertility, variety and plant uptake, but timing of N application still has to be improved. The introduction of MANAGE-N (Riethoven et al., 1995), a simulation tool, has given researchers the opportunity to do so.

Present N application in Jiangxi Province

Determination of N application amount

The amount of N to be applied (kg ha^{-1}) is determined by Eqn 1.

$$\text{Amount of N to be applied (kg ha}^{-1}\text{)} = \frac{(\text{Target grain yield} \times \text{N amount in grain}) - \text{amount of N supplied by soil}}{\text{Recovery of fertiliser N (\%)}} \quad (1)$$

$(\text{kg ha}^{-1}) \quad (\text{kg kg}^{-1}) \quad (\text{kg ha}^{-1})$

The total amount of N uptake by the plant is calculated as the product of target grain yield and N amount in grain. The amount of N supplied by the soil is an important index to evaluate soil fertility. It can be calculated from Eqn 2.

$$\text{Amount of N supplied by soil (kg ha}^{-1}\text{)} = (\text{N content of tilled soil } [\%]) \times (\text{supplied rate of soil N } [\%]) \times (\text{weight of tilled soil [kg ha}^{-1}\text{)}) \quad (2)$$

The supplied rate of soil N is calculated from Eqn 3. It is the ratio of N uptake by the plant without fertiliser N application to the total amount of N in the soil. The weight of tilled soil can be calculated according to the volume of soil.

$$\text{Supplied rate of soil N } (\%) = \frac{(\text{Grain yield without N application [kg ha}^{-1}\text{)]} \times (\text{N amount in grain [kg kg}^{-1}\text{)])}{(\text{N content of tilled soil } [\%]) \times (\text{weight of tilled soil [kg ha}^{-1}\text{)])} \quad (3)$$

As P and K stimulate uptake of soil N, the experiment for measuring the supplied rate of soil N should be conducted at the local levels of P and K application. There is a close negative correlation between the supplied rate of soil N and the N content of tilled soil (Table 1). Therefore, the supplied rate of soil N can be estimated from the N content of the tilled soil.

The recovery rate of N varied depending on the amount and timing of N application (Table 2). It is about 30-40% under current farmer practices. But it can be further improved by adjusting the amount and timing of N application.

Timing of N application

The timing of N application in Jiangxi Province and also in south China mostly depends on the growth duration of varieties, which is closely related to the panicle type (Guo, 1991). Usually 100% of fertiliser N is applied within 20 DAT for the short growth-duration varieties (100-110 d). The termination date of effective tiller production is about 20 DAT. About 70-80% of fertiliser N is applied within 20 DAT for the long growth-duration varieties (125-135 d), the remaining is applied from booting (15 d before heading) to heading.

Table 1. Relationship between N content of the tilled soil and supplied rate of soil N (Ding et al., 1987).^a

Grain yield (kg ha ⁻¹)	N content of tilled soil (%)	Supplied rate of soil N (%)
4500-4875	0.239-0.275	1.25-1.45
3750-4500	0.167-0.221	1.55-1.85
3000-3750	0.095-0.149	1.95-2.25

^aTaken from 95 experimental sites.

Table 2. Recovery rate of fertiliser N (%).

N application (kg ha ⁻¹)	Treatment	N utilisation rate (%) ^a
50	0 DAT ^b	35 (24)
50	10 DAT	67 (55)
50	25 DAT	86 (53)
50	40 DAT	97 (67)
50	Heading	61 (67)
100	Two splits	69
150	Three splits	52
120	Farmer practice	30-40

^aMeasured at harvest, figures in parentheses were measured 15 d after N application.

^bDAT = days after transplanting.

Results of present N application method

Table 3 shows that the difference between the target yield and the actual yield ranged from 1.18 to 19.66% in fields with low and medium soil fertility. The determination of target yield is based on soil fertility, variety and price of fertiliser. If the target yield is too high, the economic efficiency will be reduced. The N demand of the grain is higher at the high level of grain yield than at the low level of grain yield (Table 4).

Table 3. Comparison of the target yield and actual yield the fields with low and medium soil fertility (Ding, 1987).

Site	Target yield (kg ha ⁻¹)	Actual yield (kg ha ⁻¹)	Difference	(%)
Site 1	4500	5182	+682	15.16
	5250	5430	+180	3.43
	6000	5444	-556	9.27
Site 2	3750	3997	+247	6.59
	4500	4625	+125	2.78
	5250	4925	-325	6.19
	6000	5049	-951	15.85
	6750	5423	-1327	19.66
Site 3	4500	4740	+240	5.33
	5250	5391	+141	2.69
	6000	5929	-71	1.18
Site 4	5625	5655	+30	0.53
	6000	5897	-103	1.72
	6375	6155	-220	3.45

Table 4. N demand of grains at different yield levels.

Grain yield (kg ha ⁻¹)	N demand (kg N 100 kg grain ⁻¹)
<4500	1.8
4500-5250	1.9
5250-6000	2.0
>6000	2.1

Further improvement of the present N application method

Amount and timing of N application generated by MANAGE-N

MANAGE-N can determine the amount of N application to obtain the most economic and most efficient level of grain yield under a given grain and fertiliser price (Riethoven et al., 1995). The timing of N application can follow the curve generated by the model (Fig.1). The model recommendation indicates continuing uptake of N by plants. It can also be deduced from the model that higher yield is induced from more splits. Validation experiments showed that grain yield of the model recommendation was 10% higher than that obtained following local practices at the same N application level (Zhong & Shi), 1995) or even at lesser amount of N application (Zheng et al., 1995).

N application curve (kg ha⁻¹)

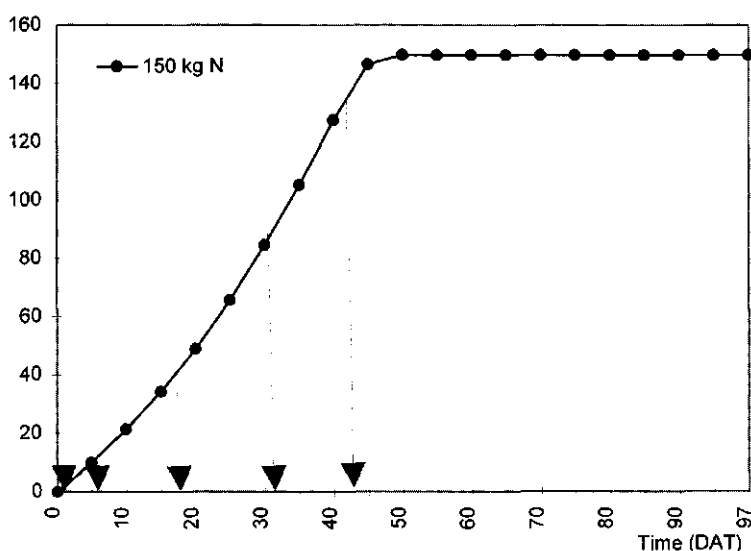


Figure 1. Nitrogen fertiliser recommendation curves corresponding to maximum economic yield for long growth-duration varieties (130-135 d).

Introduction of results generated by MANAGE-N model into rice growth chart

A rice growth chart is a combination of present advanced techniques for rice management (Guo, 1991). The growth chart is widely accepted by farmers because it is easily understood and it can result in higher yield. We introduce the MANAGE-N recommendation information for N application to the rice growth chart because the advantage of model recommendation will be more significant when other management options are also kept at optimum levels (see chart).

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Cultivation model of hybrid rice.

Time		June		July			
		11-20	21-30	1-10	11-20	21-31	1-10
Growth stage		Sowing time		Nursery stage		Trans-planting time	Tillering
							Effective tillering
Growth index					Vigorous seedling with tillers, without disease and insect injury. short, thick and white roots, transplanting at suitable time (seeding age = total leaves from main stem - 4-3)		Trans-planted plants 120-150 m ² , spacing 13x (20-23) cm 3-4 plants hill ⁻¹
Field management	Fertilizer	1. Seed treatment sunning seeds, seed selection, soaking seed for 12 h then disinfection for 12 h 2. Sowing rate: 15 g m ⁻² (for 6-7 m ² of main field) 3. Sowing time: 15 Jun to 20 Jun for 16-leaf varieties, 20 Jun to 25 Jun for 15-leaf varieties 4. Basal dressing of nursery: manure 1.2 kg m ⁻² potassium chloride 15 g m ⁻² , fused calcium-magnesium phosphate 75 g m ⁻²		Urea 4.5 g m ⁻² , potassium chloride 4.5 m ⁻² at 2-leaf stage, urea 6-7.5 g m ⁻² at 6-7 d before transplanting		Basal dressing: fresh straw 225-300 g m ⁻² , topdressing at 0 DAT: urea 3 g m ⁻² , fused calcium-magnesium phosphate 37.5 g m ⁻²	Urea 8 g m ⁻² potassium chloride 15 g m ⁻² at 6-7 DAT
	Water			Keeping the nursery surface moist before green leaf emergence, irrigation with shallow water after green leaf emergence		Recovery from transplanting with shallow water	Tillering with thin water plant
	Prevention and cure of disease, insects and weeds			Prevention and cure of rice leathopper, rice thrips, rice stem borer and rice bacterial leaf blight. Remove the weeds before third-leaf emergence			Prevention a rice stem bo together wit clearing

August		September				October		
11-20		21-31	1-10	11-20	21-30	1-10	11-20	21-31
stage		Panicle initiation and booting			Heading and ripening stage			
Ineffective tillering		Spikelets increasing	Spikelets decreasing	Heading Ripening		Grain filling		
Maximum plant number 420-500 m ⁻² before 11.1 leaves; 420-500 m ⁻² before 12.1 leaves		Vigorous roots and shoots, green leaf standing upright			Effective panicle number 260-330 m ⁻²	Green leaves during grain filling, yield components reach targeted levels		
Urea 8 g m ⁻² at 16-18 DAT			Urea 8 g m ⁻² at 30-32 DAT	Urea 5 g m ⁻² at 43-45 DAT				
Dry the field with sun at 260-330 plants m ⁻² irrigation again when 2nd leaf from top emerges		Thin water		Thin water	Shallow water	Intermittent irrigation		
Prevention and cure of rice planthopper, rice sheath blight and rice blast		Prevention and cure of rice planthopper, rice sheath blight and rice blast			Prevention and cure of rice stem borer, rice planthopper, armyworm and rice blast			

Effect of split application of N and green manure on N absorption, remobilisation and utilisation in IR72 under regulated irrigation management

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Abstract

A field experiment was carried out during the 1994-95 wet seasons in Coimbatore to study the effect of N split application and substitution of basal N with green manure on N concentration, uptake and growth of rice under regulated irrigation management after panicle initiation. Nitrogen concentrations in the leaves, stems and roots were higher between active tillering and mid-tillering stages. Leaf N had a second peak around heading and the concentration declined until maturity. The leaves and stems were the major contributors to the remobilisation pool. The panicle accounted for 67% of total N absorption. Translocation was higher in crop treated with basal green manure. In general, N absorption continued until maturity. Maximum N uptake rates of 3.0, 4.0, 1.8 and 0.4 kg N ha⁻¹ d⁻¹ were observed at active tillering, mid-heading, just after heading and at dough stage, respectively. Split applications as basal and at PI and FF were more important than at AT for tiller number, panicle weight and filled grains, respectively. Harvest index was improved by N at FF under the water management studied.

Introduction

Nitrogen management is a crucial factor in rice production since the number of tillers and spikelets is closely associated with N content of the plant (Matsushima, 1976). A large section of rice literature illustrates the effect of N availability on N uptake, growth and grain yield (e.g., Patrich et al., 1974; Marschner, 1986). Topdressing, an important agronomic practice for N, can change dramatically the N absorption of the rice plant from the early to later growth stage and can increase rice yields. Proper timing of

topdressing is very important to get the desired results. An attempt was made to find out the best stages for N split application to maximise N uptake and growth of a medium-duration rice cultivar (IR72) during the winter season.

Materials and methods

We carried out a field experiment at the Tamil Nadu Agricultural University wetland farms during the 1994-95 winter season (Oct-Feb) to determine the best stages for N application and to study the effect on growth and yield of lowland rice. Different N rates and application times comprise the treatments (Table 1). Green manure GM (neem leaf) at 6.25 t ha⁻¹ on fresh weight basis (53 kg N ha⁻¹) was applied in T7. N was applied as prilled urea. Sixty kg each of P₂O₅ (basal), K₂O (applied 50% basal and 50% at panicle initiation [PI]) and 25 kg zinc sulfate (basal) were also applied. Three seedlings per hill were transplanted at 20 × 10-cm spacing. Irrigation was assured by maintaining a standing water of 5 cm until PI; afterward irrigation was regulated 1 d after disappearance of ponded water as suggested by Ramasamy et al. (1995).

Plant samples were drawn along with roots from 0, 9, 21 (active tillering [AT]), 28, 35, 42 (PI), 51, 63 (first flowering [FF]), 76 d after flowering (DAT) and at maturity. For measurement of biomass, five hills were selected in T1, T2 and T7 plots only. Care was taken so that no loose or dead leaf material was lost from the plants during sampling. Nitrogen content of all plant organs was estimated using the microKjeldhal method. N uptake rate was calculated by plotting the time course of N uptake on a graph and joining all points to make a smooth curve. The amount of N translocated from the leaves and stem was assessed as the difference between the highest level of N accumulation in that organ and the N content at maturity. From the plotted curve, N uptake at different intervals (5 d) was derived and the rate determined.

Results and discussion

Cultivar IR72 has a field duration of 99-106 d. Total duration ranged from 134 to 141 d under varied times and levels of N application (Table 1). Maximum tillering occurred at 28 DAT in no-N applied plots while it was observed at 30-33 DAT in GM-treated plots. The panicle primordia initiation was observed during 42-48 DAT.

Crop N concentration

The N content of the leaves increased up to AT (21 DAT). It then decreased gradually as plant age advanced, except for a very brief period when split application of N was done at FF. In GM-treated plots, this concentration was higher than urea N alone (T2),

Table 1. Experimental details.^a

Treatment	N applied (kg ha ⁻¹)							Phenological growth stages of IR72 (d)				
	0 DAT	7 DAT	21 DAT	PI	MH	FF	Total N (kg ha ⁻¹)	PI	FF	Harvest	Field duration	Total duration
T1	-	-	-	-	-	-	0	44	63	23/2/95	99	134
T2	50	-	50	50	-	50	200	43	68	28/2/95	104	139
T3	-	-	50	50	-	50	150	43	69	27/2/95	103	138
T4	50	-	-	50	-	50	150	42	68	25/2/95	101	136
T5	50	-	50	-	-	50	150	43	68	28/2/95	104	139
T6	50	-	50	50	-	-	150	43	68	28/2/95	104	139
T7	GM	25	50	25	25	25	203	48	72	2/3/95	106	141
T8	-	25	50	25	25	25	150	43	70	1/3/95	105	140

^aThe experiment was conducted at 11° N, 77° E and 427 m above mean sea level; soil at experimental site is clayey and poorly drained; seedling age - 35 d; spacing 20 × 10 cm; transplanting 16 Nov 1994; GM-green manure - neem at 6.25 t ha⁻¹ (dry weight - 2.5 t; leaf N- 2.2%); design-randomised block design with four replications.

especially from PI (Fig.1). In this experiment, at the time of harvest, only 18-25% of maximum leaf N was observed in senescent leaves; the lowest was with the no-N plot. Mae (1986) reported 20% of maximum leaf blade N at maturity under good growing conditions.

The concentration of N in the stem also increased during the vegetative period. In GM-treated plots though, stem N concentration reached its peak later, owing to its slow initial recovery—it was higher just before PI (Fig.1). The total N content of stem was higher in urea N (basal) applied plots at PI which may be due to profuse tillers produced at earlier stages compared with green manure basal application. Root N concentration was also higher at AT stage. Treatment variations were not significant (Fig.1). Root N concentration was higher at FF in GM-treated plots. The dilution in concentration in later part of growth could be due to decreased root activity as reported by Dai (1988). In general, the N content of the whole crop also had the peak around AT stage, followed by a steep fall before PI due to dilution. Thereafter it was steady up to FF and then declined until maturity (Fig.2).

N uptake

In all cases, the measured N absorption continued until physiological maturity. There was an initial sluggish period. In the no-N and GM-treated plots, this period was up to 21 DAT while in urea-N basal application, it was over within 9 DAT. Roughly 50% the total N absorption occurred well before mid-heading in plots with urea-N alone compared with GM basal, which was a week later (Fig.3). There was a positive linear

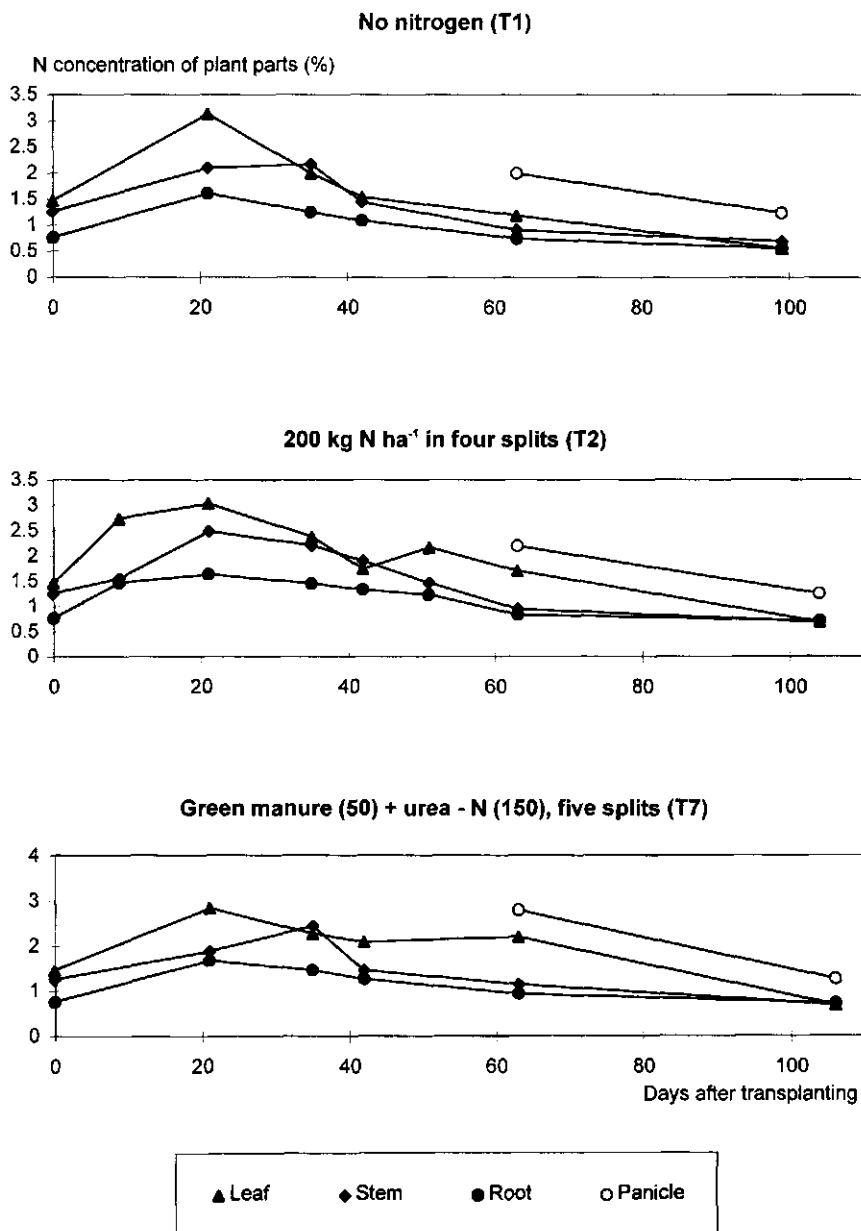


Figure 1. N concentration of plant parts as influenced by N management strategies in rice cultivar IR72, 1994-95 winter season, Coimbatore, India.

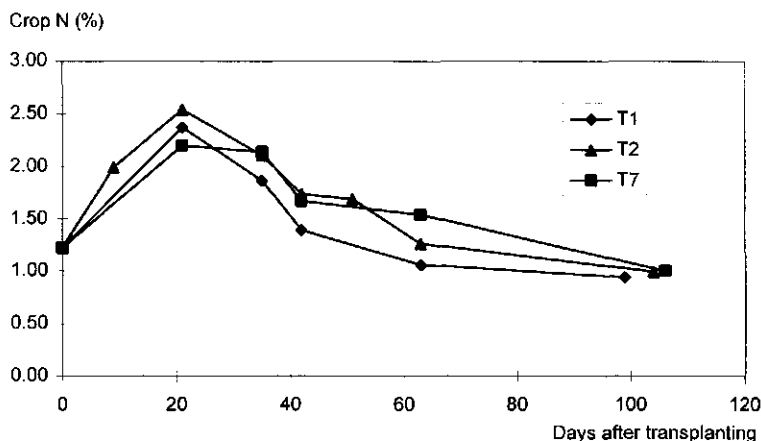


Figure 2. Crop N content of rice cultivar IR72 under different N management strategies in 1994-95 winter season, Coimbatore, India.

relationship between crop N uptake and leaf N content up to FF (Fig. 4). This relation was very strong for GM-applied crop ($Y = -0.13 + 1.59 N$, with $R^2 = 0.99^*$) followed by 200 kg N ($Y = 1.375 + 2.26 N$, $R^2 = 0.97^*$), and no-N applied crop ($Y = -4.18 + 3.84 N$, $R^2 = 0.86^*$). The positive and negative intercept values indicate early and delayed establishment of leaves after transplanting, respectively, with quicker leaf establishment in urea-N basal application.

Rate of N uptake

The peak uptake rates coincided with maximum tillering and mid-heading periods. These types of variations have already been reported (e.g., Makarim et al., 1994). These peaks were not conspicuous in the no-N manured plots. In the full urea N-applied plots, highest uptake rate occurred at maximum tillering; while in GM-urea N combination plots, it was after PI. This might be due to the early availability of soil N in the former case and the slow release in the latter. In all cases, uptake rates fell sharply as maturity approached (Fig.5).

The highest N uptake rate of $4.0 \text{ kg N ha}^{-1} \text{ d}^{-1}$ was estimated in the GM-urea N combination (T7). The maximum N uptake rate at any one time was 3.0, 4.0, 1.8 and $0.4 \text{ kg N ha}^{-1} \text{ d}^{-1}$ at maximum tillering, mid-heading, just after heading and dough stage, respectively.

Translocation

The remobilised N from green leaves ranged from 53 to 69%. Mae (1986) recorded 30-64% of total leaf N as remobilisable. A higher (69.4%) amount of leaf N content was remobilised in the GM-treated crop. Remobilisation of N from stem was estimated

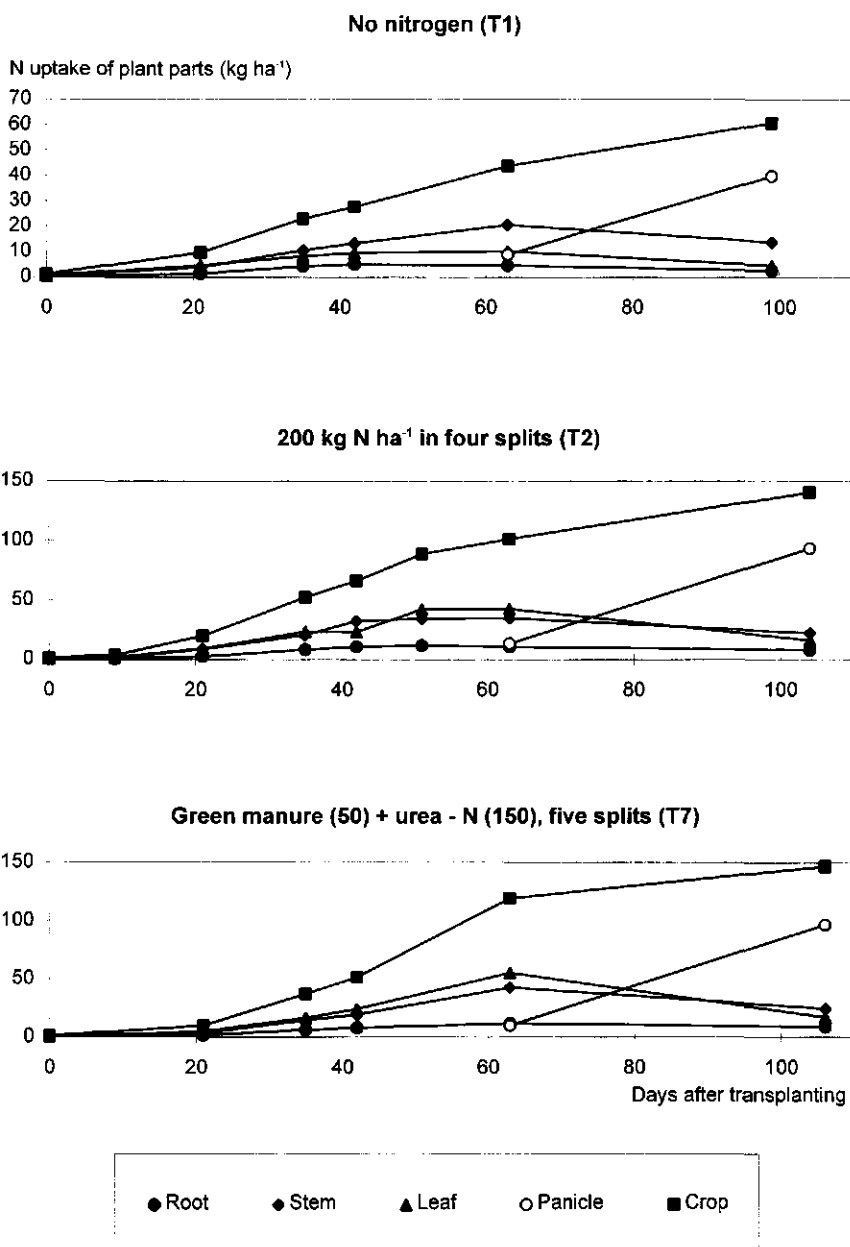


Figure 3. N uptake of plant parts as influenced by N management strategies in rice cultivar IR72, 1994-95 winter season, Coimbatore, India.

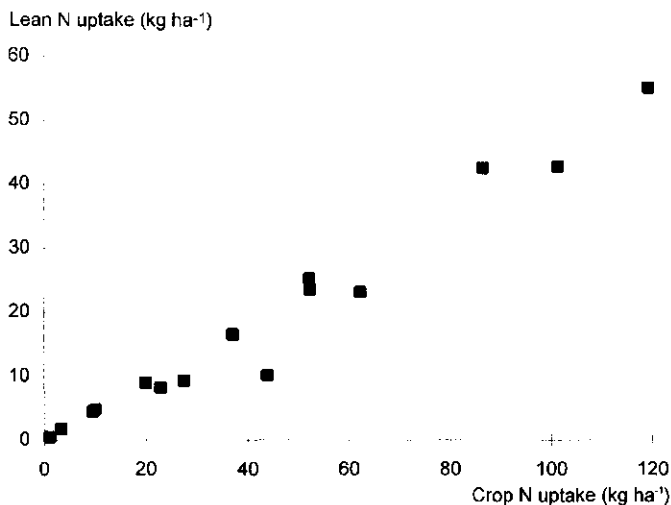


Figure 4. Leaf N uptake as a function of crop N uptake in rice cultivar IR72 in 1994-95 winter season, Coimbatore, India.

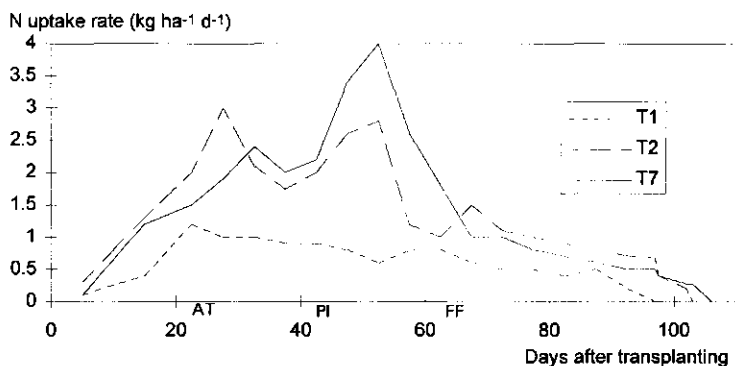


Figure 5. Crop N uptake rate of rice cultivar IR72 under different N management strategies in 1994-95 winter season, Coimbatore, India.

between 32.4 and 42.6%. The panicle contained the highest (67%) of total N absorbed. The amount of N derived from that absorbed during grain-filling period ranged from 38.5 to 63.5% of the total panicle N and the balance was from remobilisation. Greater remobilisation was observed in the GM-treated plot (61.5%), followed by urea N (54.8%) and no N (36.5%). Yoshida (1981) reported that the required leaf N can be met when N absorption by the crop is continued after heading, or when a high N content of the vegetative parts is attained before heading, so that the total amount of N absorbed by the time of heading supports translocation during ripening. Thus, the remobilised N came

mainly from the vegetative organs. The roots were of little importance in the process. Nitrogen remobilised from the roots was negatively correlated with grain yield, showing lower N remobilisation (25.9%) with higher grain production (T7). Ramasamy et al. (1994) have derived a negative relation between N remobilisation from roots and root condition. They further opined that an active rooting system after flowering is associated with smooth transfer of stored reserves from the stem and delayed leaf senescence.

Biomass production

Basally applied urea N facilitated faster growth rate in the initial periods (Fig.6). Green manure as basal dose had initial sluggish growth and after the third week of application, growth was at a higher rate than 200 kg urea N-treated plot (T2). N applied at FF could not improve total biomass production. From the results, it was obvious that for total biomass production, initial basal N is vital. Partitioning of biomass among stem, green leaves and roots continued steadily in the GM-urea N combination (T7) even after PI.

Yield and yield attributes

Withholding the initial basal N application had adverse effects on tiller production and on productive tillers. Filled spikelets per unit area were reduced by skipping N either at any of the growth stages; the effect was greater when basal N was skipped. The N applied basally encouraged more tiller production and N at PI enhanced the number of spikelets per panicle. The N at FF improved the grain-filling process under field conditions studied. Number of panicles was correlated with amount of N in plants at the neck-node initiation stage.

Neither N level nor time of application could alter the weight of individual spikelets (weight ranged from 23.0 to 23.7 mg grain⁻¹), but they had an effect on panicle weight. Skipping the N application at PI had a drastic effect on panicle weight (Table 2). The increased panicle weight was mainly due to the increased number of filled spikelets per panicle and the reduction may be attributed to limited sink size (spikelets per panicle). Wada et al. (1986) stated that the percentage of ripened grains (filled spikelets) is determined by the ratio of the amount of carbohydrate to the number of spikelets. In general, the percentage of ripened grains tends to decrease with an increase of plant N content at the late stage of spikelet initiation or at the heading stage. They also opined that in order to increase the percentage of filled spikelets, it is necessary to increase carbohydrate production.

Grain yield recorded at 14% moisture showed no significant difference between urea N in four splits (T2) and five splits with basal GM added (T7), but they were better in these two treatments than in the other. Avoiding N application at any one stage (except at AT) had affected grain yield by reduced tiller production, panicle number and filled spikelets.

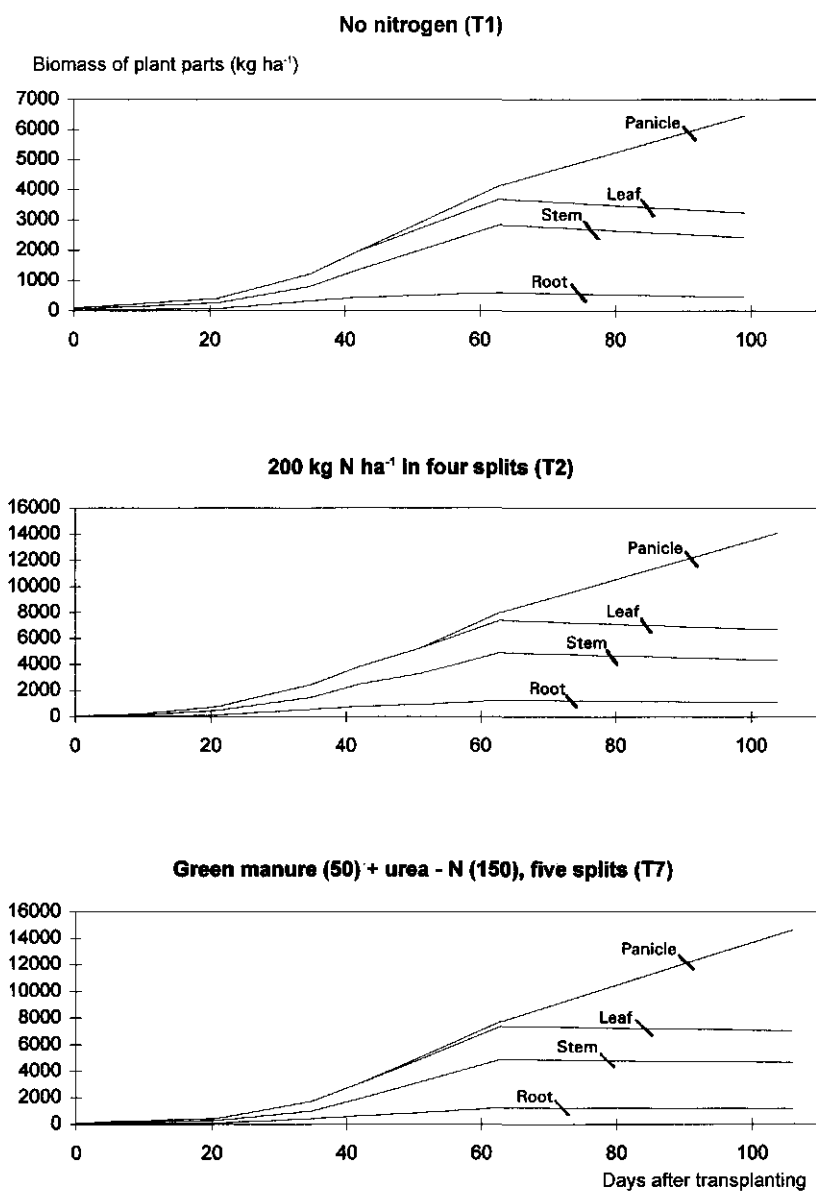


Figure 6. Biomass production of plant parts as influenced by N management strategies in rice cultivar IR72, 1994-95 winter season, Coimbatore, India.

Table 2. Effect of N level and time of application on the yield parameters of IR72 during winter season at Coimbatore.

Treatment	Productive tillers hill ⁻¹ (no.)	Filled grains panicle ⁻¹ (no.)	Filled grains m ⁻² (no.)	Weight of panicle (g)	Harvest index	Total biomass (t ha ⁻¹)	Grain yield (t ha ⁻¹)
T1	7.3	39.0	14235	0.971	48.9	6.46	3.16
T2	9.3	58.1	27017	1.432	43.3	14.03	6.08
T3	8.1	56.6	22980	1.235	47.9	11.34	5.43
T4	9.3	55.5	25697	1.259	44.6	13.17	5.88
T5	9.3	47.8	22227	1.117	42.9	12.60	5.41
T6	9.7	51.6	25075	1.198	38.9	14.20	5.52
T7	9.0	61.1	27495	1.427	42.1	14.61	6.15
T8	9.2	55.4	25484	1.249	44.5	12.94	5.76
SE	0.4	1.5	525	0.055	0.4	0.31	0.15
CD	0.9	3.1	1925	0.44	0.9	0.64	0.31

Applying 150 kg N in five splits (T8) was better than giving the same dose in three equal splits with either no basal N (T3) or no N at PI (T5), indicating the importance of N application (basal and incorporated) or at least within the period of transplanting shock (as T8) and at PI. Treatment 8 was in no way superior to 150 kg N in 3 equal splits—basal, at PI and at FF (T4).

Nitrogen application either as urea N or in combination with GM reduced harvest index (HI) through increased unproductive tillers. Poor HI was associated with skipping of N application at FF due to higher biomass production with less ripened grains per panicle. Nitrogen application at FF (T2) above a recommended N schedule (T6) improved HI positively by increased filled spikelets per unit area. This index was also affected negatively when N application was skipped at PI, mainly due to sink limitation (Fig.7).

Conclusion

Nitrogen concentration in leaves, stems and roots was highest between the AT and MT stages. At the time of harvest, 18-25% of total leaf N was recorded with dead leaves. Nitrogen absorption continued until physiological maturity, and a major portion of N uptake occurred before flowering in N-treated crops. There were two peaks in the uptake rates, one before PI and another around heading. With GM application, peak rate was after PI. Maximum uptake rate was 3.0, 4.0, 1.8 and 0.4 kg N ha⁻¹ d⁻¹, respectively, at AT, MH, just after heading and at the dough stage. Remobilisation occurred to a greater

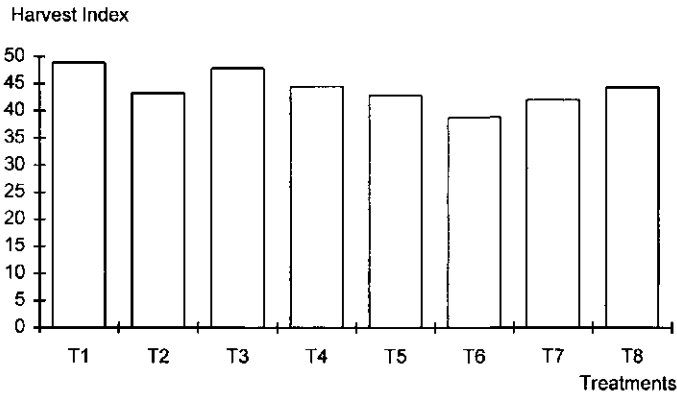


Figure 7. Harvest index in rice cultivar IR72 as influenced by N management in 1994-95 winter season, Coimbatore, India.

extent (61.5%) with GM application while the no-N crop mainly depended on absorption after heading. Withholding basal N application had an effect on biomass, productive tillers and grain yield. Green manure-urea N combination produced higher biomass, panicle weight, filled spikelets per unit area and grain yield. Harvest index was lowered when N application was skipped at FF.

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The effect of amount and timing of N application on grain yield and dry matter production of hybrid rice with long growth duration

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Abstract

A field experiment was carried out at Nanchang, China, in the 1994 late season. The results showed that the amount and timing of N application generated by ORYZA 0 model (model-recommended method) could significantly increase grain yield as much as by 9.4% compared with state-recommended method. The main reason for the yield increase was that the plants of the model-recommended treatments absorbed less N than did those of the state-recommended method before panicle initiation but they took up more N from panicle initiation to maturity. Compared with the state-recommended method, the plants of the model-recommended treatments produced fewer tillers but the panicle number remained almost the same because of death of fewer tillers. The higher N uptake during panicle differentiation resulted in more spikelets per panicle. The higher N absorption during grain filling made the plants of the model-recommended treatments produce more dry matter at that period so that additional grains could be filled up quite well. The higher number of filled grains per panicle finally raised the harvest index of the model-recommended treatments, causing higher grain yield, although it did not produce more dry matter.

Introduction

Nitrogen is the most important nutrient for rice plant growth. The chlorophyll content in the leaves, which determines the ability of the plant to utilise solar radiation, is almost parallel to leaf N content. The leaf N content depends on N uptake (Pan, 1979). Soil N usually does not meet the demand of rice plant growth. If there were no fertiliser N application, N deficiency would have occurred widely (Yoshida, 1981).

It is important to determine the dose of N application. Nitrogen overdressing often causes yield decrease as a result of higher disease incidence and more unfilled grains (Jiang et al., 1991). This not only wastes fertiliser N but also decreases profits from rice production and causes environmental pollution.

Timing is another critical factor in N application. It is well-known that applying the same amount of N at different times to the rice plant will cause different results because

the growth and development of rice plants are "periodic" (Matsushima & Manaka, 1958). For example, applying N at tillering stage will make the plant produce more tillers and the plant is likely to have more panicles; applying N during panicle differentiation will cause the plants to produce more spikelets per panicle and decrease the abortion of spikelets; and applying N after heading will raise filled grain percentage, 1,000-grain weight, etc.

To determine the amount and timing of N application, researchers have to do a number of experiments, an often costly and time-consuming process. And the results are still empirical and may only be used to quite a limited extent (Ling, 1994; Sun et al., 1994). To solve this problem, the dynamic model ORYZA_0 was recently developed by ten Berge et al. (1994). Using this model, we had obtained the optimum N application strategy for hybrid rice with long growth duration. This paper presents the results of a field experiment designed to test the recommendation by the ORYZA_0 model.

Materials and methods

The experiment was conducted at the Agronomy Research Station of the Jiangxi Agricultural University located at Nanchang, Jiangxi, China, in the 1994 late season. Sanyou 63, one of the most widely planted F_1 hybrid lines with long growth duration, was sown on 12 Jun. The seedlings were transplanted on 21 Jul with a plant spacing of 13.3×20 cm. The experiment was carried out in a complete randomised block design with four replicates. Plot size was 20 m^2 . Soil was clay loam with medium fertility. For all treatments, P fertiliser was applied basally at a rate of $60 \text{ kg P}_2\text{O}_5 \text{ ha}^{-1}$ and K fertiliser was applied at 7 d after transplanting (DAT) at a rate of $60 \text{ kg K}_2\text{O ha}^{-1}$. Nitrogen was broadcast in the form of urea.

The treatments are shown in Table 1. Of the four treatments, T1 was the control without N application, T2 was the state-recommended dose and timing, T3 was the state-recommended dose and the model-recommended timing, and T4 was the model-recommended dose and timing. In every plot, five hills were sampled at transplanting (TRP, 0 DAT), active tillering (AT, 14 DAT), panicle initiation (PI, 21 DAT), first flowering (FF, about 52 DAT) and harvest (HVST). The plants were then separated into roots, leaves, stems and sheaths and panicles. Dry weight and N content of each part were measured. Yield and yield components were also measured at harvest.

Results

Yield and yield components

The grain yield in T1 was much lower than those in T2, T3, and T4. The grain yields in

Table 1. N fertiliser application treatments, Jiangxi Agricultural University, Nanchang, China, 1994 late season.

Treatment	N application (kg N ha ⁻¹)							Total
	Basal	0 DAT ^a	7 DAT	14 DAT	21 DAT	38 DAT	52 DAT	
T1	0	0	0	0	0	0	0	0
T2	60	0	30	30	0	0	0	120
T3	0	30	0	0	30	30	30	120
T4	0	37.5	0	0	37.5	37.5	37.5	150

^aDAT = days after transplanting.

T3 and T4 were significantly higher than those in T2, with 9.4 and 9.6% increases, respectively (Table 2). It was noticeable that even at the same level of N application (T2 and T3), the model-recommended method could increase grain yield significantly. T4 did not produce more grain than T3, although dry matter in T4 was always higher than that in T3 (Fig. 1). This might be related to the deficiency of sunshine during the grain-filling period.

The number of spikelets per panicle in T3 and T4 was significantly higher than that in T2 while the difference between T3 and T4 did not reach a significant level (Table 2).

The stem number in T1 was the lowest at AT and PI and so was panicle number at maturity. In contrast, T2 had the most stems at AT and PI (Table 3). This could be well explained by the amount of N application and N uptake (Table 1, 4). Although T3 and T4 produced less tillers than T2, they got almost the same panicle number as T2. This meant that T3 and T4 had less dead tillers and the ratios of effective panicles to the highest number of stems were higher.

It was found that the single stem weight in T3 and T4 was higher than that in T2 both at AT and PI. This might be one of the reasons that T3 and T4 had larger panicles (Table 3).

Table 2. Yield and yield components and their significance between treatments, Jiangxi Agricultural University, Nanchang, China, 1994 late season.^a

Treatment	Grain yield (kg ha ⁻¹)	Panicles m ⁻² (no.)	Spikelets panicle ⁻¹ (no.)	Filled grains (%)	1,000-grain weight (g)
T1	5105 c	201.8	115.1 b	81.55	26.93
T2	6539 b	270.8	109.0 b	81.76	27.10
T3	7153 a	257.3	133.8 a	80.59	26.41
T4	7170 a	279.4	127.0 a	78.02	25.89

^aGrain yield is of 14% moisture content; significance is at the 5% level.

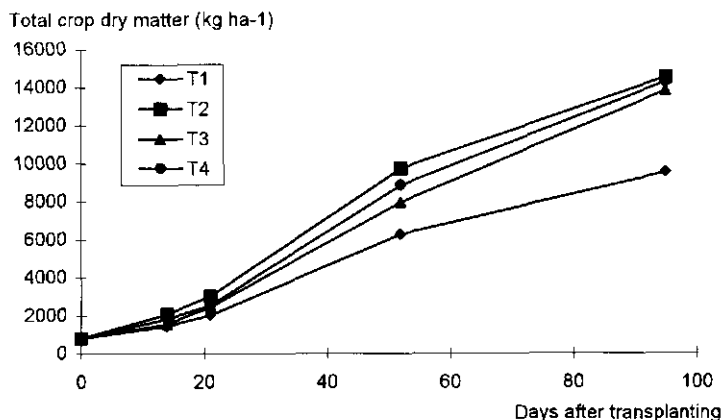


Figure 1. Effect of N application on dry matter production and total crop biomass. Rice cultivar Sanyou 63, Jiangxi Agricultural University, Nanchang, China, 1994 late season.

Table 3. Number of stems and single stem weight, Jiangxi Agricultural University, Nanchang, China, 1994 late season.

Treat- ment	Stems m ⁻² (no.)		Single stem weight (g)	
	AT	PI	AT	PI
T1	184	240	0.79	0.84
T2	296	416	0.70	0.73
T3	215	293	0.72	0.84
T4	252	283	0.73	0.89

Table 4. N uptake (kg ha⁻¹) at different crop growth stages, Jiangxi Agricultural University, Nanchang, China, 1994 late season.

Treat- ment	TRP-PI	PI-FF	FF-HVST	Total
T1	15.30	21.48	14.64	65.6
T2	61.46	48.67	11.39	135.7
T3	24.73	68.46	34.63	142.0
T4	23.02	88.61	42.89	168.7

The filled grain percentage and the 1,000-grain weight were a little lower in T3 and T4 than in T1 and T2, but there was no significant difference among the four treatments (Table 2).

Dry matter production and harvest index

There were no big differences in total biomass between T2, T3 and T4 at harvest. But the patterns of dry matter production were quite different. Compared with that in T2, the plants in T3 and T4 produced less dry matter at the early (TRP-PI) and middle (PI-FF) stages but much more at the late stage (after flowering). The lowest value of dry matter was always observed for T1 (Table 5, Fig. 1).

The highest value of harvest index was found in T1. Next to T1 were T3 and T4, which were 15 and 10% higher than T2, respectively (Table 5). Although the harvest index was highest for T1, it got the lowest grain yield because dry matter production was too low.

N uptake and N content

Higher levels of N application resulted in higher N uptake. The plants in T3 and T4 absorbed more N than did plants in T2 during the whole growth season. This did not mean that N absorption in T3 and T4 was always higher than T2 at any stages. In fact, T2 took up more—twice that taken by T3 and T4 before panicle initiation (Table 5), which caused much more tillers (Table 3).

From PI to harvest, plants in T3 and T4 took up much more N than did those in T2. During panicle differentiation, plants in T2 took up only 71 and 55% N than in T3 and T4, which could be the reason for the fewer number of spikelets per panicle in T2. After flowering, N uptake of T2 was less than one-third or one-fourth that of T3 and T4, respectively, and even less than T1 (Fig. 2, Table 4). This showed that the root's ability of T2 to take up nutrients was extremely low at that stage.

Table 5. Total biomass and harvest index, Jiangxi Agricultural University, Nanchang, China, 1994 late season.^a

Treatment	Total biomass (kg ha ⁻¹)								Harvest index
	TRP	AT	PI	FF	HVST	TRP-PI	PI-FF	FF-HVST	
T1	777	1455	2013	6262	9524	1236	4249	3262	0.47
T2	777	2076	3028	9728	14499	2251	6700	4771	0.40
T3	777	1548	2444	7949	13809	1667	5505	5860	0.46
T4	777	1831	2522	8855	14258	1745	5793	5943	0.44

^aTRP = transplanting, AT = active tillering, PI = panicle initiation, FF = first flowering (10% of the hills carrying at least one flowering panicle), HVST = harvest.

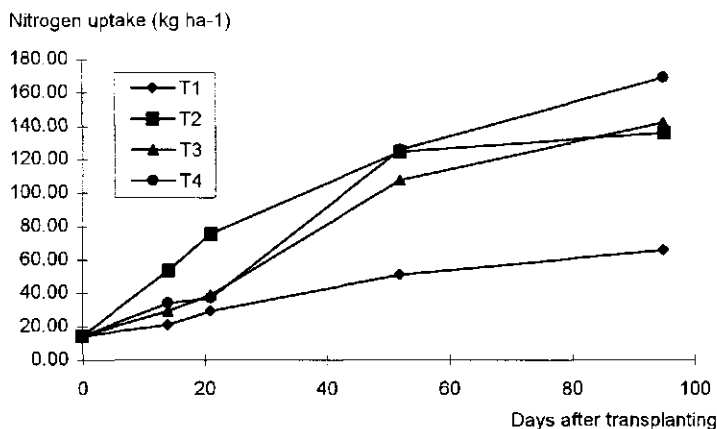


Figure 2. Effect in N application on N uptake. Rice cultivar Sanyou 63, Jiangxi Agricultural University, Nanchang, China, 1994 late season.

The differences in N content between T2, T3 and T4 had the same trend as N uptake, both for the whole plant and leaves (Table 6). The higher N content in T2 until PI stimulated the production of more dry matter and tillers, but the less N absorption during panicle differentiation could not afford to convert too much tillers to yield effective stems. So a higher proportion of tillers died and more dry matter was wasted in T2. That might be one of the reasons T2 had lower harvest index.

Higher N contents in T3 and T4 during panicle differentiation enhanced the formation of branches and spikelets and prevented their abortion. This in turn enlarged the panicles. Higher N contents in T3 and T4 during the grain-filling stage induced more

Table 6. N content of whole plant and leaves, Jiangxi Agricultural University, Nanchang, China, 1994 late season.

Treat- ment	N content of whole plant(%)					N content of leaves(%)				
	TRP	AT	PI	FF	HVST	TRP	AT	PI	FF	HVST
T1	1.82	1.45	1.46	0.81	0.69	2.99	2.59	2.45	1.70	0.67
T2	1.82	2.57	2.50	1.28	0.94	2.99	4.05	3.53	2.34	1.04
T3	1.82	1.89	1.59	1.35	1.03	2.99	3.11	2.59	2.53	1.08
T4	1.82	1.85	1.47	1.42	1.18	2.99	2.97	2.50	2.66	1.28

photosynthesis and more dry matter production at that stage. So the grains in T3 and T4 could be filled quite well and the filled grain percentage and 1,000-grain weight at harvest did not decrease seriously although the spikelets per panicle in T3 and T4 were much higher.

Discussion and conclusion

Rice grain yield is determined by four yield components—i.e., the number of panicles per unit area, number of spikelets per panicle, filled grain percentage and the 1,000-grain weight. Increase in the four components will increase grain yield if the other ones are kept unchanged.

In this experiment, the model-recommended amount and timing of N application could significantly increase number of spikelets per panicle while keeping the other yield components relatively stable. The grain yield of the model-recommended treatments were higher than that of the state-recommended treatment.

The patterns of N uptake were quite different between different N application methods. In comparison with the state-recommended method, the model-recommended method suggests applying less N to the crop at the early stage but more at the middle and late stages. This conforms with earlier findings that more N should be applied during panicle differentiation and grain filling when yield level is high and/or growth duration is long (Jiang, et. al., 1991; Shi et al., 1994).

The crop absorbed N following a pattern similar to that of N application. The whole crop and leaves of the model-recommended treatments contained less N at the early stage but more at the middle and late stages. Though less tillers were produced in the model-recommended treatments, the percentage of dead tillers was lower and hence panicle number was almost the same as that in the state-recommended treatment.

The heavier single stem weight at PI and the larger N uptake during panicle differentiation made it possible for plants in the model-recommended treatments to form larger panicles with more spikelets and consequently attain higher harvest indexes. Although T1 had higher single stem weight at PI, it had the lowest spikelet number per panicle because of the low level of N absorption during panicle differentiation.

The larger amounts of N absorption and the higher leaf N contents after flowering made the crops in model-recommended treatments produce more dry matter at that stage to feed the grains.

In this experiment, T4 did not obtain higher grain yield than T3. This might be the result of inadequate sunshine during ripening.

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Effects of N on source-sink relations in rice

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Abstract

Data collected from a series of experiments conducted at the Jiangxi Agricultural University, People's Republic of China, during 1988-95 were used to study the effect of N on sink-source relationships in hybrid rice. There was a negative relationship between N uptake before 25 DAT and tiller-panicle ratio ($R^2=0.135^*$, $n=36$). Higher N application at the early stages should be avoided as it leads to more ineffective tillers. Nitrogen uptake before heading had a close correlation with total spikelets and sink capacity. Dry matter production was affected by N uptake both before and after heading. At a certain range of LAI, grain yield increased as spikelet-leaf ratio increased.

Introduction

Since the theory of source and sink was put forward by Mason, scientists have considered it important to understand the relationship between source and sink in order to increase crop yield. Normally, leaf area and leaf weight are known as a source size. Spikelets per panicle (single plant level) and number of spikelets or sink capacity (number of spikelets \times grain weight) per unit area (population level) are known as a "sink." Yield increase is related to increase in LAI (Enyi, 1962; Kriedemann, 1966) and sink size (Evens, 1972; Yoshida, 1973). Ling (1991) reported that the spikelet-leaf ratio could be used as an index to determine if the ratio of source to sink is suitable. When maximum LAI reaches a certain value, yield could be increased by increasing spikelet-leaf ratio.

In rice cultivation, N is one of the main nutrients essential for growth. Only a few reports (Wada et al., 1986; Akita, 1986; Shi et al., 1995) that specially focus on N and source-sink relations are available. In this paper we present results of our research on N and rice growth in recent years which aimed to understand source-sink relations with respect to N supply. The source-sink relation due to N application as recommended by MANAGE-N (Riethoven et al., 1995) and as practised locally is also discussed.

Materials and methods

The experiments were conducted at the Jiangxi Agricultural University, Nanchang, People's Republic of China, in the late seasons of 1988, 1989, 1993, 1994 and 1995. The experiment plot was a clay loam soil containing 3.12-3.78% organic matter, 0.12-0.2% total N, 81.0-150.3 ppm available N, 21.3-48.4 ppm available P, and 44.9-77.4 ppm available K. pH was 5.5-6.0. Nitrogen was applied in the form of urea, at the rate of 0-300 kg ha⁻¹. The varieties used were hybrid rice Ganhua7 (124-129 d), Sanyou 63 (131-136 d), V64 (105-108 d), Jiang1068 (122 d) and F131xG37 (126 d).

Plant samples were taken from five hills for each treatment at each sampling time. The plant material was separated into panicles, leaves, stems and roots. The dry weight of plant organs, LAI and grain yield were measured. The N content of plants was analysed by the Kjeldahl method.

Results and discussion

Relationship between N uptake and the formation of sink

Effect of N on total sink size Both spikelets (no. m⁻²) and sink capacity (g m⁻²) increased with increase in N uptake before heading (Fig. 1, 2). But as the amount of N uptake approached 20 g m⁻² (300 kg N application), spikelet number and sink capacity did not increase any more. A similar phenomenon was also observed in another study by Shi & Akita (1993). This suggests that 20 g m⁻² before heading would be enough for the sink increase in present rice varieties. There was a significant logarithmic correlation between N uptake before heading and total spikelet number ($R^2=0.48^{**}$, $n=46$) and sink capacity ($R^2=0.4934^{**}$, $n=46$).

Effect of N on formation of panicles In the population level, the number of spikelets per unit area (m²) involves number of panicles (m²) and number of spikelets per panicle. The number of panicles is determined by the number of main stem and tillers. Tiller number increased with increase in N uptake (Fig. 3). There was a linear correlation between N uptake before 25 DAT and total tiller number ($R^2=0.6123^{**}$, $n=36$). The relationship between number of panicles and N uptake before 25 DAT was logarithmic ($R^2=0.5457^{**}$, $n=36$), indicating that the ineffective tillers increased with increase in N uptake before 25 DAT. Fig. 4 showed clearly that the ratio of tillers to panicles decreased as increase N uptake before 25 DAT ($R^2=0.3621^{**}$, $n=36$). On the other hand, there was positive linear correlation between the ratio of tillers to panicles and N uptake during PI ($R^2=0.1353^*$, $n=36$) (Fig. 5). The ratio of tillers to panicles had a close correlation with dry matter production after heading, number of spikelets per unit area, effective leaf area and grain yield (Ling, 1995). Therefore, too much N application at the early stage is not good for maintaining a higher tiller-panicle ratio.

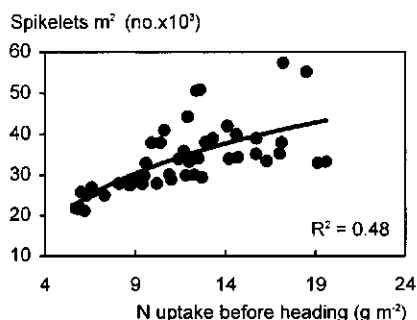


Figure 1. Relationship between N uptake and spikelets.

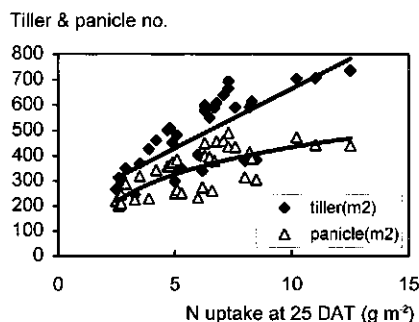


Figure 3. Relationship between N uptake at 25 DAT and tiller, panicle.

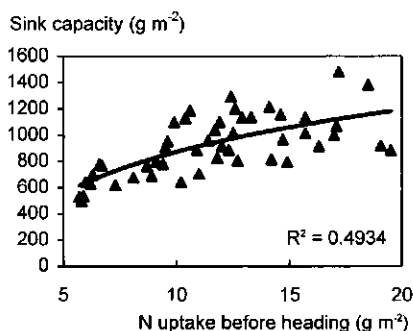


Figure 2. Relationship between N uptake and sink capacity.

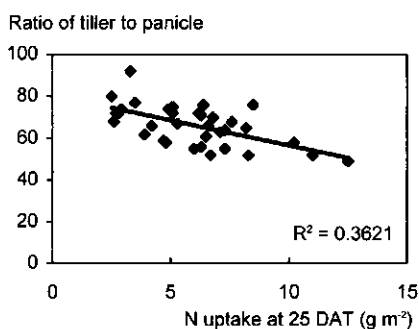


Figure 4. Relationship between N uptake and the ratio of tiller to panicle.

Effect of N on formation of spikelets The number of spikelets per panicle decreased as N uptake before 25 DAT increased (Fig. 6). The negative correlation between the two factors was significant ($R^2=0.1378$, $n=36$). The reduced spikelets per panicle was due to the production of more tillers under higher N uptake. Too large a population changes the microclimate of the ricefield. Therefore, although the population is composed of single plants, the single plants are also affected by population size. There was positive correlation between N uptake during PI and number of spikelets per panicle (Fig. 7), although spikelet number per panicle was reduced when N uptake was more than 10 g m^{-2} (300 kg N ha^{-1} application). Nitrogen uptake during PI contributed to higher tiller-panicle ratio as well as number of spikelets per panicle. It is thus important to apply some N at this growth stage.

At the population level, the number of spikelets per unit area (m^2) increased with increase in N uptake around 25 DAT except with 300 kg N application (Fig. 8). The spikelet increase related to the N uptake around 25 DAT was mainly due to the increase

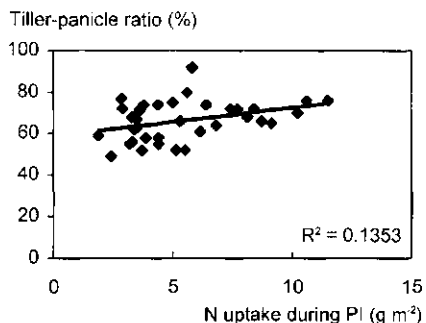


Figure 5. Relationship between N uptake during PI and tiller-panicle ratio

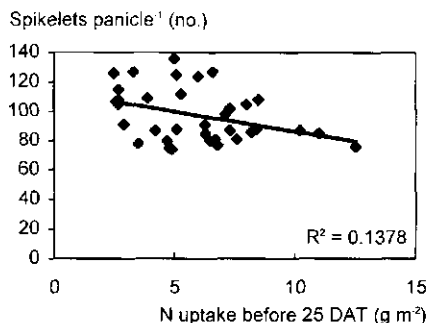


Figure 6. Relationship between N uptake before 2 DAT and spikelets per panicle.

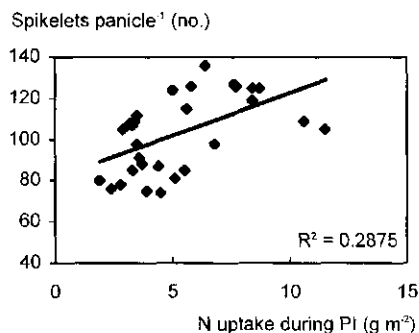


Figure 7. Relationship between N uptake during PI and spikelets per panicle.

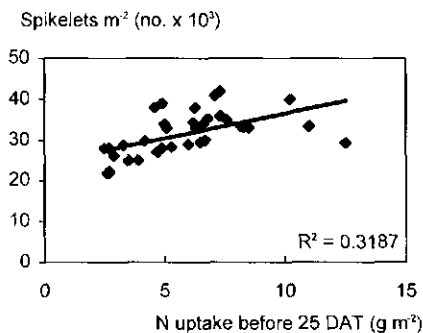


Figure 8. Relationship between N uptake before 25 DAT and spikelets.

in panicle number (Fig. 3). The contribution of N uptake to the increase in panicle number was larger than that of decrease in spikelets per panicle, which was affected by population size. More detailed analysis by Ling (1995) showed that N uptake during the end stages of effective tillering to panicle initiation did not significantly contribute to spikelet formation. There was a significant correlation between number of spikelets (m^2) and the N uptake during PI ($R^2=0.1439^*$, $n=30$) (Fig. 9). Table 1 shows that the effects of N application on spikelet generation at panicle initiation (neck-node differentiation stage) were much higher than at pollen mother cell formation stage. The degenerated spikelets were less when N was applied at the pollen mother cell formation stage than at panicle initiation stage. The developed spikelets per panicle were only slightly higher when N was applied at the spikelet generation stage than at the pollen mother cell differentiation stage. It also showed that too much application of N at panicle initiation is not necessary for increasing the number of spikelets. Less N applied per split and more splits may be good to increase the number of developed spikelets.

Table 1. Effects of N application on spikelet formation.

Treat- ment	Amount of N applied (g m ⁻²) ^a	Generated spikelets (no. panicle ⁻¹)	Degenerated spikelets (no. panicle ⁻¹)	Degeneration rate (%)	Developed spikelets (no. panicle ⁻¹)
T1	0+6+3+0+0	324	59	18.2	265
T2	0+6+6+0+0	322	67	20.8	255
T3	0+6+9+0+0	326	61	18.7	265
T4	0+6+-+3+0	266	31	11.7	235
T5	0+6+0+6+0	282	26	9.2	256
T6	0+6+-+9+0	284	23	8.1	261
T7	2.2+3+3+3.8+3	321	37	11.5	284
T8	6+7.5+0+0+1.5	257	50	19.5	207
T9	0+0+0+0+0	235	31	13.2	204

^aN applied at transplanting (0 DAT), tillering (7 DAT), panicle initiation (neck node differentiation, 20 DAT, booting (pollen mother cell formation, 35 DAT) and heading, respectively.

Relationship between N and formation of source

Effect of N on LAI The leaf area per unit area of land (LAI) is the usual index for measuring source size. There was a significant positive correlation between N uptake before heading and LAI ($R^2=0.7805^{**}$, $n=30$) (Fig. 10). One gram of N (m²) can increase 0.601 of the LAI. Fig. 11 shows the dynamic effect of N uptake on LAI development. The effect of N uptake on increase of LAI was more evident before 25 DAT than after 25 DAT. Similar results were also indicated by Ling (1995). Leaf weight was correlated with N uptake ($R^2=0.9234^{**}$, $n=30$) (Fig. 12) as it included the leaf thickness factor. Therefore, leaf weight could be considered a better index for measuring the source (Shi et al., 1995).

Effect of N on dry matter production after heading About 70% of the grain yield is contributed by dry matter production after heading. There was a significant positive correlation between N uptake after heading and dry matter production after heading (Fig. 13). The amount of N uptake before heading had also a positive effect on dry matter production after heading (Fig. 14). The effects of N uptake before heading on dry matter production after heading and grain yield were also affected by the radiation after heading (ten Berge, 1995). The suitable amount of N uptake before heading to attain highest grain yield in certain varieties will be determined by the radiation after heading. Inasmuch as there is close correlation between LAI and N uptake before heading, LAI is usually used as the measurement index if the population is suitable.

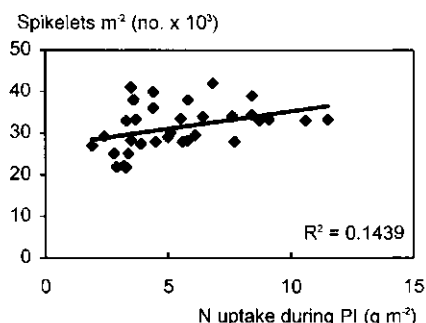


Figure 9. Relationship between N uptake during PI and spikelets.

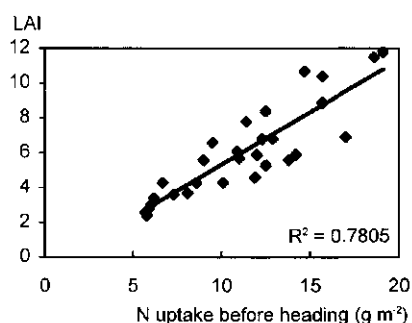


Figure 10. Relationship between N uptake before heading and LAI.

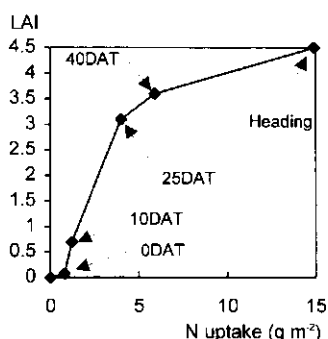


Figure 11. Effects of N uptake on the dynamic change of LAI.

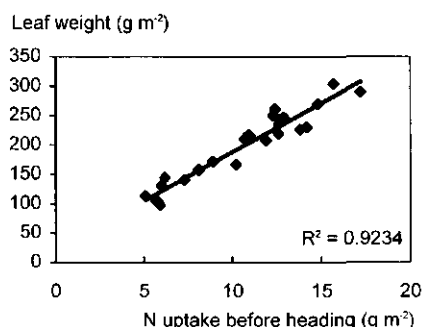


Figure 12. Relationship between N uptake before heading and leaf weight.

Effect of N on translocation rate of stem reserves Translocation of dry matter from stem to panicle after heading is also a part of source. The single stem weight and translocation rate of stem reserves of V64 (short growth duration) decreased with the increase in N uptake of a single plant (Fig. 15a). There was no evident effect of N uptake on single stem weight and translocation rate of stem reserves of Sanyou 63 (long growth duration) (Fig. 15b). In both varieties, translocation rate of stem reserves was related to single stem weight. In rice cultivation, it is important to keep the population at a certain level and increase single stem weight.

Ratio of source to sink

Relationship between spikelet-leaf ratio and grain yield Fig. 16 shows that grain yield decreased as spikelet-leaf ratio increased. There was a significant negative correlation between grain yield and spikelet-leaf ratio ($R^2=0.3415^{**}$, $n=45$). If the LAI range was

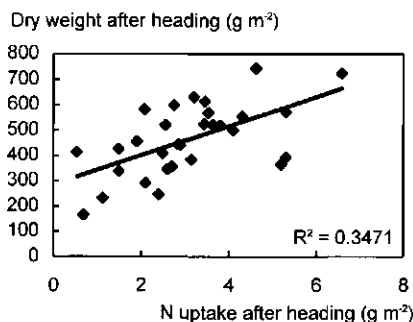


Figure 13. Relationship between N uptake after heading and dry matter production after heading.

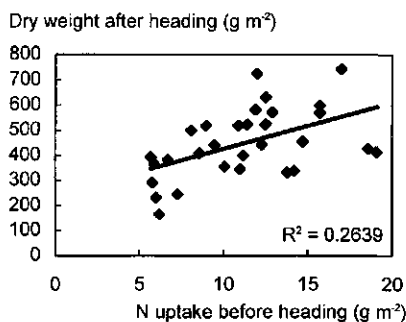


Figure 14. Relationship between N uptake before heading and dry matter production after heading.

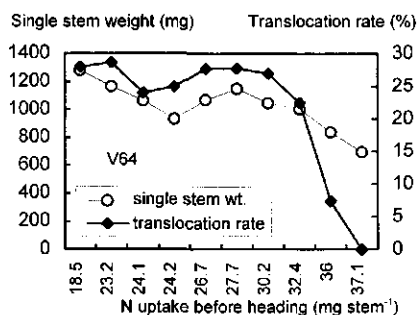


Figure 15a. Effects of N uptake before heading on stem weight and translocation rate (V64).

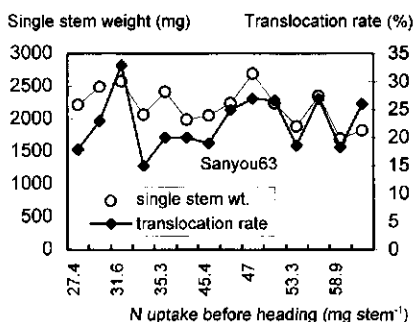


Figure 15b. Effects of N uptake before heading on stem weight and translocation rate (Sanyou63).

maintained at 6-8, grain yield increased as spikelet-leaf ratio increased, both in short- and long-growth duration varieties (Fig. 17a,b).

Effect of N on spikelet-leaf ratio The spikelet-leaf ratio was both affected by N uptake before 25 DAT and during PI. There was a negative correlation between N uptake before 25 DAT and during PI and the spikelet-leaf ratio, respectively ($R^2=0.5233^{**}$, 0.5277^{**} , $n=30$) (Fig. 18, 19). The decrease in spikelet-leaf ratio is due to the fact that the increase in LAI is faster than the increase in spikelets with increased N uptake (Takeda, 1984). There were obvious differences in spikelet-leaf ratio, LAI and grain yield between the N application at PI (panicle initiation) and BO (booting) (Table 2). Nitrogen application at BO resulted in lower LAI, higher spikelet-leaf ratio and higher grain yield than at PI. Therefore, the effects of N application at different times during PI on spikelet-leaf ratio were different.

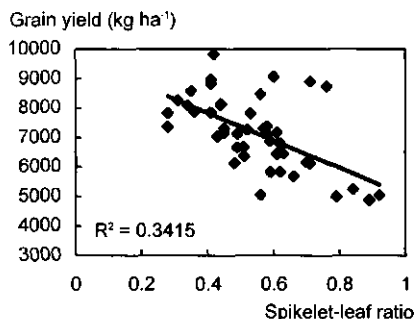


Figure 16. Relationship between the spikelet-leaf ratio and grain yield.

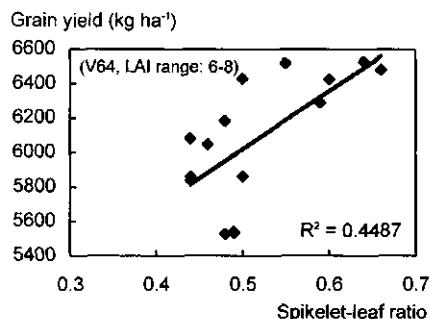


Figure 17a. Relationship between the spikelet-leaf ratio and grain yield (LAI range: 6-8).

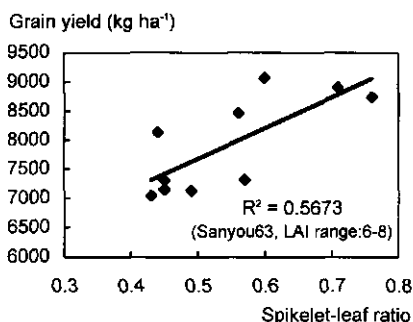


Figure 17b. Relationship between the spikelet-leaf ratio and grain yield.

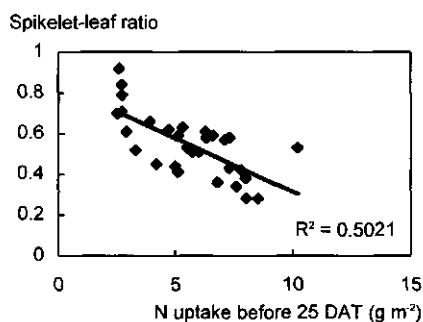


Figure 18. Relationship between N uptake before 25 DAT and spikelet-leaf ratio.

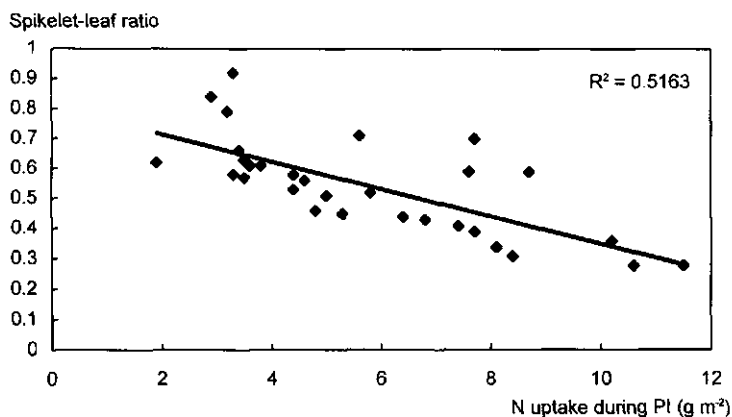


Figure 19. Relationship between N uptake during PI and spikelet-leaf ratio.

Table 2. Effects of N application on spikelet-leaf ratio.

Stage of N application ^a	Amount of N applied (g m ⁻²)	Spikelet-leaf ratio	LAI	Grain yield (g m ⁻²)
PI	3	0.78	4.90	6885
BO	3	0.81	4.31	6960
PI	6	0.80	5.39	6739
BO	6	0.82	4.68	7314
PI	9	0.72	6.42	6799
BO	9	0.83	5.11	7451

^aPI = panicle initiation (neck-node differentiation) (20 DAT), BO = booting (pollen mother cell formation) (35 DAT).

Characteristics of sink-source ratio in the model-recommended N management strategy

Tiller-panicle ratio, spikelet-leaf ratio, spikelet number per panicle, dry matter production after heading and grain yield were all higher in MANAGE-N treatment than in local practise for two varieties (Table 3). But the number of panicles per unit area was almost the same or even less in MANAGE-N treatment than in local practise. These were attributed to N applied at the early stage and more N applied at the later stage. In recent years, scientists have paid more attention to late application of N (Zhen, 1993). At the high N application level, the reduction of N in early stage can reduce the number of ineffective tillers. Therefore, tiller-panicle ratio, spikelet-leaf ratio and spikelet number per panicle will be higher.

Table 3. Comparison between model-recommended split N application and that following local practise.

Treatment	N application ^a (kg ha ⁻¹)	Tiller panicle ratio	Grain leaf ratio	Dry matter produced after heading (kg ha ⁻¹)	Panicles (no. m ⁻²)	Spikelets (no. panicle ⁻¹)	1000 grain weight (g)	Grain yield (kg ha ⁻¹)
Model recommended ^b	2.2+3+3+3.8+3	0.71	0.88	5143	253	210	24	8848
Local practice ^b	6+7.5+0+0+1.5	0.61	0.58	5081	276	155	25.7	8017
Model recommended ^c	2.2+3+3+3.8+3	0.77	0.95	5929	209	212	28.9	7926
Local practice ^c	6+7.5+0+0+1.5	0.6	0.65	4885	209	186	29.1	7536

^aN applied at transplanting 0 DAT), tillering 7 (DAT), panicle initiation (neck node initiation, 20 (DAT), booting (pollen mother cell formation, 35 DAT) and heading, respectively.

^bF131xG37; ^cJiang 1068

Conclusions

Nitrogen uptake before heading had a close correlation with total spikelets and sink capacity. Although tiller number increased as N uptake before 25 DAT increased the tiller-panicle ratio decreased. Too much N application at an early stage will increase ineffective tillers. The number of spikelets per panicle decreased as N uptake before 25 DAT increased, although the total spikelets increased. The increase in N uptake during PI increased the tiller-panicle ratio, the number of spikelets per panicle and the total spikelets. There was close correlation between N uptake before heading and leaf area and leaf weight. Dry matter production after heading was both affected by N uptake before and after heading. Translocation rate was affected by stem weight at heading. The spikelet-leaf ratio decreased as N uptake increased. There was close negative correlation between spikelet-leaf ratio and grain yield. But at a certain LAI range, grain yield increased as spikelet-leaf ratio increased. More splits of N application as recommended by MANAGE-N resulted in higher yield than that obtained using local practise.

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Use of ORYZA_0 model for optimising fertiliser N application to irrigated rice

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Abstract

A field experiment was conducted at Cuttack, India, to test the fertiliser N recommendation generated by the model ORYZA_0 against the state-recommended practise during the 1995 dry season. Variations in grain yield resulting from varying doses and timings of N application were mainly due to differences in number of panicles per m² and number of spikelets per panicle. The dose and timing generated by model ORYZA_0 was found to be superior to the state-recommended practise in increasing grain yield. The higher level of N combined with appropriate timing might have resulted in increased grain yield under computer-generated N application as compared with state-recommended practise.

Introduction

To increase overall N use efficiency in rice production systems, recovery of applied N should be increased. Under field conditions, productivity of rice is often constrained by a limited supply of N. A detailed strategy and a systems approach to fertiliser N management and subsequent crop production are needed to achieve greater efficiency of crop production.

The model ORYZA_0 (ten Berge et al., 1994) was used by Rao et al. (1995) for optimising N fertiliser application to irrigated rice at Cuttack, India. The present study was taken up to test such computer-based recommendation against current recommended practise.

Materials and methods

A field experiment was conducted during the 1995 dry season at the same site where a 1993 experiment was conducted to generate fertiliser recommendation. It aimed to evaluate the advantages, if any, of the computer-based recommendation for fertiliser N application in contrast to state-recommended practise. Thirty-day-old seedlings of medium-duration rice cultivar IR36 were transplanted in puddled soil on Feb 1995.

Seedlings were uprooted from a nursery sown on 2 Jan 1995 which received 10 kg N ha⁻¹ as urea 15 d after sowing (DAS). P₂O₅ and K₂O fertilisers were applied basally at the rate of 40 kg ha⁻¹ each. Nitrogen was applied as per treatment schedule (Table 1). Adequate plant protection measures were taken throughout the growth period of the crop. Tiller counts were made at 10-d intervals starting from 20 d after transplanting (DAT). Five hills were sampled at each sampling date as per the sampling procedure given by Thiyagarajan et al. (1995) to determine dry weights of leaves, stem, roots, panicles and grain at 0, 30, 40, 62 and 96 DAT. Yield (harvest area: 10 m² per plot) and yield components (from five hills) were recorded at harvest.

Results and discussion

The yield components and yield of rice variety IR36 as affected by dose and timing of fertiliser N application during the 1995 dry season are presented in Fig. 1. It was found that the dose and timing generated by ORYZA_0 where the crop received 120 kg N ha⁻¹ in three equal splits at 45, 60 and 70 DAS produced significantly higher grain yield than did the state-recommended practise of giving 80 kg N ha⁻¹ in three equal splits (50% at basal, 25% at active tillering and the rest at panicle initiation). The higher level of N combined with the appropriate timing might have resulted in increased grain yield under computer-generated N application. In the state-recommended practise, the crop received a major portion of the applied N (50%) at planting which might have been lost through leaching and other processes. The crop suffered due to inadequate supply of N at later stages of growth and this was clearly reflected in the periodic tiller production (Fig. 2) and less grain yield. Basal application of N fertilisers involves risk of losses since the nutrient uptake in transplanted rice does not accelerate until 2-3 wk after

Table 1. Treatment details of verification experiment, Cuttack, 1995 dry season.

Treatment	Details
T1	Zero N
T2	State-recommended dose (80 kg N ha ⁻¹) and timing (50% at basal, 25% at active tillering and the rest 25% at panicle initiation)
T3	State-recommended dose (80 kg N ha ⁻¹) and timing (three equal splits at 45, 60 and 70 d after sowing) generated by ORYZA_0
T4	Dose (120 kg N ha ⁻¹) and timing (three equal splits at 45, 60 and 70 d after sowing) generated by ORYZA_0 to reach target yield
T5	120 kg N ha ⁻¹ in two equal splits at 40 and 70 d after sowing
T6	200 kg N ha ⁻¹ in four equal splits as basal, at active tillering, at panicle initiation and at flowering

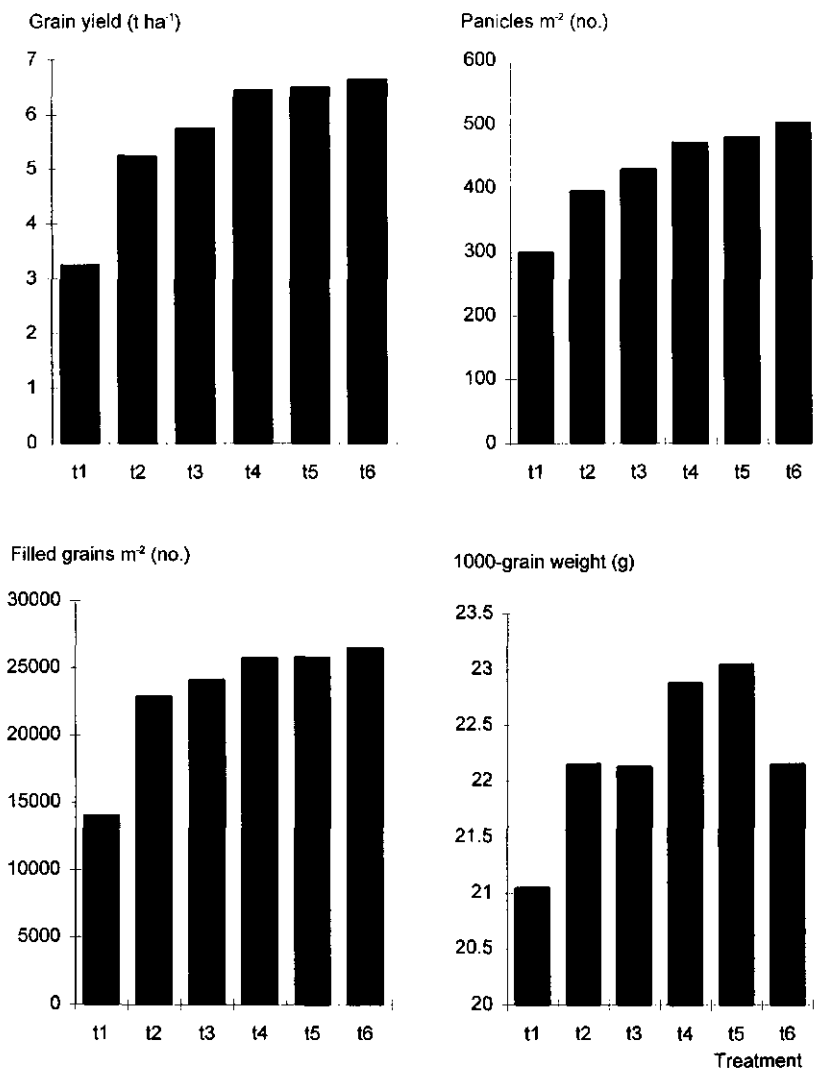


Figure 1. Yield and yield components of IR36 as affected by dose and timing of N application during 1995 dry season.

planting and losses of added N fertiliser could be considerable during this period. This could be further confirmed as the crop which received the same amount of N in three equal splits at growth stages other than the basal (T3) could benefit more in terms of higher grain yield. The beneficial effect of dose and timing generated by the ORYZA_0 model was amply demonstrated through the increase in number of panicles, number of

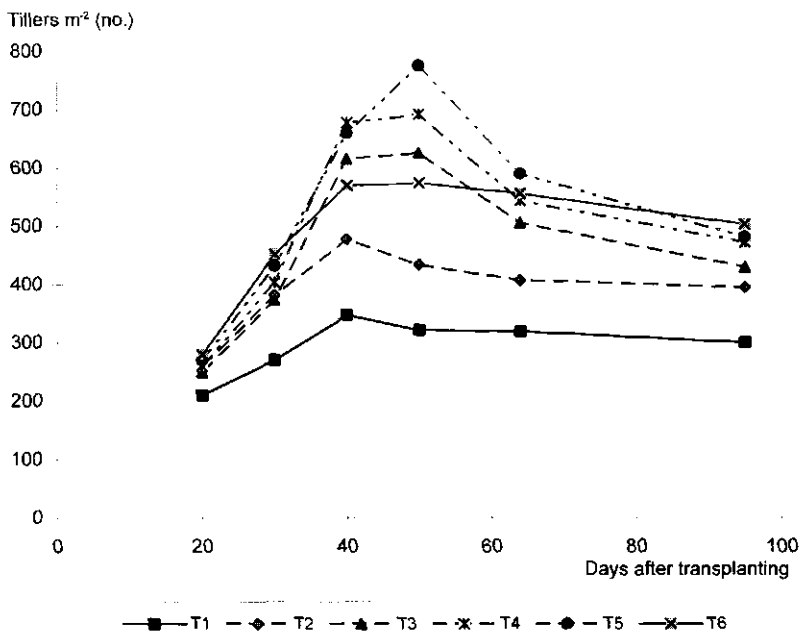


Figure 2. Periodic tiller production of IR36 as affected by dose and timing of N application during 1995 dry season.

filled grains per panicle and 1,000-grain weight (Fig. 1), which ultimately resulted in higher grain yield of the crop.

These experimental evidences emphasise the disadvantage of applying greater quantity of N particularly at planting (basal) when the capacity of the plant to utilise applied N is very low. This suggests that total or even a part of N application at the planting stage (basal) of the crop should be avoided. Furthermore, for best crop responses, N should be applied in three equal splits at 45 DAS (around seedling establishment), at 60 DAS (around active tillering stage) and at 70 DAS (5-6 d before panicle initiation).

Conclusions

- The model ORYZA_0 could be used to optimise the N management strategy for a specific cultivar under a specific cultivation environment.
- An application of 120 kg N ha⁻¹ in three equal splits at 45, 60 and 70 DAS was found optimum to produce a grain yield of 7 t ha⁻¹ during the dry season for rice cultivar IR36.

- The dose and timing of N application generated by the model ORYZA_0 (i.e., 120 kg N ha⁻¹ in three equal splits at 45, 60 and 70 DAS gave 24% extra grain yield over the current state-recommended practise of 80 kg N ha⁻¹ in three splits (50% at planting, 25% at active tillering and the rest at panicle initiation).

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Numerical optimisation of fertilizer N application to irrigated rice with ORYZA_0: experiences at Jinhua, China

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Abstract

A field experiment was conducted to verify the effectiveness of fertiliser N recommendation given by the ORYZA_0 model. Consisting of four treatments, the experiment compared model recommendation with local practise. The variations in grain yield as a result of different doses and timings of N applications were mainly attributed to the differences in number of panicles m⁻² and number of spikelets panicle⁻¹. Higher N application had significantly favourable effects on dry matter production and N uptake during vegetative stage but the effects were not reflected in the final yield. With model recommendation, the crop enhanced translocation of stored N from leaf to panicle and achieved greater N availability and higher spikelet-leaf ratio. This represented good source-sink coordination and greater photosynthetic rate among the crop population. As a result, maximum grain yield was attained with the model recommendation.

Introduction

The efficiency of rice production, as of the other crops, is basically determined by the ability of the crop to intercept and convert solar energy into chemical compounds which are essential for growth. It is well-established that light use efficiency as well as expansion of growing tissue of a species are considerably determined by crop nitrogen (N) content (Sinclair & Horie, 1989; Moorby & Besford, 1983; Mengel & Kirkby, 1978). Under field conditions, rice productivity is often constrained by a limited supply of N. Research has been continuously conducted to investigate factors and processes affecting N availability in the soil, its distribution within the crop and its effects on growth and yield (IRRI, 1979). The findings have led to significant improvement in rice management and productivity. It was observed, however, that high rates of N application do not always ensure a proportional increase in yield due to high N losses resulting in low N recoveries (Patrick & Reddy, 1976; Stutterheim et al., 1994). Moreover, complex

crop-environment interactions and economic and environment aspects must also be considered (Pannangpetch & ten Berge, 1994). Therefore a detailed strategy and a systematic approach to fertiliser N management and subsequent crop production are needed to achieve greater efficiency in crop production, while maintaining sustainability of the system and the environment.

Using the summary model ORYZA_0 (ten Berge et al., 1994), fertiliser N recommendation curves for hybrid rice Xieyou 46 were generated by Zheng et al. (1995). The present study was carried out to compare the model recommendation with local practises.

Materials and methods

Based on the response curve resulting from EXP93 (Zheng et al., 1995), total input level A_{tot} was the best that could be determined in view of local economic and environmental considerations. The transformation of this selected curve into a discrete number of split dose applications, each of a specified size and at a specified time, can be identified with the approach that ten Berge et al., (1994) suggested.

Thirty-five-d-old seedlings of hybrid rice Xieyou 46 were transplanted on 25 Jul to 30-m² plots. The trial consisted of a randomised complete block with four replications. The different treatments were as follows: T0 = the control without fertiliser N application; T1 = state-recommended dose (180 kg N ha⁻¹) and timing (three splits at 0, 5, and 25 DAT); T2 = state-recommended dose and timing generated by ORYZA_0 model (four splits at 8, 19, 27, and 38 DAT); T3 = computer-recommended dose (150 kg N ha⁻¹) and timing.

Plants were sampled at transplanting (TP), active tillering (AT), first flowering (FF), panicle initiation (PI) and harvest. Crop N was determined using the Kjeldahl method (Manual, 1988). Tiller dynamics and physiological maturity were recorded. Weather data were collected from a local weather station 5 km away from the experimental field.

From the fertiliser N recommendation curves generated for the site and cultivar (Zheng et al., 1995) and considering local economic, environmental, and other conditions, 150 kg N ha⁻¹ was taken as the best input level at Jinhua region. To transform this curve into a discrete number of split-dose applications, the continuous recommendation curve was segmented into time intervals, each of which was associated with one split-dose application. The recommendation curve showed how much N must be applied during that time segment. The time when cumulative N was halfway the total increment associated with a certain time interval was chosen as the time of application of the split. The recommended timings of N application were at 8, 19, 27 and 38 DAT.

Results and discussion

Dry matter production

Dry weights of leaf biomass and total crop biomass for various N application doses and timings are presented in Table 1. Leaf biomass of Xieyou 46 given doses according to local practise (T1) and of those given state-recommended N application dose and computer-generated timing (T2) were higher than that of model recommendation (T3) before first flowering (47 DAT). The trend was reversed after first flowering. Total crop biomass increased with increase in N application at any crop stage. The results imply that higher fertiliser N application (T1 and T2) did not lead to an increase in leaf biomass during the reproductive stage, which greatly contributed to grain yield formation.

Crop N uptake

Time courses of leaf N accumulation and total crop N uptake are shown in Table 2. Varying the dose and timing of N application mainly affected N uptake during the vegetative stage, while a slight decrease was observed at first flowering onward comparing state recommendation (T1) with model recommendation (T3). The leaf N accumulation for T1 and T2 where the same doses of N were applied but at different times differed considerably during crop growth stage. The highest leaf N accumulation occurred at first flowering for model recommendation (T3), whereas it was lowest at harvest except in the treatment without N application, indicating that most of the N was transferred from the leaf to the panicles. The proportion of crop N uptake from the soil ranged from 50.91 to 62.88% for T1 and from 51.06 to 73.95% for T3 (Table 3). Contribution from fertiliser varied from 37.12 to 49.09% for T1 and from 29.05 to 48.94% for T3.

Grain yield and yield components

Details of grain yield and yield components are listed in Table 4. Various N application

Table 1. Effect of N application on leaf biomass and total crop biomass for hybrid Xieyou 46, Jinhua, 1994.

Days after transplanting	Leaf biomass (kg ha ⁻¹)				Total crop biomass (kg ha ⁻¹)			
	T0	T1	T2	T3	T0	T1	T2	T3
13	456.5	592.6	584.4	560.7	1041.1	1367.8	1349.4	1297.5
28	1030.7	1756.6	1697.1	1670.2	3192.8	4392.1	4243.4	4097.7
47	1614.8	2388.0	2400.0	2381.3	6319.9	8640.8	8572.6	8372.5
90	1095.1	1732.4	1756.5	1783.1	9500.0	13386.8	13562.7	13214.1

Table 2. Effect of N application on total crop N uptake and leaf N accumulation for hybrid Xieyou 46, Jinhua, 1994.

Days after transplanting	Total crop N uptake (kg ha ⁻¹)				Leaf N accumulation (kg ha ⁻¹)			
	T0	T1	T2	T3	T0	T1	T2	T3
13	22.43	35.67	32.86	30.33	13.42	19.47	17.96	16.87
28	47.92	84.02	79.69	74.13	19.12	41.52	40.34	38.30
47	74.23	142.83	144.28	141.32	24.21	44.89	46.60	46.97
90	80.56	158.23	161.26	157.78	9.64	23.21	23.19	21.75

Table 3. Proportion of total crop N uptake from 'native' soil N supply and from fertiliser N for hybrid Xieyou 46, Jinhua, 1994.

Days after transplanting	T1: 180 kg N ha ⁻¹ (local practise)	
	Soil N (% of total N uptake)	Fertiliser N (% of total N uptake)
13	62.88	37.12
28	57.03	42.97
47	51.97	48.03
90	50.91	49.09
T3: 150 kg N ha ⁻¹ (model recommendation)		
13	73.95	29.05
28	64.64	35.36
47	52.53	47.47
90	51.06	48.94

doses and timings significantly affected grain yield by affecting yield components. Highest yield was attained when 150 kg ha⁻¹ fertiliser N was applied in four splits (8, 19, 27 and 38 DAT) due to highest number of spikelets per panicle and filled grain. For the treatments that received 180 kg ha⁻¹ fertiliser N, greater number of panicles per m² and a slight increment in 1,000-grain weight were obtained but the lower spikelets per panicle and setting percentage consequently did not lead to an increase in grain yield. Grain yields were not significantly different among T1 and T2 where the same doses of fertiliser N were applied in different splits.

The impact of the different doses and timings of N application on spikelet-leaf ratio at heading stage are shown in Table 5. The crop that was given model-recommended

Table 4. Comparison of grain yield^a of Xieyou 46 with and without model recommendation, Jinhua, 1994.

Treat- ment	Panicles m ⁻² (no.)	Spikelets panicle ⁻¹ (no.)	Filled grains (%)	1,000-grain weight (g)	Calculated yield (kg ha ⁻¹) ^b	Actual yield (kg ha ⁻¹) ^b
T0	259.9	90.4	86.20	28.10	4951.2 c	4870.3 c
T1	316.6	101.7	80.08	27.79	6230.8 b	6045.6 b
T2	309.9	106.7	80.11	27.70	6383.7 ab	6296.5 b
T3	307.1	113.0	80.14	27.64	6678.3 a	6410.4 a

^aGrain yield at 0% moisture.

^bYield difference is significant at the 5% level.

treatment (T3) had better source-sink coordination and higher photosynthetic activity at heading onward, resulting in higher grain yield.

Conclusions

Combined with a numerical optimisation procedure, ORYZA_0 could be used to predict attainable crop biomass or grain yield and to optimise the N management strategy for a specific cultivar under a specific cultivation environment. The best fertiliser N recommendation curve for Xieyou 46 at Jinhua was 150 kg N ha⁻¹ in view of both the resulting N response curve and considerations of local economic and environmental conditions. The fertiliser N recommendation curve corresponding to the selected N application was transformed into doses of equal proportions to be applied at 8, 19, 27 and 38 DAT.

Variation in crop biomass, crop N uptake and grain yield resulting from varying doses and timings of N application was observed in the verification trials (Tables 2, 3

Table 5. Comparison of spikelet-leaf ratio of hybrid Xieyou 46 at heading stage with and without model recommendation, Jinhua, 1994.

Treat- ment	Spikelets ha ⁻¹ (no.)	Leaf weight (kg ha ⁻¹)	Specific leaf weight (mg cm ⁻²)	LAI	Spikelet- leaf ratio (kg ha ⁻¹)	Yield (kg ha ⁻¹)
T0	2.35 x 10 ⁸	1614.8	28.58	5.65	0.41	4870.3
T1	3.22 x 10 ⁸	2388.0	33.92	7.04	0.46	6045.5
T2	3.30 x 10 ⁸	2400.1	34.00	7.06	0.47	6296.5
T3	3.47 x 10 ⁸	2386.4	34.76	6.85	0.51	6410.4

and 5). Higher N application (180 kg N ha⁻¹) had significantly favourable effects on dry matter production and N uptake during the vegetative stage of the crop but these were not reflected in the final yield. Increasing the number of times of N application induced higher yield. Yield differences among treatments were mainly due to differences in number of panicles per m² and number of spikelets per panicle. Maximum grain yield was attained with the model recommendation, possibly due to better translocation of stored N from leaf to panicle, higher N availability and higher spikelet-leaf ratio representing good coordination of source-sink and higher photosynthetic activity of the crop population.

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Field and simulation study to evaluate effects of brown planthopper feeding on rice plants

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Abstract

A field experiment was conducted at IRRI in the 1994 dry season to quantify the growth response of rice plants infested with brown planthopper (BPH) populations. Infestation of 10 pairs of BPH adults was timed in such a way that the 5th-instar nymphal period coincides with these stages: 10 d before flowering, at flowering and 10 d after flowering. Destructive sampling was done when BPH 1st-instar and 5th-instar nymphs emerge and this was continued at weekly intervals until harvest. The growth rate of BPH population decreased with plant age. Of the three treatments, the growth of rice plants infested before flowering was much affected by BPH feedings. In the infested rice plants, the area and dry weight of green leaves were significantly reduced. Similarly, shoot dry weight decreased continuously after infestation. In addition to the normal decline of N content in the green leaves due to aging, the decline was accelerated by BPH infestation. The N reduction was more significant in the lower than in the upper leaves. The plant growth simulation model coupled with BPH feeding was used to analyse these results.

Introduction

The brown planthopper (BPH) *Nilaparvata lugens* Stål is one of the most serious pests of rice in Asia. The BPH is a phloem sap feeder. At high population density, BPH feeding causes death of the rice plant. The phloem sap feeding may also cause several physiological effects on rice growth and yield. One direct effect is drainage of photosynthates. Other indirect effects were blockage of photosynthates, translocation, reduction of photosynthetic rate, and increase in maintenance respiration. There are a few studies that quantify these important effects on rice growth. In addition, data on the interaction between rice plant growth and BPH population in the field are inadequate. To quantify this relationship, a field experiment was conducted at IRRI. The data were used

to evaluate the effect of different infestation periods at a given environmental condition with the use of simulation models described in this paper.

Materials and methods

An experiment was conducted in a 2500-m² field in IRRI during the dry season of 1994. Variety IR22, susceptible to BPH, was sown on 7 Jan. It was transplanted on 25 Jan at the rate of three seedlings per hill, with 25- x 25-cm spacing. There were three treatments: BPH was infested at 10 d before flowering (T1), at flowering (T2) and 10 d after flowering (T3). Uninfested plants were used as control. Each treatment had four replicates. The sampling plots (2 x 2 hills) were covered with nylon mesh, 50 x 50 cm wide and 150 cm tall, supported by bamboo sticks. Ten pairs of BPH adults per hill were released into each cage. When 80% of the nymphs were at the 5th-instar stage, all BPH in the cage were collected.

The rice plants were sampled when the 1st-instar nymphs emerged and the 5th-instar nymphs were collected. This destructive sampling was continued at weekly intervals until harvest. At each sampling, leaf area (green and dead), aboveground biomass and number of tillers (productive and unproductive) were measured and recorded. Nitrogen and carbon concentration in each plant part were also determined.

Results and discussion

The later the infestation on rice plants started, the lower the population growth rate of BPH (Fig. 1). Kisimoto (1977) showed similar changes in BPH population growth rate on a japonica variety. The highest BPH population growth rate was observed at T1. However, LAI reduction was observed just after infestation (58 DAT) and at flowering (64 DAT) (Fig. 2). Shoot dry weight and panicle dry weight were also reduced after infestation at T1. The differences between the infested plot and the control increased at later infestation. Moreover, even at initial sampling when the 1st-instar nymphs emerged, LAI and shoot dry weight in the infested plot at T2 and T3 were lower than those in the control. The growth of the rice plants may have been affected by infested BPH adult feedings. There were no differences in dry weight of dead parts in all treatments.

The N content in the leaves decreased with plant age (Fig. 3). The leaf N contents measured after infestation was also reduced at T1 when compared with the control (Fig. 4). The reduction in N content of the lower leaf layer (3rd and 4th leaves) was greater than that of the upper leaf layer (flag, 1st and 2nd leaves). The leaf chlorophyll content measured by a chlorophyll meter (SPAD 502) also decreased in infested plants.

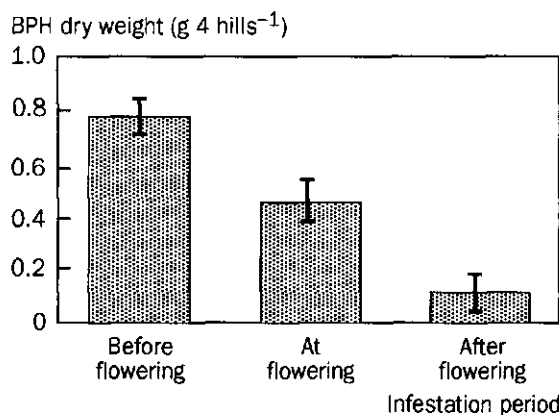


Figure 1. Dry weight of BPH collected at the end of infestation.

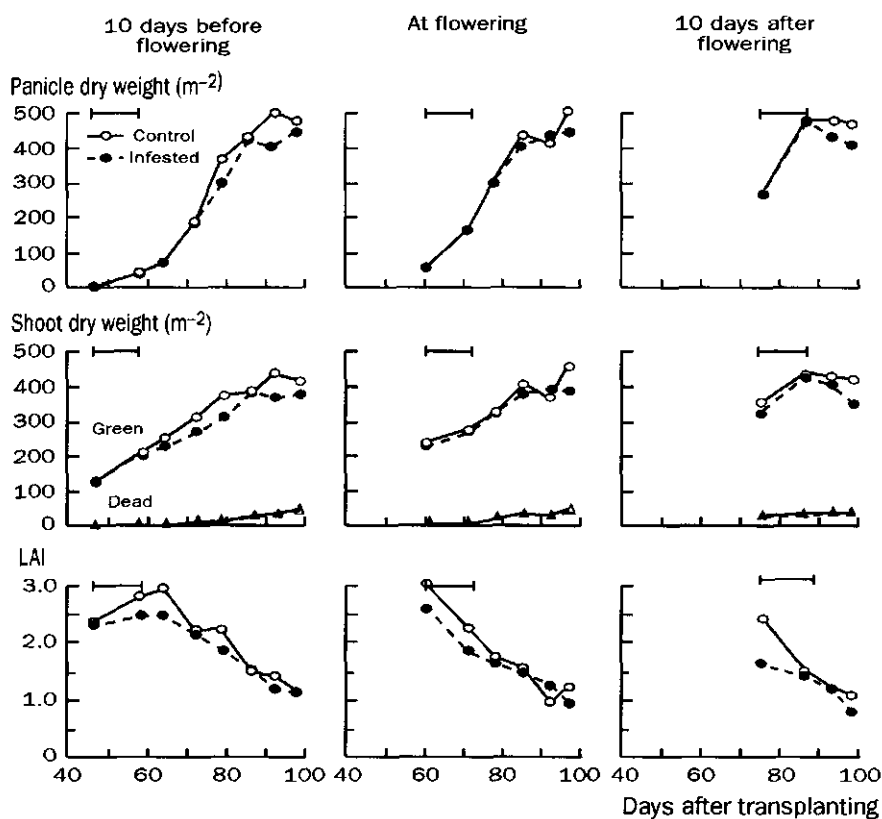


Figure 2. Changes in panicle dry weight, shoot dry weight and LAI observed in three infestation periods. Horizontal bar indicates the infestation period, 1st-instar nymphs to 5th-instar nymphs of BPH.

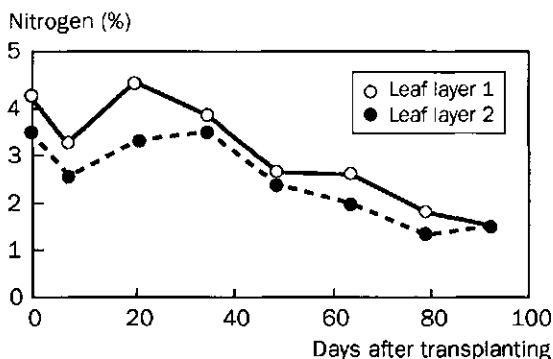


Figure 3. Nitrogen content in the leaves of the control.

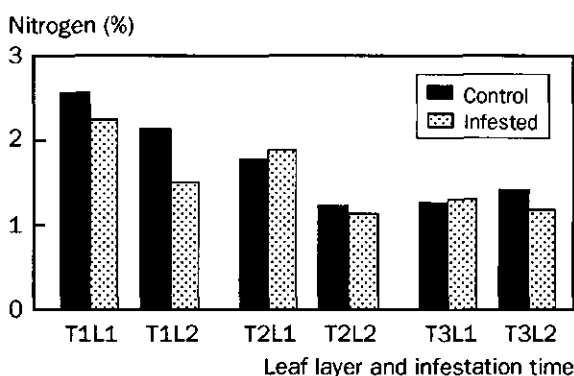


Figure 4. Nitrogen content in the leaves at each treatment after infestation. T1: infestation started 10 d before flowering, T2: at flowering, T3: 10 d after flowering. L1: leaf layer 1 (flag, 1st and 2nd leaves), L2: leaf layer 2 (3rd and 4th leaves).

Kuno (1968) observed that BPH nymphs and adults usually stay and feed on the lower sheaths near the water surface. This may have resulted in higher BPH sucking rate on the lower leaf sheaths than on the upper leaf sheaths. Therefore, the effect of BPH feeding on the lower leaf layer was much severe than that on the upper leaf layer. Although BPH were removed before flowering at T1, production of shoot dry weight and panicles continuously decreased after infestation. We applied the simulation model coupled with plant growth and BPH feedings (Watanabe, 1995) to evaluate the effects of reduction of LAI and shoot dry weight at flowering on grain growth. The simulation initial values of 2.5 and 3.0 for LAI and shoot dry weight of 430 and 480 g m⁻², for the control and infested, respectively, were obtained from sampling at flowering. The daily mean temperature and radiation recorded at IRRI were also used. The simulated grain weight and LAI were closely related to observed values (Fig. 5). These results show that

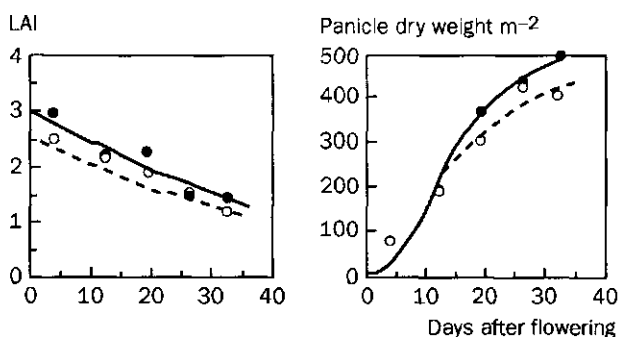


Figure 5. Simulated and observed LAI and grain growth of T1. Circles are observed data, ●: control, ○: infested. Lines are simulated output, solid line: control, broken: infested.

LAI and biomass reduction due to BPH feeding before flowering accounted for the differences in panicle weight between the infested and the control plants.

The results did not show a clear relationship between infestation period and reduction in biomass and panicle weight because BPH density varied with plant age, even if an equal number of adults were released at each treatment. Another field experiment was conducted to further determine the effect of different BPH infestation rates and times of BPH feeding on the growth of the rice plant and grain yield.

Acknowledgment

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Simulation study to quantify brown planthopper feeding effects on growth and yield of rice plants

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Abstract

The brown planthopper *Nilaparvata lugens* Stål is an important pest of rice in many countries. Recent studies showed that *N. lugens* feeding activity is significantly influenced by crop development stage. *N. lugens* feeding affected photosynthesis and leaf senescence. This paper identifies knowledge gaps and future activities for *N. lugens* research.

Introduction

The brown planthopper (BPH) *Nilaparvata lugens* (Stål) is a phloem sap feeder of the rice plant. BPH feeding causes reduction in plant growth and yield. It is difficult to simulate the actual damage of BPH by artificial methods. Therefore, coupling the feeding effect of BPH with the rice growth model is not only a useful way to verify the hypothesis about physiological changes in the rice plant but also an important tool to quantify crop damage by BPH under varying weather and planting conditions. In addition, these approaches will contribute to the improvement of integrated pest management strategies to control BPH in areas planted to rice in Asian countries. This paper gives an update of the status of BPH damage and identifies research gaps and future activities of the SARP research group working on BPH.

Summary of activities conducted

Laboratory experiment

The rate of honeydew excretion by BPH increased with increase in % leaf N and temperature. The maximum rate was maintained up to maximum tillering. Two weeks before flowering, it started to decline until flowering (Sogawa 1992, 1994).

The effect of feeding by BPH was assessed by infesting rice plants in a pot using several densities per plant. Zero to 20 BPH female adults were released at three plant stages, 10 d before flowering, at flowering and 10 d after flowering. The dry weights of BPH were significantly correlated with most plant biomass parameters, weight of green

leaves, dead leaves, stems and total green leaf area. The increase in percentage of dead leaves' dry weight was significantly correlated with percentage of BPH dry weight in three infestation times (Fabellar et al., unpubl.). Plant matter was removed by BPH feeding (Sogawa, 1994). Similar high reduction in plant biomass due to WBPH feeding was observed (Watanabe and Sogawa, 1994).

The effects of phloem feeding by BPH on rice canopy photosynthesis were measured by using stable isotope ^{13}C . BPH infestation started at the booting stage. One hundred large nymphs were released at each plant and were allowed to feed for 10 d. After the infestation period, $^{13}\text{CO}_2$ was fed at each plant. The excess ^{13}C abundance per leaf area was an index of photosynthetic activity of the leaves. These values decreased gradually from the top to the lower leaves in both treatments. The significant differences between treatments were observed at the lower leaves (Watanabe and Kitagawa, unpubl.).

Field experiment

At IRRI. BPH female adults were released 10 d before flowering, at flowering and 10 d after flowering at the IRRI field. After one generation, insects and plants were sampled. The later the infestation on rice plants started, the lower the population growth rate of BPH. The highest growth rates were observed at 10 d before flowering. Leaf area index, shoot dry weight and panicle dry weight were reduced after infestation at 10 d before flowering of rice plant decreased in the infested plot. The N% reduction in lower leaves by BPH feeding was larger than that in upper leaves (Watanabe et al., 1995).

At Japan. At the panicle initiation stage, BPH adults were released at several densities under field conditions. After flowering, panicle and shoot dry weight and insect density were measured at 2-3-wk-intervals. Both yield and crop growth rate (CGR) of shoot and panicle decreased linearly when BPH incidence (density \times observation interval) increased. The reduction rate in panicle CGR was lower than that in shoot CGR. It was assumed that phloem feeding by BPH did not affect panicle growth rate directly (Watanabe, 1995).

Simulation approach. Extended MACROS-LID, with five leaf layer photosynthesis processes and BPH feeding could describe not only grain weight reduction but also plant death (hopperburn). By using this model, we showed the differences in yield due to changes in infestation period and climatic conditions, even though initial plant biomass and planthopper infestation levels were stable (Watanabe, 1994, 1995).

Research gaps

The following issues should receive the highest priority for BPH model improvement:

- Relationship between the leaf senescence process and BPH feeding
- Nitrogen uptake and nonstructural carbohydrate (NSC) accumulation change by BPH

- Relationship between spatial distribution of BPH and its effect on rice plant growth and yield
- Acquisition of plant and grain growth data to validate the model output

Future activities of the BPH research group

Experiment

- Several sets of field data (e.g., BPH density, LAT, biomass, % N, etc.) are needed to validate/improve the model.
- An intensive study must be done to assess BPH feeding effect on % N and NSC performance in the greenhouse or laboratory.
- If possible, some physiological information must be obtained to improve the model (e.g., relationship between % N of phloem and % N of leaves, changes in maintenance respiration of infested plants, etc.).

BPH Model

- The BPH model should be validated under various conditions.
- The model should include the function of N movement.

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Interaction of N and bacterial leaf blight management

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Abstract

Bacterial leaf blight (BLB) of rice incited by *Xanthomonas oryzae* pv. *oryzae* is one of the foliar diseases that limit rice production. To understand the effect of BLB onset at three crop growth stages and two N regimes, normal (125 kg ha⁻¹) and high (250 kg ha⁻¹), a crop growth simulation model, BLIGHT_1 was used. The model was validated using data from a field experiment conducted during the 1994-95 wet seasons, using IR64. BLB was inoculated following the clip method of inoculation at early tillering (57 DAS), late tillering (81 DAS) and flowering (92 DAS) crop stages. For periodic samplings, the crop canopy was divided in two layers to measure leaf area of healthy, diseased (healthy and dead) and dead leaves and dry weights of leaves, stem and panicles. Disease severity and leaf N contents were determined and used as inputs for the model. Analysis of green leaf area and the diseased dead leaf area in two layers of the canopy revealed that under normal N, the bottom layer had lesser green leaf area for the early-inoculated plot whereas the top layer had more green leaf area than the healthy plot or other treatments. Diseased dead leaf area increased up to flowering. More diseased dead leaf area was observed at the top layer after flowering. No yield loss was observed for the early-inoculated plot but yield reduction was pronounced in the late-inoculated plot. Under high N, early inoculation increased the diseased dead leaf area of the bottom layer with concomitant reduction of green leaf area; but the top layer had more green leaf area. Late inoculation increased the dead leaf area at the top layer. The loss of dry matter and grain yield was highest for late followed by early inoculation. The presence of more dead leaf area at the top layer of canopy resulted in reduced light use efficiency and thereby loss of dry matter production and grain yield. BLIGHT_1 model simulated well the field situation and could be used for application studies. The present study showed that the late tillering stage of the crop is critical for disease management.

Introduction

Bacterial leaf blight (BLB) of rice incited by *Xanthomonas oryzae* pv. *oryzae* is one of the foliar diseases that limit rice production. Degree of cultivar susceptibility, time of disease

onset, crop development stage and N application methods influence disease buildup, and extent of damage and yield loss. Estimates of yield loss ranged from 2 to 74% (Srivastava et al., 1966; Reddy, 1974; Exconde et al., 1973). Disease onset at late tillering stage causes more losses than at the flag leaf stage (Reddy et al., 1994). The objective of the present study is to understand the effect of BLB, with onset at three different stages of crop growth under normal and high levels of N (125 and 250 kg N ha⁻¹) using a crop growth simulation model incorporating the disease damage mechanism BLIGHT. A field experiment was conducted and data on various crop growth parameters with and without the disease pressure were collected. The model was used to analyse the experiment and understand the differential effect of disease onset on crop yield.

Materials and methods

Field experiment

A field experiment was conducted during 1994-95 wet season (October to February) at Tamil Nadu Rice Research Institute, Aduthurai, Tamil Nadu, India. Cultivar IR64 was sown on 13 Oct and 30-d-old seedlings were transplanted at the rate of 2 seedlings per hill with a hill spacing of 0.2 x 0.15 m on 12 Nov. The field was divided into eight plots each measuring 18 m². Normal recommended level of N (125 kg ha⁻¹) and a high N level (250 kg ha⁻¹) were applied as urea in five split doses on 29, 40, 55, 70 and 90 d after sowing (DAS). Phosphorus and potash were applied basally at the rate of 60 kg each of P₂O₅ and K₂O ha⁻¹. Treatments were as follows: without BLB, BLB inoculation at early tillering stage (early inoculation, 57 DAS), late tillering stage (late inoculation, 81 DAS) and inoculation at flowering stage (flowering inoculation, 92 DAS). The BLB pathogen was inoculated following the clip method (Kauffman et al., 1973). Early tillering, late tillering and flowering received three, two and one inoculation, respectively.

Crop and disease characteristics were observed periodically by destructive sampling of 5 hills in three adjacent rows, starting from 27 d after transplanting on day of the year 343, 352, 363, 14, 30 and 46. Crop characteristics observed include leaf area and dry weights of leaves, stems and panicles. The crop canopy was initially considered as a single layer and after the start of inoculation divided into two layers to account for a vertical gradient of injury: bottom layer (L1) constituted two-thirds and the top (L2) one-third, based on actual height of plants observed (Elings, 1994). In each layer, healthy, diseased and dead leaves were separated. Disease severity was determined based on the fraction of diseased leaf area relative to total leaf area (Elings, 1993). Leaf N content of healthy leaves (with and without disease) were determined periodically.

Anthesis and physiological maturity of the crop occurred on 16 Jan and 15 Feb 1995, respectively. Analysis of the data on disease characteristics was done for each treatment.

Model validation

The effects of BLB on crop growth and production were simulated using BLIGHT model (Elings & Rubia, 1994; latest version Jul 1995), which is based on ORYZA_1 (Kropff et al., 1993). The BLIGHT model incorporates reduction of photosynthesis of diseased leaf area due to BLB and simulates crop growth under given disease progress (Elings et al., 1994). Observed healthy, diseased and dead leaf areas were used as input. The calculated crop development rates on the basis of observed phenology for the vegetative (DVRV) and reproductive (DVRR) phases of IR64, 0.000703 d⁻¹ and 0.00202 d⁻¹, respectively, were introduced. Specific leaf weight was calculated from leaf area (LAI) and dry weight of leaves. Dry matter partitioning into leaves, stems and panicles was taken from field observations. Fraction of carbohydrates allocated to the stems (FSTR) that is stored as reserves was calculated from the difference between maximum stem weight and stem weight at harvest.

Results

Field experiment

Normal N application (125 kg N ha⁻¹) Total green leaf area up to flowering was highest for plants inoculated at flowering, followed by plants inoculated at late tillering, healthy plants and plants inoculated at early tillering (Table 1). Green leaf area for early-inoculated plants and healthy plants was almost the same (Fig.1-A). At the bottom layer (L1), early-inoculated plants showed less green leaf area before flowering whereas at the top layer (L2), there was more green leaf area than in healthy plants or at late tillering and flowering (Fig.1B-C). The diseased dead leaf area for early-inoculated plants showed a gradual increase up to flowering. After flowering, the diseased dead leaf area for late-inoculated plants was larger than plants inoculated at early tillering or flowering and it continued to increase up to physiological maturity. Layerwise analysis showed that the bottom layer of the canopy also followed a similar trend. After flowering, more diseased dead leaf area was observed in late-inoculated plots than in early-inoculated plots (Fig.2A-C).

Total dry matter production were 8729, 8664, 7633 and 7901 kg ha⁻¹; final stem weights were 2801, 2819, 2697 and 2985 kg ha⁻¹ and grain yield were 5347, 5355, 4479 and 4538 kg ha⁻¹, respectively, for healthy plants, and those inoculated at early tillering, late tillering and flowering (Table 2). Grain yield in early-inoculated plants was not reduced when compared with healthy plants whereas yield reduction was pronounced in late- and flowering-inoculated plants (Fig.3A-B).

High N application (250 kg N ha⁻¹) Total green leaf area up to flowering was highest for healthy plants, followed by those inoculated at flowering, late and early tillering

Table 1. Total leaf area and green and diseased dead leaf area in relation to rice development stage at three BLB onset times (125 kg N ha⁻¹).

Inoculation	Leaf area (kg ha ⁻¹) ^a	Days after sowing					
		57	66	77	93	109	125
		Development stage					
		0.57	0.67	0.79	0.96	1.45	2.01
Healthy	LAIT	0.59	1.77	2.99	3.29	2.11	1.25
	LAIGT	0.59	1.73	2.93	3.20	2.01	1.15
	LAIDSD	0.00	0.00	0.00	0.00	0.00	0.00
Early	LAIT	0.58	2.01	3.40	3.62	1.74	1.05
	LAIGT	0.58	1.89	3.03	3.15	1.38	0.70
	LAIDSD	0.00	0.02	0.14	0.39	0.18	0.20
Late	LAIT	0.58	2.22	3.30	3.67	1.79	1.24
	LAIGT	0.58	2.16	3.24	3.18	1.17	0.60
	LAIDSD	0.00	0.00	0.00	0.43	0.46	0.48
Flowering	LAIT	0.45	2.08	3.55	3.86	1.83	1.31
	LAIGT	0.45	2.04	3.48	3.75	1.45	0.70
	LAIDSD	0.00	0.00	0.00	0.00	0.27	0.40

^aLAIT = total leaf area, LAIGT = total green leaf area of whole canopy, LAIDSD = total diseased dead leaf area.

(Table 3). Early inoculation resulted in greater reduction of green leaf area of the whole canopy or of the bottom layer followed by late inoculation. However, early-inoculated plants showed greater green leaf area at the top layer than late-inoculated plants (Fig.4A-C). At the bottom layer, early-inoculated plants showed a steady increase of diseased dead leaf area up to flowering whereas late-inoculated plants showed a continuous increase in diseased dead leaf area until physiological maturity (Fig.5A-C).

Table 2. Influence of N and BLB onset times on final dry weights of total dry matter, storage organ, and stem (125 kg N ha⁻¹).

Inoculation at	Dry matter (kg ha ⁻¹)		Storage organ (kg ha ⁻¹)		Stem (kg ha ⁻¹)	
	Obs	Sim	Obs	Sim	Obs	Sim
Healthy	8729	9275	5347	5161	2801	2424
Early tillering	8664	8564	5355	4508	2819	2360
Late tillering	7663	8091	4479	3738	2697	2590
Flowering	7901	8492	4538	4097	2985	2805

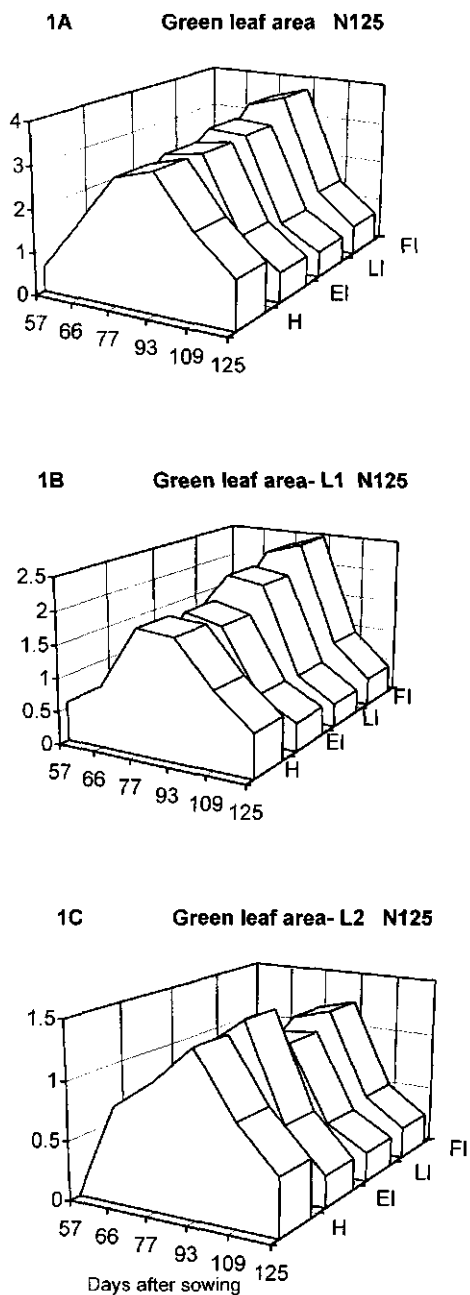
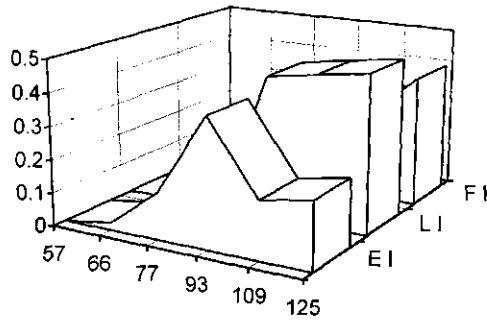
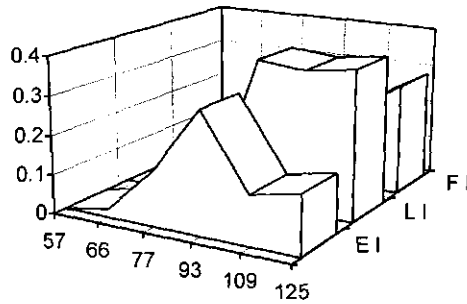


Figure 1. Green leaf area for crop canopy for healthy (H), early (EI), late (LI) and flowering (FI) inoculations under normal N application (125 kg N ha^{-1}).

2A Diseased dead leaf area N125



2B Diseased dead leaf area-L1 N125



2C Diseased dead leaf area-L2 N125

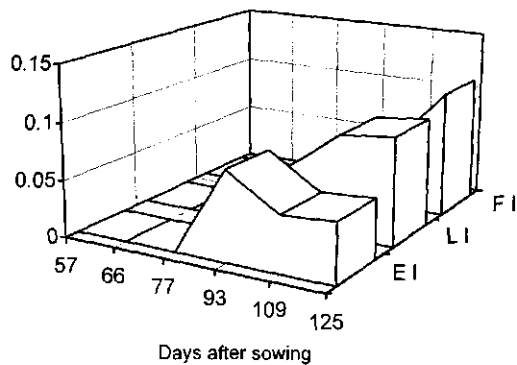


Figure 2. Diseased dead leaf area for crop canopy for healthy (H), early (EI), late (LI) and flowering (FI) inoculations under normal N application (125 kg N ha⁻¹).

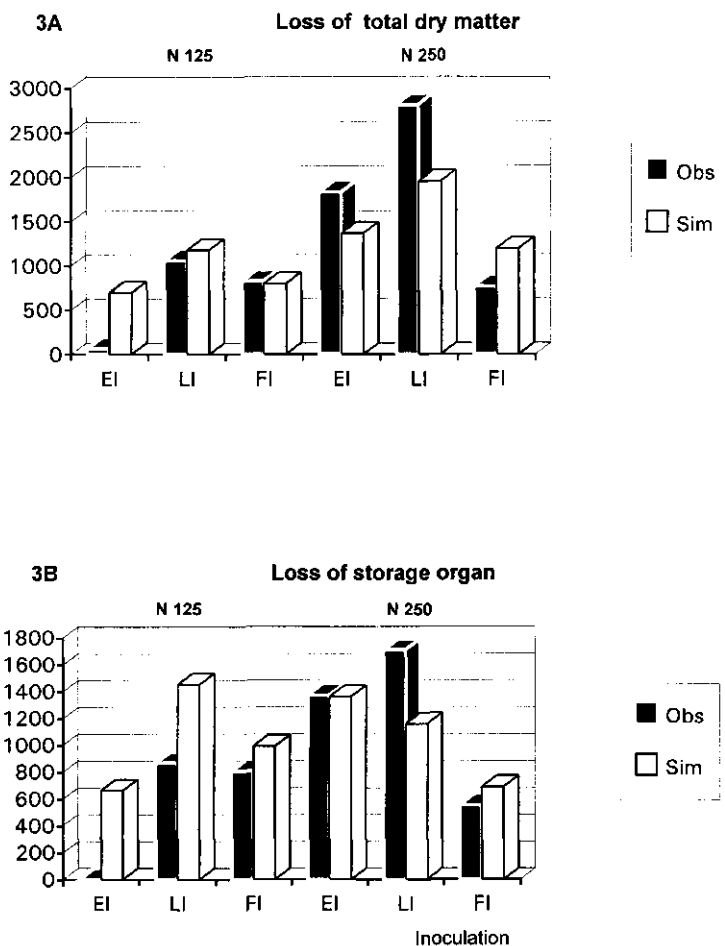
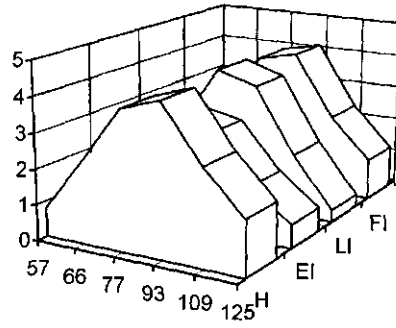


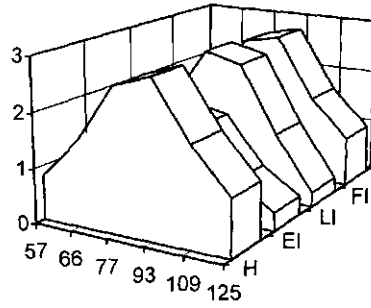
Figure 3. Simulated and observed loss of total dry matter and storage organ due to early (EI), late (LI) and flowering (FI) inoculations under normal (125 kg N ha⁻¹) and high (250 kg N ha⁻¹) N applications.

The observed dry matter production for healthy plants and early, late and flowering-inoculated plots was 11129, 9293, 8513 and 10362 kg ha⁻¹; the stem weights were 3513, 2993, 2657 and 3547 kg ha⁻¹ and the grain yield were 6837, 5464, 5128 and 6284 kg ha⁻¹ (Table 4). The loss in dry matter and grain yield due to BLB inoculation was highest for late-inoculated plants followed by early-inoculated plants and plants inoculated at flowering (Fig.3A-B).

4A Green leaf area N250



4B Green leaf area- L1 N250



4C Green leaf area- L2 N250

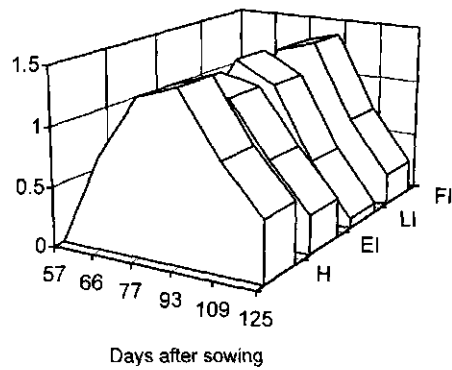


Figure 4. Green leaf area for crop canopy for healthy (H), early (EI), late (LI) and flowering (FI) inoculations under high N application (250 kg N ha⁻¹).

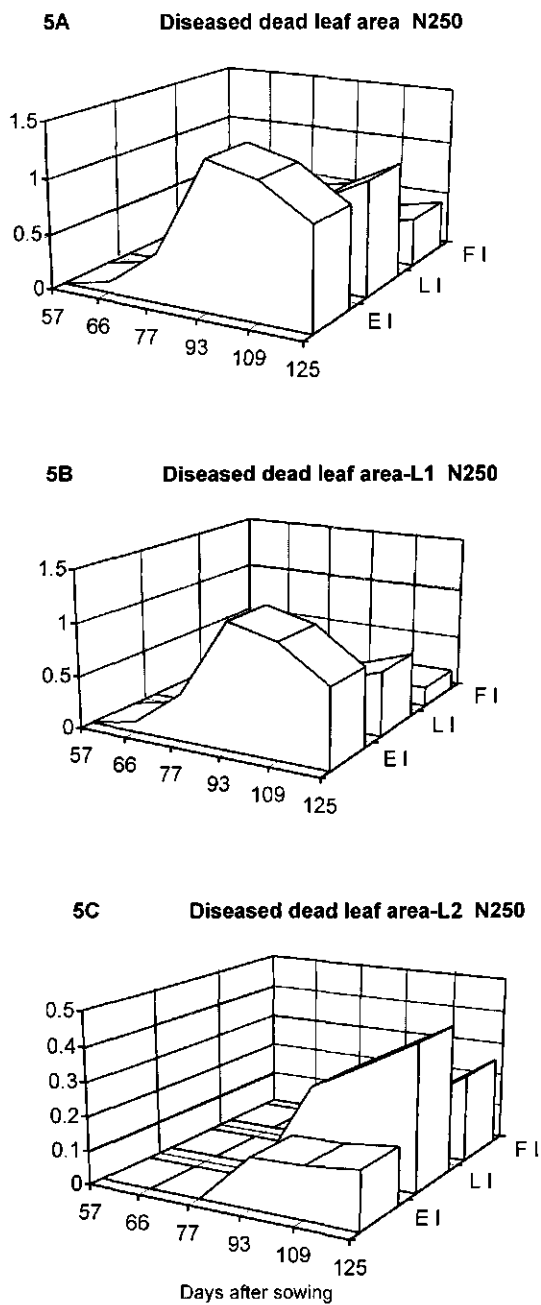


Figure 5. Diseased dead leaf area for crop canopy for healthy (H), early (EI), late (LI) and flowering (FI) inoculations under high N application (250 kg N ha^{-1}).

Table 3. Total leaf area and green and diseased dead leaf area in relation to rice development stage at three BLB onset times (250 kg N ha⁻¹).

Inoculation	Leaf area (kg ha ⁻¹) ^a	Days after sowing					
		57	66	77	93	109	125
		Development stage					
		0.57	0.67	0.79	0.96	1.45	2.01
Healthy	LAIT	0.80	2.37	3.96	4.34	2.81	1.64
	LAIGT	0.80	2.34	3.92	4.29	2.74	1.57
	LAIDSD	0.00	0.00	0.00	0.00	0.00	0.00
Early	LAIT	0.79	2.29	3.89	4.29	2.82	1.71
	LAIGT	0.78	2.15	3.06	2.85	1.54	0.67
	LAIDSD	0.00	0.10	0.44	1.32	1.21	0.92
Late	LAIT	0.90	2.38	4.07	4.43	2.70	1.55
	LAIGT	0.90	2.32	3.99	3.64	1.79	0.35
	LAIDSD	0.00	0.00	0.00	0.71	0.80	1.04
Flowering	LAIT	0.45	2.28	3.91	4.19	2.83	1.69
	LAIGT	0.45	2.28	3.66	4.13	2.34	1.19
	LAIDSD	0.00	0.00	0.00	0.00	0.34	0.44

^aLAIT = total leaf area, LAIGT = total green leaf area of whole canopy, LAIDSD = total diseased dead leaf area.

Simulation

Normal N application (125 kg N ha⁻¹) Simulated dry matter production were 9275, 8564, 8091 and 8492 kg ha⁻¹ and simulated grain yield were 5161, 4508, 3738 and 4097 kg ha⁻¹, respectively, for healthy plants and plants inoculated at early tillering, late tillering and flowering (Table 2). Simulated values of dry matter reduction due to BLB damage were 711, 1184 and 783 kg ha⁻¹ and grain yield reductions were 653, 1143 and

Table 4. Influence of N and BLB onset times on final dry weights of total dry matter, storage organ, and stem (250 kg N ha⁻¹).

Inoculation at	Dry matter (kg ha ⁻¹)		Storage organ (kg ha ⁻¹)		Stem (kg ha ⁻¹)	
	Obs	Sim	Obs	Sim	Obs	Sim
Healthy	11129	12257	6837	6490	3513	3471
Early tillering	9293	10887	5464	5129	2993	3225
Late tillering	8313	10302	5128	5333	2657	2850
Flowering	10362	11062	5801	5801	3547	3354

1064 kg ha⁻¹ respectively, for early, late and flowering inoculations (Fig.3A,B). The total dry matter and stem weights for all the treatments were slightly underestimated. Grain yield was well-simulated at the beginning of grain filling and final grain yield was slightly underestimated. The observed and simulated weights of total dry matter followed a similar trend (Fig.6A-D).

Dry matter production as a function of cumulative absorbed radiation revealed that the amounts of cumulative absorbed radiation for all treatments were almost the same but the amount of dry matter produced differed between treatments. Analysis of average crop light use efficiency (AVCLUE) for various treatments showed that late and flowering inoculation resulted in reduction in AVCLUE at least for a short period (Fig.7A).

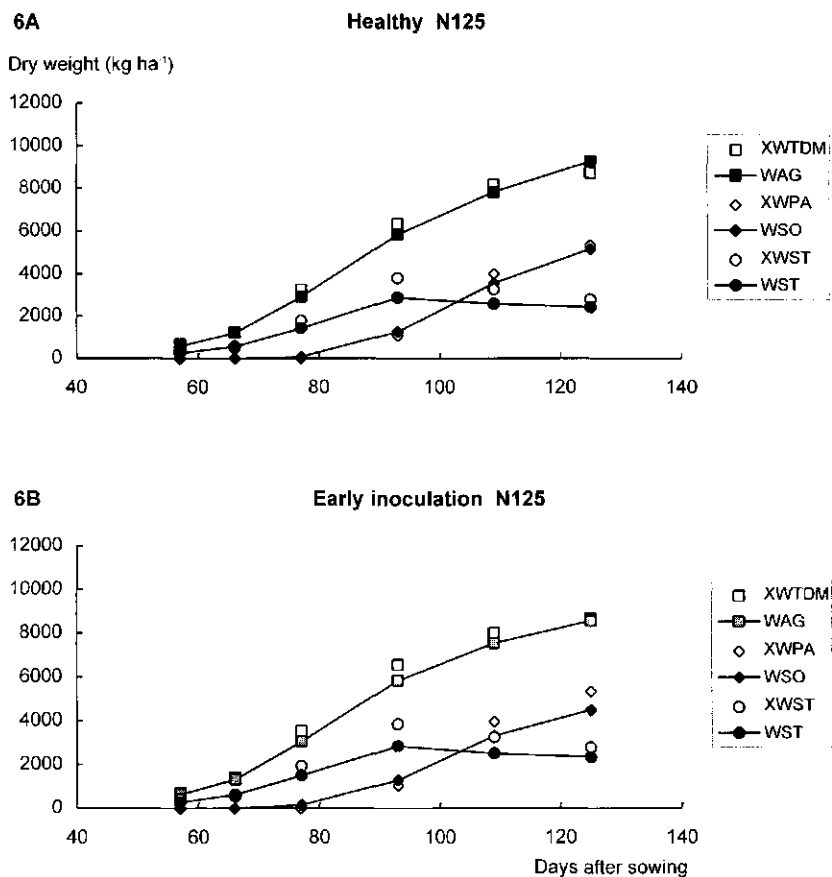
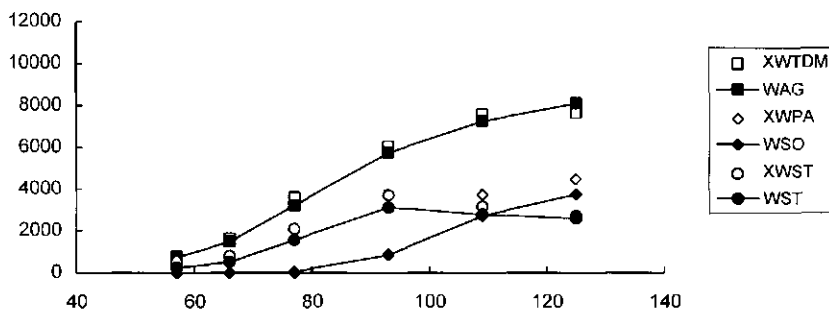


Figure 6. Simulated and observed dry weights of total dry matter, stem and storage organ under normal N application (125 kg N ha⁻¹).

6C

Late inoculation N125

Dry weight (kg ha⁻¹)

6D

Flowering inoculation N125

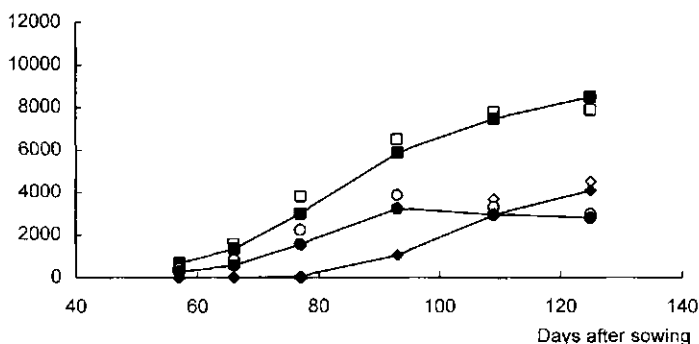


Figure 6. Simulated and observed dry weights of total dry matter, stem and storage organ under normal N application (125 kg N ha⁻¹).

High N application (250 kg N ha⁻¹) Simulated dry matter production was 12257, 10887, 10302 and 11062 kg ha⁻¹ and simulated grain yield was 6490, 5129, 5333 and 5801 kg ha⁻¹, respectively, for healthy plants and plants inoculated at early tillering late tillering, and flowering (Table 4). Simulated values of dry matter loss were 1370, 1955 and 1195 kg ha⁻¹ and those of grain yield loss were 1361, 1157 and 689 kg ha⁻¹, respectively, for early tillering, late tillering and flowering (Fig.3A-B).

The total dry matter production for all treatments was slightly overestimated while grain yield and stem weights were well-simulated compared with treatments under normal N applications (Fig.8A-D).

The AVCLUE for various treatments showed that the late and flowering inoculations resulted in reduction in AVCLUE between 77 and 93 DAS (Fig.7B).

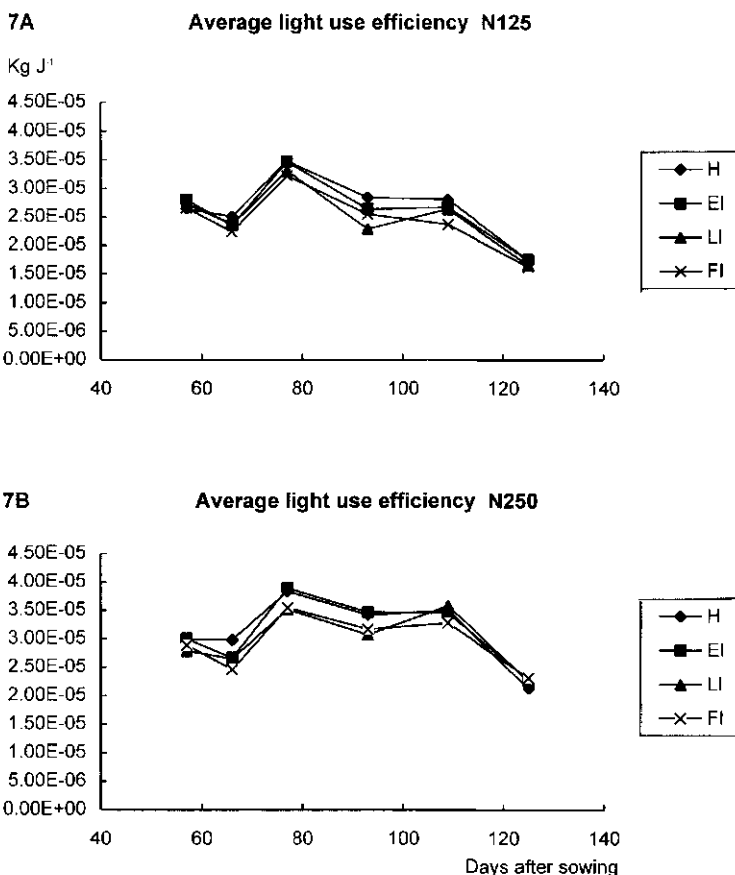


Figure 7. Average crop light use efficiency for healthy (H), early (EI), late (LI) and flowering (FI) inoculations under normal (125 kg N ha⁻¹) and high (250 kg N ha⁻¹) N applications.

Discussion

Using normal N application, despite early-inoculated plots showing an increase in diseased leaf area up to flowering, yield was similar to that of healthy plots. Furthermore, the green leaf area at the top layer of early-inoculated plants showed greater green leaf area just before and after flowering, which might have resulted in higher interception of radiation and higher photosynthetic activity. The observed dry matter loss for the early-inoculated plot was only 65 kg ha⁻¹ as against 1096 kg ha⁻¹ for late-inoculated plants. In the late-inoculated plants, the dead and diseased leaf tissue at the top of the canopy caused reduction of crop light use efficiency resulting in yield

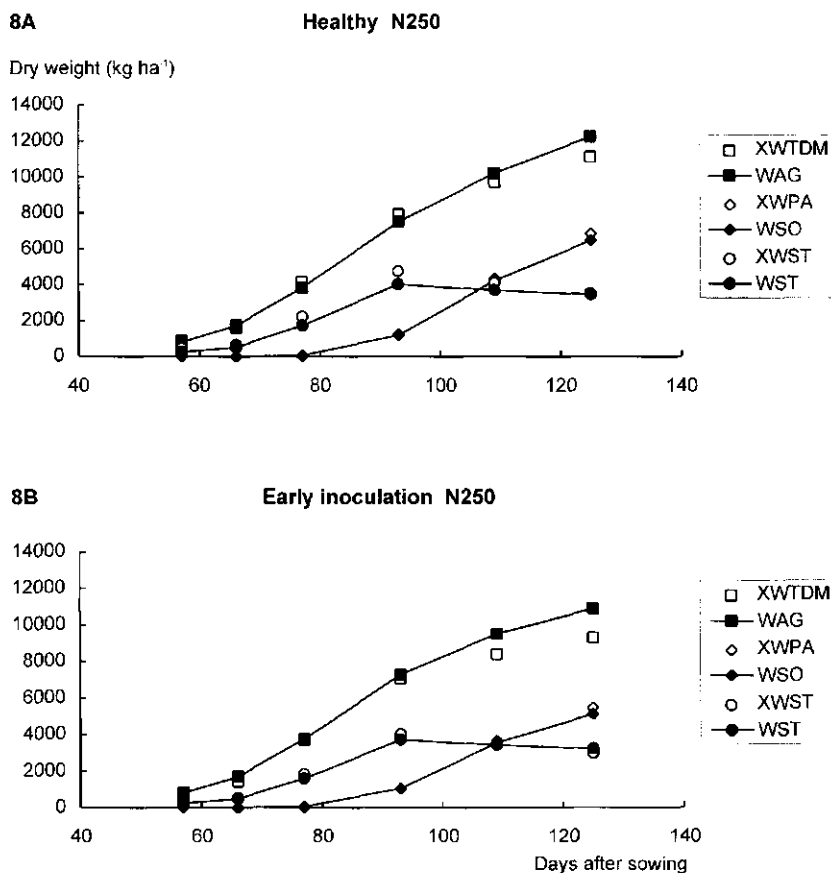


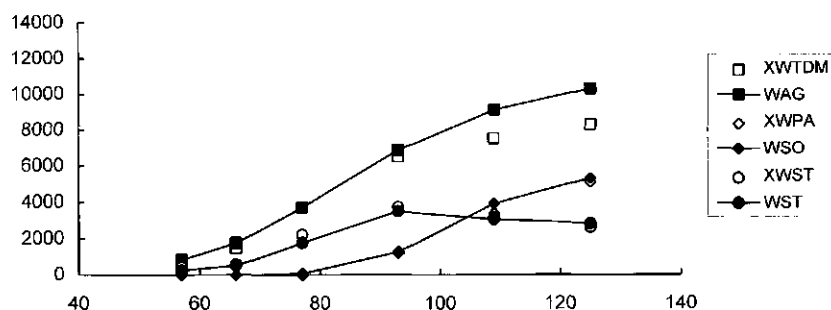
Figure 8. Simulated and observed dry weights of total dry matter, stem and storage organ under high N application (250 kg N ha⁻¹).

reduction. Similar observations were also made by Teng (1988) and Reddy (1994). Crop growth rate is linearly related to absorbed photosynthetically active radiation (PAR_a) by green foliage (Monteith, 1977) under potential production which results in a constant amount of biomass produced per unit of PAR_a (Biscoe & Gallagher, 1977) or crop light use efficiency (CLUE) (Rossing et al., 1992). Reduction in CLUE indicates that the activity per unit of photosynthetic area is altered (Waggoner & Berger, 1987); this was also indicated in the present study.

Under high N application, early inoculation had greater reduction of green leaf area for the canopy as a whole or for the bottom layer than late inoculation. However, the observed dry matter loss was higher when the onset of disease started at the late tillering

8C

Late inoculation N250

Dry weight (kg ha⁻¹)

8D

Flowering inoculation N250

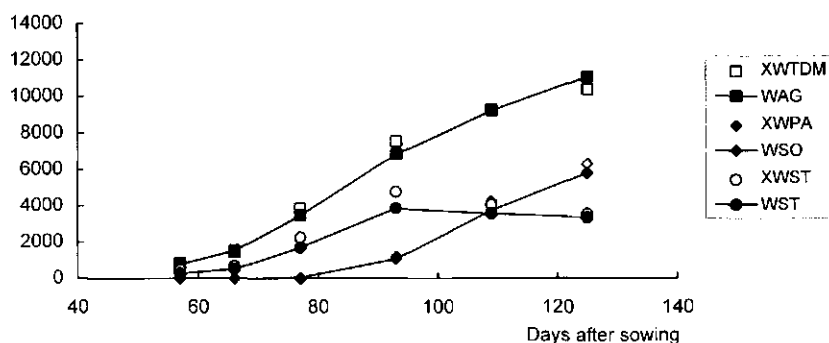


Figure 8. Simulated and observed dry weights of total dry matter, stem and storage organ under high N application (250 kg N ha⁻¹).

stage than at early tillering because plants inoculated at tillering stage compensated for it by producing extra leaves. But under simulated conditions, the loss of grain yield was slightly higher in early inoculation than in late inoculation. It might be due to the larger green leaf area available for early-inoculated plots. Since the disease was introduced at late tillering stage, the diseased dead leaf area at the top layer of the canopy was larger than that of early-inoculated plants. The possibility of crop compensation cannot be excluded since at the early onset of disease under normal N management, available green leaf area was slightly higher than in healthy plants. However, under high N management the losses in dry matter and grain yield were more during the early than during the late onset of the disease since spread of the disease is faster under high N.

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Current status and future of simulation of bacterial blight disease

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Introduction

Bacterial blight disease of rice caused by *Xanthomonas campestris* pv. *oryzae*, is one of the major foliar diseases of rice that hinder increase in rice production. Disease occurrence is very common in most rice-growing countries of the world. The disease is manifested in two forms—kresek or wilt and leaf blight phase. Blighting of the leaves is the most commonly observed symptom under field conditions. Symptoms are initiated normally in the leaf tips when the pathogen enters the leaf through wounds or hydathodes and multiplies in the epithem. After initial multiplication, it enters the xylem vessels and multiplies blocking water transport (Horino & Kaku, 1989; Mew et al., 1993). Lesion formation usually begins at the leaf tips or margins of the leaf blade as water-soaked stripes. Water-soaked area turns yellow and becomes necrotic within a few days while new water-soaked area forms (Ou, 1985). The lesion expands longitudinally downward the leaf base, depending on the bacterial multiplication in different rice varieties. Typically, a diseased leaf blade has a stretch of yellow dead leaf area followed by water-soaked area and green leaf area at the leaf base. Dead and water-soaked leaf area together form the lesion, with the lesion tips pointing toward the leaf base. On susceptible genotypes, the lesion may cover the entire leaf blade even extending to the leaf sheaths (Ou, 1985).

Research in the last several decades has been mostly to understand the basic aspects of the disease occurrence and its intensity or severity on different rice varieties grown around the world. Emphasis has been on pathogen survival and its transmission to the subsequent crop and disease epidemiology and host plant resistance. Studies on pathogenic variability or identification of pathotypes have been conducted in some countries and some are still in progress to understand the molecular nature of the variability through biotechnological techniques. Research on disease epidemiology has been mainly to relate the progress and spread of the disease in field conditions to climatic factors and cultural practices of rice cultivation (e.g., influence of N application to the crop on disease spread and temperature and rainfall relationship to the decrease or increase of the disease). However, detailed studies on the ultimate product of disease epidemiology—crop loss assessment and understanding the underlying factors responsible

for crop growth reduction—are minimal. Earlier researchers, in general, have correlated approximate yield reduction to the time of disease occurrence and severity (Srivastava, 1966; Reddy, 1974). Later, it has been reported to cause 50% yield reduction in severely infected rice crop (Mew et al., 1993; Ou, 1985). More commonly, however, plants are infected at the maximum tillering stage, thus reducing grain yield by 10-20% (Mew et al., 1993). High N application rates enhance pathogen development and lesion enlargement (Reddy et al., 1979; Mohanty, 1981) if the cultivar-pathotype combination is compatible (Mew et al., 1993).

Studies through systems analysis

With the advent of the concept of systems analysis and simulation of crop growth in 1986 under the SARP project, studies were taken up to understand damage relations to reductions in crop growth and yield. It started with the concept of leaf area damage and monitoring the damage due to the disease at different intervals throughout the crop growth period. The amount of diseased leaf area and its severity form basic inputs to the amount of yield reduction. During SARP III (the extension phase of the project, in early 1990s), relevant damage mechanisms were prioritised (Heong & Rossing, 1993). Reductions in maximum photosynthesis rate and shading by dead leaf area on the top of the canopy were hypothesised as the most important damage mechanisms; reduction in green leaf area, reduction in leaf N content in the diseased leaf tissue and accelerated leaf senescence were considered as damage mechanisms of medium priority; and disruption of translocation of carbohydrates in leaf sheaths, disruption of translocation of carbohydrates to the panicles and reduced tiller density were considered as the least important damage mechanisms (Elings et al., 1995). Reduction in maximum photosynthesis rate at the whole leaf level can be the consequence of loss of photosynthetically active green leaf area due to lesion formation or reduction of net photosynthesis rate per unit green leaf area due to bacterial presence in the remaining green leaf area. These mechanisms interact with environmental conditions and farm management practises such as incoming solar radiation and temperature (which vary within and among seasons) and N application rate which may lead to increased CO₂ assimilation at the increased level of leaf N content (van Kuelen & Selignan, 1987).

Disease management requires understanding of damage relations that relate increased disease incidence to grain yield reduction at harvest. Established relations between disease pressure and grain yield reduction are generally valid only for a limited range of environmental conditions, leading to much variation in relations among years and regions. Yield loss studies by ten Have and Kauffman (1972); Reddy et al. (1979a) and Reddy et al. (1979b) have quantified the relations between N application rate, disease

severity, season and grain yield. This has resulted in qualitative understanding of the host-pathogen-environment interactions and in disease management recommendations such as optimum N application rate. However, the validity of such recommendations is limited as they are strongly influenced by disease onset time, spreading rate, farm management practices, environmental conditions and their interaction.

The systems analytical approach enables integration of these factors and increases understanding of damage by identification and quantification of the dominant underlying mechanisms which have normally a wider validity than correlative relations. Infected leaf blade for photosynthesis measurements has been described as follows: dead leaf tissue at the leaf tip does not photosynthesise; water-soaked tissue toward the leaf base is expected not to photosynthesise or to maintain a low photosynthesis rate if photosynthetic processes have not come to a complete halt; green leaf tissue that borders the lesion and invaded by the bacteria may photosynthesise at a reduced rate and photosynthesis of green not invaded leaf tissue is expected to be unaffected. Thus, an increasing photosynthesis rate is expected from the tip to the base of the leaf blade (Elings et al., unpubl.). The concept of virtual lesion which was previously developed for rice blast (Bastiaans, 1991) was introduced for bacterial blight (BLB) lesion. It has been found that maximum rate of gross CO₂ assimilation, dark respiration and initial light use efficiency decrease with increasing disease severity. The major reason for this is the increase in the fraction of dead leaf area which does not photosynthesise.

Model development

The BLIGHT model was developed by Elings and Rubia (1994) based on the ORYZA1 model for rice (Kropff et al., 1994). It is a crop growth model with sections on crop growth and development and sections that account for plant-pathogen interaction. BLIGHT does not simulate disease development in time but requires as input a detailed definition of leaf area covered by the disease. Therefore, three types of leaf area covered are distinguished: healthy, diseased and dead leaf area. Healthy leaf area is entirely green, dead leaf area is entirely dead and diseased leaf area is partly green and partly dead as defined by the disease severity. These leaf area types are introduced into the model as fractions of healthy and diseased leaf area from which the fraction of dead leaf area is calculated. The crop is divided into three canopy layers which are separately characterised by the fractions of healthy and diseased leaf area, leaf N contents, and specific leaf weights. This allows a more precise simulation and analysis of events compared with a single canopy layer approach as diseases are mostly unevenly distributed over canopy depth.

Field evaluations

Field experiments were conducted following a design that had been agreed upon by collaborating researchers (Elings, 1993b; 1994). The rice varieties included were IR64, Annada and ADT38. Experiments were conducted in both wet and dry seasons. Periodical samplings were adapted to obtain the leaf area characteristics of both healthy and diseased leaves at different canopy leaf layers. Dry weights of leaves, stems and storage organs were determined. From these data, specific leaf weight was derived. Leaf N contents of healthy and diseased leaf fractions were determined. The experiments by Marimuthu and Rossing (1995) and Reddy (1995) were aimed at determining the consequences of increased soil N availability on the reduction of total aboveground dry matter and grain yield due to BLB. Inoculations were started at early tillering, late tillering, flag leaf appearance, booting, panicle initiation and anthesis. Disease development varied (Elings et al., 1994; Marimuthu et al., 1995; Reddy 1994; Reddy 1995). In general, it was reported that disease spread was fast in early and late tillering inoculations in different leaf layers. It was also observed that higher green leaf area characterised in the early-inoculated treatments caused reduction in overall disease severity and may have compensated for earlier growth rate reduction.

Terminating rather than starting inoculations at different moments resulted in reductions in total aboveground dry matter production and grain yield in line with the type of epidemic imposed on the crop of Annada (Reddy, 1995). This also suggests that the compensatory capacity of the crop at the end of the growth period is weaker than that at the beginning.

Model evaluation

The BLIGHT model has been successfully calibrated on the basis of field experiments reported by Elings et al. (1994), Reddy et al. (1994) and Marimuthu et al. (1995). Total aboveground dry matter production of both healthy and diseased crops are slightly overestimated. Grain yield of healthy crop is on the average correctly simulated while that of diseased crops is on the average underestimated. In general, it can be concluded that the BLIGHT model simulated growth and production of rice crop sufficiently well and covered a wide range of varieties, locations and N application rates to justify analysis of these rice systems and application of the model to disease management recommendations.

Scenario studies

An attempt was made to quantify grain yield reductions as a consequence of a variety of epidemics under diverse growing conditions using the BLIGHT simulation model. As disease development cannot be dynamically simulated by the BLIGHT model, predefined epidemics were superimposed on crop growth. Leaf area development was simulated to enable interaction with disease pressure. Thus, crop growth was simulated for two rice varieties, two years, two seasons, three disease onsets and three levels of leaf N. The relatively strong simulated effects on grain yield reductions are confirmed by field scenario studies conducted by Reddy (1994, 1995). There was interaction between variety, season and leaf N content. At low N application rates, disease onsets at early and late tillering cause similar reductions in grain yield. It was also found that early disease presence may cause enhanced leaf growth which limits yield reduction. Inoculation at later developmental stages caused the most damage. Thus, high level of leaf N causes an earlier disease onset and a faster disease spreading rate, which results in greater grain yield reductions. This offsets a higher yield potential that is also an effect of high N availability. Thus, disease management through optimisation on N application becomes all the more important. Timing of N application or resumption of N application depending on the disease progress comes as an alternative suggestion to grow a rice crop with minimum disease pressure.

Further studies

1. Response of more number of rice varieties to disease-N interaction is needed before translating the results to farmers' field conditions.
2. Research on the amount and timing of N application is needed to minimise disease pressure on the crop and to formulate disease management recommendations.
3. Field experiments and model application studies should go side by side to have a better understanding of the rice bacterial blight pathosystem.

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Quantification of the effects of bacterial blight disease on rice crop growth and grain yield

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Abstract

Computer simulation of bacterial leaf blight epidemics in rice showed that disease onset at early or late tillering stages at high levels of N caused greater reductions in grain yield and total dry matter production than disease onset at flag leaf appearance. Field experiments were conducted with cultivar Annada during the 1995 dry season to validate simulation results. In the first experiment, disease onset time was varied. The trend of reductions in grain yield and total dry matter in the field experiment was similar to that observed in the simulated results. Higher levels of N application favour larger amounts of green leaf area which becomes damaged by the disease. Increasing the damaged leaf area leads to increased losses. Early and mid-disease onsets coinciding with early and late tillering stages of the crop caused more damage than the infection at flag leaf appearance. In the second experiment, the same disease onset time was used but duration was varied to create three levels of bacterial blight disease epidemics at different N levels. The epidemics were maintained for the entire crop growth, up to late tillering and early tillering stages. The results on total dry matter production and grain yield indicated higher reductions in the plots where the disease was maintained throughout crop growth followed by inoculations up to late and early tillering stages of crop growth. This was more pronounced at higher levels of N application. Modelling therefore suggests that it would be more appropriate to grow the crop at moderate levels of N to delay disease onset, reduce severity and, in turn, increase production.

Introduction

Bacterial blight (BLB) disease of rice, caused by *Xanthomonas campestris* pv. *oryzae* is one of the major foliar diseases that limit increase in rice production. Disease severity, the crop development stage at which initial infection occurs and the rate of subsequent disease spread determine yield loss. Increased crop N content has a positive effect on infection and disease spread (Mohanty, 1981). A susceptible cultivar grown at high levels of N has more chances of early initial infection and fast spread of the disease. Conventionally, empirical damage functions were used to estimate yield losses as an effect of single or multiple pests (Pinnschmidt et al., 1995). However, physiologically

based systems analysis and simulation can be applied to understand the mechanisms of damage due to the disease and analyse its effects on crop growth and yield of rice. Actual data on crop and disease characteristics obtained through field experiments conducted during the 1993 wet season were used as default input into the BLIGHT model developed by Elings and Rubia (1994). The model has been satisfactorily calibrated (Reddy, 1994). Attempts are being made for model application through generation of disease scenarios as an effect of N x disease interaction. Therefore, the objectives of the research reported here are to understand the simulated effects of different disease epidemics and to validate the simulation results through field experiments.

Materials and methods

Simulation model

The BLIGHT model (Elings and Rubia, 1994) which was based upon the ORYZA_1 model (Kropff et al., 1993) was used to analyse the effects of bacterial blight disease on total dry matter production and grain yield. The crop characteristics of cultivar Annada used earlier for model calibration were also used for the scenario studies. Disease levels were introduced into the model in two ways. First, leaf area was divided into either healthy (H) or diseased leaf area for each of three canopy layers. For each canopy layer, fraction of diseased leaf area (FDSL) was calculated as

$$\text{FDSL} = \frac{\text{Diseased leaf area}}{\text{Diseased leaf area} + \text{Healthy leaf area}}$$

Second, diseased leaves in each canopy layer were visually assessed for percent severity using all the leaves in the canopy sample and a mean disease severity value for blight was calculated for each layer. Leaf area was simulated by the model. A value of 0.006 was used for relative growth rate of leaf area. Development rates of vegetative (DVRV) and reproductive (DVRP) phases used in the model were 0.000719 and 0.001522, respectively, for cultivar Annada calculated from its observed phenology. A value of 0.3 was used for the fraction of carbohydrates allocated to the stem as reserves.

Disease scenarios were created for three infection times—early tillering (early onset), late tillering (mid onset), and flag leaf appearance (late onset). Yield reductions were studied at various levels of leaf N content—0.06, 0.04, 0.02 and 0.01 g g⁻¹. For each level of leaf N content, different disease epidemics were assumed because of the fact that higher N application results in early infection and fast spread of the disease.

Simulation of early disease onset in dry season was initiated at the early tillering stage at a fraction of diseased leaf area in the lower canopy layer of 0.05. This fraction

increased up to 0.50. Later, the second and third leaf layers are infected, which results in 55-75% of the leaf area being infected at harvest, respectively.

Simulation of the mid-disease onset was initiated at the late tillering stage at a fraction of diseased leaf area in the second canopy layer of 0.15. The bottom layer was assumed to remain healthy. Disease spread to the top canopy layer resulting in a fraction of diseased leaf area of 0.75 at harvest.

Simulation of late disease onset was initiated at flowering in the top canopy layer. Fraction of diseased leaf area reached 0.75 with a severity of 0.65 (Table 1).

Field experiment

Two field experiments were conducted to quantify the effect of BLB on rice growth and yield. The first was designed to determine BLB onset time and subsequent epidemic on rice. The second experiment was designed to determine the effect of BLB epidemic durations with the same onset time on rice.

Table 1. Fraction of diseased leaf area and severity in different disease onsets in simulated crop growth of the cultivar Annada in 1991 dry season.

Treatment	Leaf area	Development stage								
		0.39	0.49	0.61	0.75	0.88	1.00	1.27	1.60	2.00
		Day of the year								
		60	68	76	85	94	102	110	120	132
Early onset										
Fraction of diseased leaf area	Layer 1	0	0	0.05	0.15	0.25	0.25	0.35	0.50	0.50
	Layer 2	0	0	0.15	0.25	0.25	0.35	0.40	0.50	0.55
	Layer 3	0	0	0	0.15	0.25	0.45	0.65	0.75	0.75
Severity	Layer 1	0	0	0.07	0.10	0.15	0.25	0.30	0.35	0.35
	Layer 2	0	0	0.05	0.15	0.20	0.25	0.25	0.35	0.35
	Layer 3	0	0	0	0.10	0.25	0.25	0.30	0.45	0.65
Mid onset										
Fraction of diseased leaf area	Layer 2	0	0	0.15	0.25	0.25	0.35	0.40	0.50	0.55
	Layer 3	0	0	0	0.15	0.25	0.45	0.60	0.70	0.75
Severity	Layer 2	0	0	0.05	0.15	0.20	0.25	0.25	0.35	0.35
	Layer 3	0	0	0	0.10	0.25	0.25	0.30	0.45	0.65
Late onset										
Fraction of diseased leaf area	Layer 3	0	0	0	0.15	0.25	0.45	0.65	0.75	0.75
Severity	Layer 3	0	0	0	0.10	0.25	0.25	0.30	0.45	0.65

The two field experiments were conducted during the dry season (January-May) of 1995 at Central Rice Research Institute, Cuttack, India. Cultivar Annada was sown for both experiments on 2 Jan and 29-d-old seedlings were transplanted on 31 Jan to a well-puddled field in 28 plots. Single plots measured $1.8 \times 4.2 \text{ m}^2$ and were separated by an open space of 2 m. One plant per hill was planted, hill distance was $15 \times 15 \text{ cm}$ and plant density was 444,000 plants ha^{-1} . Nitrogen fertiliser was applied in different doses as shown in Table 2. Treatments were allocated to plots in a randomised block design. Out of 28 plots, four (one plot for each N level) were not inoculated and treated as completely healthy plots. The remaining 24 plots were divided into 12 plots each for two experiments.

Experiment 1 Different epidemics of bacterial blight were created in individual plots of different levels of N application to understand the impact of the timing of disease initiation and spread over time at different crop growth stages. These epidemics were initiated at three different crop development stages (at early tillering - early onset [62 DAS], at late tillering - mid onset [78 DAS] and at flag leaf appearance - late onset [86 DAS]). The plots inoculated at early tillering stage were repeatedly inoculated (4 times) to maintain bacterial blight throughout the crop growth period. Inoculations were made thrice in the plots at late tillering stage and single inoculation in the plots of flag leaf appearance.

Experiment 2 Epidemics were induced in individual plots of different N levels by inoculating all the 12 plots at the same time—i.e., at early tillering stage of crop growth. Maintenance of the epidemics ended in a phased manner: (i) throughout crop growth, (ii) up to late tillering stage and (iii) only for early tillering stage so as to understand the extent of natural disease spread for different periods on the crop and its impact on production. The plots meant to maintain the disease for the entire growth period were inoculated repeatedly (4 times). Disease was maintained up to late tillering stage by inoculating thrice (twice inoculated for early tillering stage) after which disease progress was maintained by natural spread.

Table 2. Amount and timing of N application in the field.

Split no.	Days after transplanting	Date of application	Total amount of N application (kg N ha^{-1})			
			65	145	200	250
1	10	10 February	20	40	50	50
2	21	21 February	15	35	50	50
3	28	1 March	15	35	50	50
4	38	11 March	15	35	50	50
5	55	28 March	0	0	0	50

The disease was induced in both experiments by inoculating the rice plants through clipping method (Kauffman et al., 1973).

Crop and disease characteristics were observed periodically on five plants in three adjacent rows, starting at 20 d after transplanting (on days 50, 64, 71, 79, 87, 102, 113 and 123 for experiment 1 and on days 50, 64, 73, 80, 89, 107, 117 and 123 for experiment 2). Observed crop characteristics included leaf area and dry weights of leaves, stems and panicles. The crop canopy was separated into three leaf layers, depending on crop height. The canopy was initially considered as a single layer and was later split in two and three layers. In each layer, healthy, diseased and dead leaves were separated. Diseased leaf area is considered to be the total area of all leaves that are partially covered by lesions. Disease severity of the diseased leaves was considered visually as the ratio of the diseased leaf area to the total leaf area. Anthesis and physiological maturity were reached on 4 Apr and 2 May, respectively, and the crop was harvested on 4 May.

Results

Simulated disease scenarios

Nitrogen effect Higher levels of leaf N generally increased growth and yield of rice. Cultivar Annada grown in the dry season gave a simulated total dry matter production of 11,800 kg ha⁻¹ at a leaf N content of 0.06 g g⁻¹ and it gradually decreased to 3752 kg ha⁻¹ with a decreasing leaf N content of 0.01 g g⁻¹ (Fig. 1a).

Simulated grain yield of Annada in dry season at a leaf N content of 0.06 g g⁻¹ was 7904 kg ha⁻¹. Reduction of leaf nitrogen content caused reduction of grain yield to 2340 kg ha⁻¹ at a leaf N content of 0.01 g g⁻¹ (Fig. 1b).

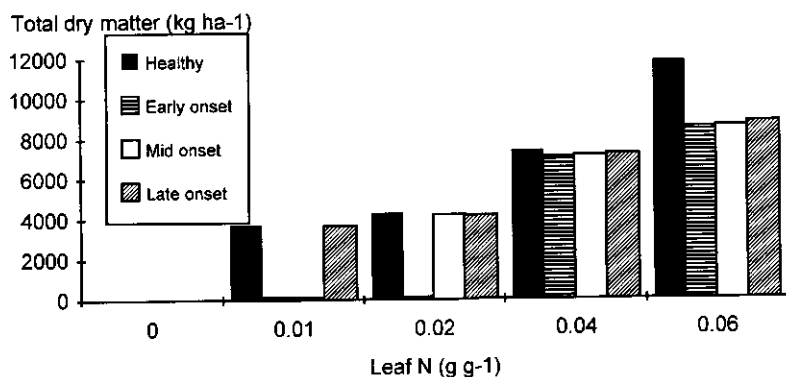


Figure 1a. Simulated total dry matter of cultivar Annada during 1993 dry season for different moments of disease onset.

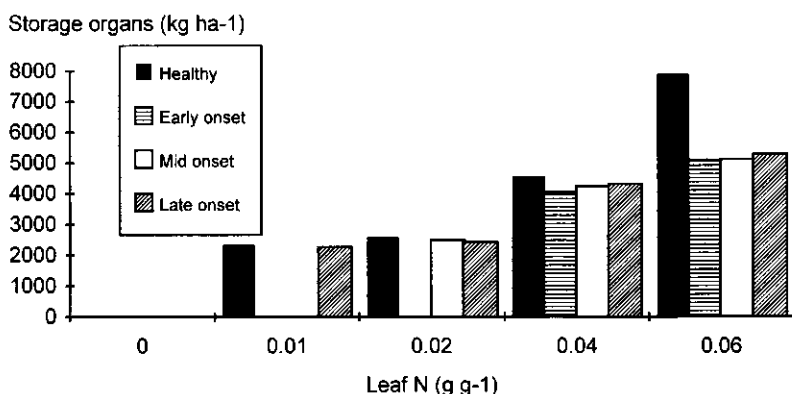


Figure 1b. Simulated weight of storage organs of cultivar Annada during 1993 dry season for different moments of disease onset.

Effect of disease buildup Introduction of the disease at three growth stages of the crop gave an overview of the effects of disease presence on total dry matter production and grain yield. Disease initiation at the early growth stages of the crop caused more damage, followed by mid and late onsets.

Simulated total dry matter production of Annada in the dry season was 11,800 kg ha⁻¹ at leaf N content of 0.06 g g⁻¹. Early, mid and late disease onsets reduced total dry matter to 8495, 8538 and 8752 kg ha⁻¹, respectively (Fig. 1a). Total dry matter production was further reduced in healthy and diseased model runs with the decreased leaf N level.

Simulated grain yield of a healthy crop of Annada in the dry season was 7904 kg ha⁻¹ at a leaf N content of 0.06 g g⁻¹ and decreased to 5057, 5091 and 5254 kg ha⁻¹ at early, mid and late disease onsets, respectively. Yield reductions relative to healthy were in the range of 2650 and 2847 kg ha⁻¹. At 0.04 g g⁻¹ N level, simulated yield of a healthy crop was 4557 kg ha⁻¹. It was reduced to 4025, 4210 and 4288 kg ha⁻¹ under different disease pressures. The yields were further reduced with disease at leaf N levels of 0.02 and 0.01 g g⁻¹. In general, yield reductions were lower at low N levels coupled with late disease onsets (Fig. 1b).

The simulation results show that higher leaf N enhances green leaf area which in turn becomes more susceptible to the disease than leaf area with a lower N content. Therefore, green leaf area gets reduced rapidly due to higher levels of disease. It is reflected in the marked reductions in grain and total dry matter production. The green leaf area also varies at different disease onsets. The later the disease initiation, the higher the green leaf area available for crop production. Generally, early and mid disease onsets caused more reduction in leaf area and consequently greater reduction in grain yield and total dry matter. With late disease onset, only a limited period of crop growth is available for disease spread and consequently, the reduction in grain yield is smaller.

Disease scenarios induced in the field at different levels of nitrogen application

Experiment 1. Early tillering epidemic - early onset At higher levels of N application (200 and 250 kg N ha⁻¹), fraction of diseased leaf area increased from 0.20 to 0.75 in the lower leaf layer and from 0.29 to 0.90 in the middle layer while it was 0.46-0.75 in the top leaf layer. Progress of the disease was fast leading to maximum severity levels of 85-90% in different leaf layers (Table 3).

Table 3. Fraction of diseased leaf area and severity of the early tillering epidemic at different growth stages of crop cultivar Annada under different levels of N application, Field experiment 1.

N application (kg N ha ⁻¹)	Disease	Leaf layer	Day of the year							
			50	64	71	79	87	102	113	123
			Development stage							
			0.54	0.70	0.77	0.86	0.95	1.3	1.66	2.0
250	Fraction of diseased leaf area	Layer 1	0	0	0.22	0.36	0.25	0.47	0.58	0.75
		Layer 2	0	0	0	0	0.29	0.69	0.57	0.85
		Layer 3	0	0	0	0	0	0.27	0.58	0.75
	Severity	Layer 1	0	0	0.35	0.75	0.85	0.85	0.90	0.90
		Layer 2	0	0	0	0	0.25	0.60	0.75	0.85
		Layer 3	0	0	0	0	0	0.50	0.65	0.85
	Fraction of diseased leaf area	Layer 1	0	0	0.20	0.36	0.25	0.39	0.55	0.75
		Layer 2	0	0	0	0	0.29	0.78	0.67	0.90
		Layer 3	0	0	0	0	0	0.46	0.60	0.75
200	Severity	Layer 1	0	0	0.35	0.75	0.85	0.85	0.87	0.85
		Layer 2	0	0	0	0	0.25	0.60	0.75	0.87
		Layer 3	0	0	0	0	0	0.67	0.87	0.90
	Fraction of diseased leaf area	Layer 1	0	0	0.20	0.46	0.25	0.38	0.50	0.75
		Layer 2	0	0	0	0	0.29	0.40	0.60	0.70
		Layer 3	0	0	0	0	0	0.40	0.62	0.75
	Severity	Layer 1	0	0	0.25	0.50	0.50	0.65	0.75	0.75
		Layer 2	0	0	0	0	0.25	0.50	0.75	0.80
		Layer 3	0	0	0	0	0	0.50	0.75	0.80
145	Fraction of diseased leaf area	Layer 1	0	0	0.26	0.41	0.32	0.25	0.48	0.65
		Layer 2	0	0	0	0	0.20	0.30	0.50	0.65
		Layer 3	0	0	0	0	0	0.42	0.51	0.45
	Severity	Layer 1	0	0	0.15	0.35	0.35	0.50	0.65	0.65
		Layer 2	0	0	0	0	0.25	0.50	0.55	0.50
		Layer 3	0	0	0	0	0	0.50	0.65	0.65
	Fraction of diseased leaf area	Layer 1	0	0	0.26	0.41	0.32	0.25	0.48	0.65
		Layer 2	0	0	0	0	0.20	0.30	0.50	0.65
		Layer 3	0	0	0	0	0	0.42	0.51	0.45
65	Severity	Layer 1	0	0	0.15	0.35	0.35	0.50	0.65	0.65
		Layer 2	0	0	0	0	0.25	0.50	0.55	0.50
		Layer 3	0	0	0	0	0	0.50	0.65	0.65

Application of 145 kg N ha⁻¹ resulted in a fraction of diseased leaf area from 0.20 to 0.75 in the bottom leaf layer. It was 0.29-0.70 and 0.60-0.75 in the middle and top leaf layer, respectively. Disease severity was between 75 and 90% in different leaf layers.

Fraction of diseased leaf area ranged from 0.26 to 0.65 in the bottom leaf layer while it was 0.20-0.75 in the middle and 0.42-0.50 in the top leaf layers at the N level of 65 kg N ha⁻¹. Disease severity in different leaf layers was between 50 and 75% at crop maturity (Table 3).

Late tillering epidemic - mid onset Disease development at the level of 200-250 kg N ha⁻¹ has shown 0.50-0.85 fraction of diseased leaf area at crop maturity in different leaf layers and 75-85% of disease severity (Table 4).

Table 4. Fraction of diseased leaf area and severity of the late tillering epidemic at different growth stages of crop cultivar Annada under different levels of N application, Field experiment 1.

N appli- cation (kg N ha ⁻¹)	Disease	Leaf layer	Day of the year							
			50	64	71	79	87	102	113	123
			0.54	0.70	0.77	Development stage				
						0.86	0.95	1.3	1.66	2.0
250	Fraction of diseased leaf area	Layer 1	0	0	0	0	0.22	0.35	0.65	0.60
		Layer 2	0	0	0	0	0.35	0.65	0.85	0.85
		Layer 3	0	0	0	0	0	0.25	0.65	0.75
	Severity	Layer 1	0	0	0	0	0.50	0.75	0.80	0.75
		Layer 2	0	0	0	0	0.35	0.65	0.75	0.85
		Layer 3	0	0	0	0	0	0.25	0.65	0.75
200	Fraction of diseased layer area	Layer 1	0	0	0	0	0.22	0.25	0.75	0.50
		Layer 2	0	0	0	0	0.35	0.70	0.75	0.75
		Layer 3	0	0	0	0	0	0.30	0.63	0.75
	Severity	Layer 1	0	0	0	0	0.50	0.75	0.80	0.77
		Layer 2	0	0	0	0	0.25	0.67	0.75	0.85
		Layer 3	0	0	0	0	0	0.30	0.68	0.75
145	Fraction of diseased layer area	Layer 1	0	0	0	0	0.10	0.25	0.50	0.65
		Layer 2	0	0	0	0	0.35	0.45	0.50	0.50
		Layer 3	0	0	0	0	0	0.30	0.48	0.65
	Severity	Layer 1	0	0	0	0	0.25	0.50	0.65	0.85
		Layer 2	0	0	0	0	0.25	0.50	0.50	0.65
		Layer 3	0	0	0	0	0	0.35	0.65	0.75
65	Fraction of diseased leaf area	Layer 1	0	0	0	0	0.20	0.30	0.65	0.65
		Layer 2	0	0	0	0	0.22	0.33	0.35	0.55
		Layer 3	0	0	0	0	0	0.50	0.50	0.55
	Severity	Layer 1	0	0	0	0	0.35	0.50	0.50	0.50
		Layer 2	0	0	0	0	0.25	0.35	0.40	0.45
		Layer 3	0	0	0	0	0	0.25	0.50	0.55

Similarly, there was a steady progress at 145 kg N ha⁻¹ with 0.50-0.65 fraction of diseased leaf area at crop maturity. Maximum disease severity was also in the range of 65-85 %.

At low level of N application (65 kg N ha⁻¹), fraction of diseased leaf area increased from 0.20-0.65 to 0.22-0.55 in lower and middle leaf layer, respectively. It was in the 0.50-0.55 range in the top leaf layer. Severity of the disease gradually increased between 40 and 55% in different leaf layers at crop maturity (Table 4).

Epidemic at flag leaf appearance - late onset The amount of diseased leaf area was more in the middle and top leaf layers at higher levels of N application than in the bottom layers. Fraction of diseased leaf area ranged between 0.43 and 0.65 in the middle and between 0.48 and 0.85 in the top leaf layer. Similarly, disease severity ranged from 65 to 75% and from 75 to 85% in the middle and top leaf layer, respectively.

Inoculation at flag leaf appearance, in general, resulted in disease only for the last 30 d of crop growth period. Maximum diseased leaf area fraction was 0.50 at maturity in the top leaf layer in the plots applied with 65 kg N ha⁻¹.

At 145 kg N ha⁻¹, disease caused more damage in the middle and top leaf layers in terms of fraction of diseased leaf area. Severity of the disease was 55-65 % in the top leaf layer (Table 5).

In general, it is seen that progress of the disease was fast at the higher levels of N application. However, at crop maturity, fraction of diseased leaf area did not differ in the lower leaf layers among all N treatments. Variation in the amount of diseased leaf area was observed in inoculations made at late tillering and flag leaf appearance at low levels of N application.

Experiment 2. Inoculations for the entire crop growth period In plots where higher levels of N (200 and 250 kg N ha⁻¹) were applied, disease progress was fast with a fraction of diseased leaf area from 0.15 to 1.0 in the lower layer and from 0.11 to 0.85 and 0.35 to 0.75 in the middle and top leaf layers, respectively. Similarly, disease severity ranged between 75 and 85% at crop maturity.

There was moderate disease progress in plots where 145 and 65 kg N ha⁻¹ were applied. Diseased leaf area fraction ranged between 0.19 and 0.65 at crop maturity in different leaf layers. Severity was, however, high in the diseased leaves (Table 6).

Inoculations up to late tillering stage Disease progress was high at higher levels of N application, with fraction of diseased leaf area ranging between 0.12 and 1.0 in lower and middle leaf layers. It ranged between 0.15 and 0.65 in the top leaf layer.

At the N level of 145 and 65 kg N ha⁻¹, fraction of diseased leaf area was high (0.17-1.0) in the lower leaf layer and less in the middle and top layers. Infected leaves had 50-75% disease severity at crop maturity (Table 7).

Inoculations only at early tillering stage At higher levels of N application, fraction of diseased leaf area was high in the lower leaf layer. The disease spread moderately to the middle and to a less extent to the top leaf layer.

Table 5. Fraction of diseased leaf area and severity of epidemic at flag leaf appearance at different growth stages of crop cultivar Annada under different levels of N, Field experiment 1.

N appli- cation (kg N ha ⁻¹)	Disease	Leaf layer	Day of the year							
			50	64	71	79	87	102	113	123
			0.54	0.70	0.77	Development stage				
						0.86	0.95	1.3	1.66	2.0
250	Fraction of diseased leaf area	Layer 1	0	0	0	0	0	0.10	0.35	0
		Layer 2	0	0	0	0	0	0.35	0.50	0.75
		Layer 3	0	0	0	0	0	0.45	0.65	0.85
	Severity	Layer 1	0	0	0	0	0	0.50	0.25	0.
		Layer 2	0	0	0	0	0	0.50	0.75	0.85
		Layer 3	0	0	0	0	0	0.65	0.75	0.85
200	Fraction of diseased leaf area	Layer 1	0	0	0	0	0	0.09	0.23	0.0
		Layer 2	0	0	0	0	0	0.43	0.55	0.65
		Layer 3	0	0	0	0	0	0.48	0.66	0.85
	Severity	Layer 1	0	0	0	0	0	0.80	0.75	0
		Layer 2	0	0	0	0	0	0.65	0.85	0.75
		Layer 3	0	0	0	0	0	0.75	0.75	0.85
145	Fraction of diseased leaf area	Layer 1	0	0	0	0	0	0.11	0.33	0.25
		Layer 2	0	0	0	0	0	0.35	0.48	0.55
		Layer 3	0	0	0	0	0	0.40	0.60	0.75
	Severity	Layer 1	0	0	0	0	0	0.55	0.55	0.45
		Layer 2	0	0	0	0	0	0.75	0.65	0.75
		Layer 3	0	0	0	0	0	0.65	0.55	0.65
65	Fraction of diseased leaf area	Layer 1	0	0	0	0	0	0.08	0.26	0.50
		Layer 2	0	0	0	0	0	0.38	0.50	0.65
		Layer 3	0	0	0	0	0	0.50	0.50	0.50
	Severity	Layer 1	0	0	0	0	0	0.50	0.50	0.45
		Layer 2	0	0	0	0	0	0.50	0.65	0.65
		Layer 3	0	0	0	0	0	0.50	0.50	0.65

On the other hand, at lower levels of N application, moderate disease spread was observed in the lower layer and it was least in the top leaf layers (Table 8).

Observed effects of disease scenarios

Experiment 1 Initiation of the disease at three growth stages of the crop (early, mid and late) showed the pattern of disease spread and its impact on total dry matter production and grain yield. Disease initiation at early growth stages of the crop caused more damage followed by mid and late disease onsets.

Table 6. Fraction of diseased leaf area and severity under inoculation treatment throughout crop growth of cultivar Annada at different N levels in the 1995 dry season, Field experiment 2.

N appli- cation (kg N ha ⁻¹)	Disease	Leaf layer	Day of the year							
			50	64	71	79	87	102	113	123
			0.54	0.70	0.79	Development stage				
						0.87	0.97	1.47	1.80	2.0
250	Fraction of diseased leaf area	Layer 1	0	0	0.20	0.35	0.50	0.75	1.00	0.
		Layer 2	0	0	0	0.25	0.45	0.80	0.85	0.75
		Layer 3	0	0	0	0	0	0.35	0.65	0.75
	Severity	Layer 1	0	0	0.22	0.65	0.75	0.85	0.95	0.
		Layer 2	0	0	0	.15	0.50	0.75	0.75	0.85
		Layer 3	0	0	0	0	0	0.50	0.75	0.85
	Fraction of diseased leaf area	Layer 1	0	0	0.15	0.30	0.21	0.80	1.00	0.
		Layer 2	0	0	0	0.11	0.27	0.62	0.79	0.85
		Layer 3	0	0	0	0	0	0.48	0.64	0.75
200	Severity	Layer 1	0	0	0.25	0.75	0.75	0.75	0.85	0.
		Layer 2	0	0	0	0.25	0.50	0.50	0.75	0.75
		Layer 3	0	0	0	0	0	0.50	0.80	0.85
	Fraction of diseased leaf area	Layer 1	0	0	0.19	0.33	0.28	0.29	0.50	0.
		Layer 2	0	0	0	0.16	0.30	0.65	0.50	0.65
		Layer 3	0	0	0	0	0	0.43	0.58	0.60
	Severity	Layer 1	0	0	0.20	0.75	0.75	0.50	0.35	0.
		Layer 2	0	0	0	0.05	0.35	0.65	0.75	0.75
		Layer 3	0	0	0	0	0	0.50	0.75	0.75
145	Fraction of diseased leaf area	Layer 1	0	0	0.17	0.28	0.19	0.29	0.25	0.
		Layer 2	0	0	0	0.08	0.51	0.85	0.29	0.35
		Layer 3	0	0	0	0	0	0.39	0.57	0.50
	Severity	Layer 1	0	0	0.35	0.65	0.50	0.50	0.65	0.
		Layer 2	0	0	0	0.05	0.25	0.65	0.50	0.30
		Layer 3	0	0	0	0	0	0.75	0.50	0.65
	Fraction of diseased leaf area	Layer 1	0	0	0.17	0.28	0.19	0.29	0.25	0.
		Layer 2	0	0	0	0.08	0.51	0.85	0.29	0.35
		Layer 3	0	0	0	0	0	0.39	0.57	0.50
65	Severity	Layer 1	0	0	0.35	0.65	0.50	0.50	0.65	0.
		Layer 2	0	0	0	0.05	0.25	0.65	0.50	0.30
		Layer 3	0	0	0	0	0	0.75	0.50	0.65

The grain yield of cultivar Annada was 6900 kg ha⁻¹ at the N level of 250 kg N ha⁻¹. It was reduced to 4500, 5300 and 6500 kg ha⁻¹ under disease pressure at early, mid and late stages of crop growth, respectively. Thus the extent of yield reductions over healthy was in the range of 2300 to 400 kg ha⁻¹ at different disease onsets. The yield was 6500 kg ha⁻¹ at the N level of 200 kg N ha⁻¹. It was 5000 kg ha⁻¹ at early, 4900 kg ha⁻¹ at mid and 5700 kg ha⁻¹ at late disease onsets. The yield reductions relative to healthy were in the

Table 7. Fraction of diseased leaf area and severity, inoculation treatment up to late tillering stage of Annada at different N levels in the 1995 dry season, Field experiment 2.

N appli- cation (kg N ha ⁻¹)	Disease	Leaf layer	Day of the year							
			50	64	73	80	89	107	117	123
			Development stage							
			0.54	0.70	0.79	0.89	0.97	1.47	1.80	2.0
250	Fraction of diseased leaf area	Layer 1	0	0	0.10	0.17	0.20	0.40	0.75	0
		Layer 2	0	0	0	0	0.25	0.36	0.65	0.75
		Layer 3	0	0	0	0	0	0.20	0.45	0.65
	Severity	Layer 1	0	0	0.25	0.25	0.50	0.75	0.85	0
		Layer 2	0	0	0	0	0.15	0.50	0.75	0.75
		Layer 3	0	0	0	0	0	0.45	0.55	0.65
200	Fraction of diseased leaf area	Layer 1	0	0	0.12	0.21	0.15	0.47	1.0	0
		Layer 2	0	0	0	0	0.15	0.55	1.0	1.0
		Layer 3	0	0	0	0	0	0.15	0.20	0.50
	Severity	Layer 1	0	0	0.20	0.75	0.75	0.75	0.85	0.85
		Layer 2	0	0	0	0	0.25	0.50	0.50	0.65
		Layer 3	0	0	0	0	0	0.50	0.50	0.75
145	Fraction of diseased leaf area	Layer 1	0	0	0.21	0.29	0.23	0.17	0.45	0
		Layer 2	0	0	0	0	0.32	0.26	0.29	0.65
		Layer 3	0	0	0	0	0	0.13	0.29	0.35
	Severity	Layer 1	0	0	0.20	0.75	0.75	0.50	0.50	0
		Layer 2	0	0	0	0	0.35	0.75	0.75	0.75
		Layer 3	0	0	0	0	0	0.25	0.50	0.55
65	Fraction of diseased leaf area	Layer 1	0	0	0.17	0.28	0.14	0.33	0	0
		Layer 2	0	0	0	0	0.20	0.26	0.40	0.45
		Layer 3	0	0	0	0	0	0.15	0.15	0.25
	Severity	Layer 1	0	0	0.25	0.75	0.75	0.55	0.50	0
		Layer 2	0	0	0	0	0.25	0.55	0.65	0.65
		Layer 3	0	0	0	0	0	0.50	0.50	0.50

range of 1500 to 800 kg ha⁻¹. At the N level of 145 kg ha⁻¹, grain yield was 5600 kg ha⁻¹. It was reduced to 4500, 4600 and 5000 kg ha⁻¹ at early, mid and late disease onsets, respectively. The reductions were in the range of 1100-600 kg ha⁻¹. The grain yield was 5200 kg ha⁻¹ at the level of 65 kg N ha⁻¹. It was 4900, 4700 and 4600 kg ha⁻¹ at different disease onsets and reductions were in the range of 370-657 kg ha⁻¹ (Fig. 2a and Table 9).

Table 8. Fraction of diseased leaf area and severity under inoculation treatment up to early tillering stage of cultivar Annada at different N levels in the 1995 dry season, Field experiment 2.

N appli- cation (kg N ha ⁻¹)	Disease	Leaf layer	Day of the year							
			50	64	73	80	89	107	117	123
			Development stage							
			0.54	0.70	0.79	0.87	0.97	1.47	1.80	2.0
250	Fraction of diseased leaf area	Layer 1	10	0	0.20	0.25	0.20	0.35	0.50	0
		Layer 2	0	0	0	0	0.15	0.40	0.55	0.65
		Layer 3	0	0	0	0	0	0.15	0.35	0.30
	Severity	Layer 1	0	0	0.15	0.35	0.50	0.45	0.50	0
		Layer 2	0	0	0	0	0.45	0.50	0.50	0.65
		Layer 3	0	0	0	0	0	0.25	0.55	0.50
200	Fraction of diseased leaf area	Layer 1	0	0	0.16	0.21	0.17	0.41	0.31	0
		Layer 2	0	0	0	0	0.11	0.52	0.53	0.45
		Layer 3	0	0	0	0	0	0.08	0.30	0.25
	Severity	Layer 1	0	0	0.25	0.65	0.75	0.55	0.75	0
		Layer 2	0	0	0	0	0.50	0.50	0.50	0.50
		Layer 3	0	0	0	0	0	0.25	0.65	0.50
145	Fraction of diseased leaf area	Layer 1	0	0	0.12	0.23	0.21	0.45	0.35	0
		Layer 2	0	0	0	0	0.08	0.29	0.25	0.35
		Layer 3	0	0	0	0	0	0.10	0.30	0.30
	Severity	Layer 1	0	0	0.20	0.65	0.75	0.75	0.50	0
		Layer 2	0	0	0	0	0.55	0.50	0.50	0.45
		Layer 3	0	0	0	0	0	0.50	0.75	0.55
65	Fraction of diseased leaf area	Layer 1	0	0	0.16	0.41	0.08	0.32	0	0
		Layer 2	0	0	0	0	0.09	0.40	0.20	0
		Layer 3	0	0	0	0	0	0.13	0	0
	Severity	Layer 1	0	0	0.15	0.75	0.65	0.75	0	0
		Layer 2	0	0	0	0	0.05	0.50	0.50	0
		Layer 3	0	0	0	0	0	0.25	0	0

Maximum amount of total dry matter production for cultivar Annada was 11,900 kg ha⁻¹ in dry season when the crop was given 250 kg N ha⁻¹ in the field. It was reduced to 9800, 9700 and 10700 kg ha⁻¹ at early, mid and late disease onsets. At 200 kg N ha⁻¹, total dry matter production was 11,300 kg ha⁻¹ and it was 9500, 8900 and 9700 kg ha⁻¹ at different disease onsets. Total dry matter production was 9700 and 9300 kg ha⁻¹ at the N levels of 145 and 65 kg N ha⁻¹, respectively. As a result of early, mid and late disease onsets, it was 8600, 8500 and 9000 kg ha⁻¹, respectively, at 145 kg N ha⁻¹ and 9000, 8200 and 8200 kg ha⁻¹, respectively, at 65 kg N ha⁻¹ (Fig. 2b).

Early, mid and late disease onsets of simulated disease scenarios were compared with epidemics induced at the stages of early tillering, late tillering and flag leaf appearance in the field experiments. Observed and simulation results indicated higher reductions in grain yield and total dry matter production, as a consequence of early and

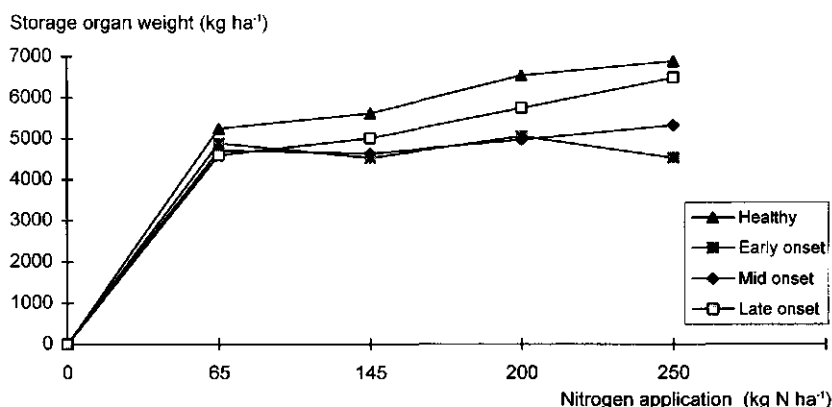


Figure 2a. Observed weights of storage organs of cultivar Annada during 1995 dry season for healthy crop and different diseases onsets, Field experiment 1.

mid disease scenarios. In general, reductions were lower at low levels of N application due to less disease. Similarly, the effect was less marked for the late disease onset at flag leaf appearance, as it is for a short duration of crop growth.

Experiment 2. The grain yield obtained from the healthy Annada crop was 6890 kg ha⁻¹ at N level of 250 kg N ha⁻¹. The yield was reduced to 4367 kg ha⁻¹ under the disease pressure throughout the crop growth period. It was 5244 and 5728 kg ha⁻¹ when the inoculations were up to late tillering and early tillering stages, respectively. The extent of yield reductions over that of the healthy crop were 2353, 1646 and 1162 kg ha⁻¹ under

Table 9. Observed reductions in total dry matter (WAG) and grain yield (WSO) over healthy crop due to disease epidemics at different levels of N application of cultivar Annada (kg ha⁻¹) in 1995 dry season.

Disease onset	N application (kg N ha ⁻¹)							
	250		200		145		65	
	WSO	WAG	WSO	WAG	WSO	WAG	WSO	WAG
<i>Experiment 1</i>								
Early tillering	2358	2050	1477	1872	1096	1083	368	280
Late tillering	1558	2139	1565	2405	988	1212	546	1012
Flag leaf appearance	402	1161	790	1628	607	683	657	1030
<i>Experiment 2</i>								
Entire crop growth	2535	3681	1032	2169	830	1334	1613	1950
Up to late tillering	1646	1957	1388	1506	385	856	813	599
Up to early tillering	1162	1177	943	970	385	856	813	1206

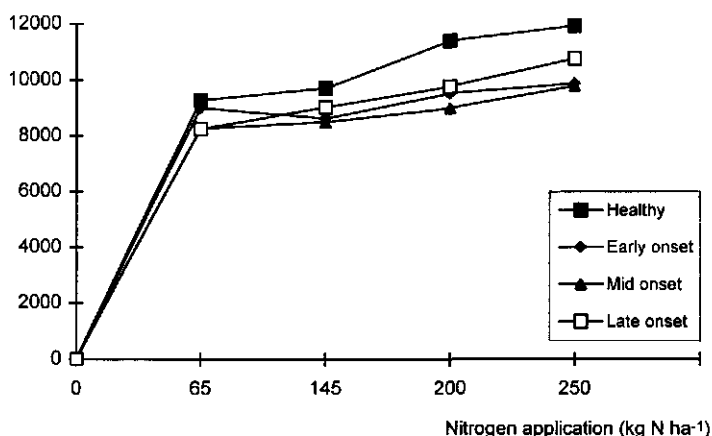


Figure 2b. Observed weights of total dry matter of cultivar Annada during 1995 dry season for healthy crop and different diseases onsets, Field experiment 1.

the three epidemic levels. At 200 kg N ha⁻¹, the healthy crop yielded 6543 kg ha⁻¹. It was reduced to 5511, 5156 and 5728 kg ha⁻¹ when disease was induced for the entire crop growth and up to late tillering and early tillering. The reductions were in the range of 1032-943 kg ha⁻¹. The grain yield obtained from the healthy crop at the N level of 145 kg ha⁻¹ was 5630 kg ha⁻¹. When the disease was induced for the entire crop growth and up to late tillering and early tillering stages, the yields were reduced to 4800, 5244 and 5244 kg ha⁻¹. The reductions were in the range of 829 to 385 kg ha⁻¹. At 65 kg N ha⁻¹, the grain yield was 5257 kg ha⁻¹. Under the three different disease epidemics, the yields were reduced to 3644, 4444 and 4444 kg ha⁻¹ and the reductions were in the range of 1613-812 kg ha⁻¹ (Fig. 3a and Table 9).

Total dry matter production at 250 kg ha⁻¹ was 11917 kg ha⁻¹. It was reduced to 8236, 9960 and 10739 kg ha⁻¹ when disease was induced for the entire growth, and up to late tillering and early tillering stages, respectively. At 200 kg N ha⁻¹, total dry matter production of a healthy crop was 11380 kg ha⁻¹. It was 9214, 9876 and 10413 kg ha⁻¹ at different disease epidemics. Total dry matter production was 9700 kg ha⁻¹ at N level of 145 kg N ha⁻¹. As a result of disease pressure for varying periods, it was reduced to 8300, 8800 and 8800 kg ha⁻¹. For the healthy crop grown at 65 kg N ha⁻¹, total dry matter production was 9200 kg ha⁻¹. It was reduced to 7300, 8600 and 8000 kg ha⁻¹ under disease pressure applied at different growth stages of crop (Fig. 3b).

In general, higher reductions in grain yield and total dry matter production were observed at increased levels of N application, when disease pressure was maintained for the entire crop growth period. When the disease was allowed to spread naturally as a consequence of few artificial inoculations up to late tillering and early tillering stages, the effect on grain yield and total dry matter production was less marked.

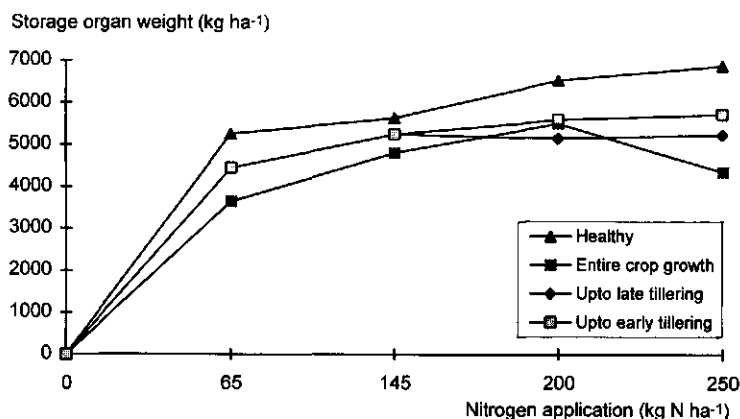


Figure 3a. Observed weights of storage organs of cultivar Annada during 1995 dry season for healthy crop and different diseases epidemics, Field experiment 2.

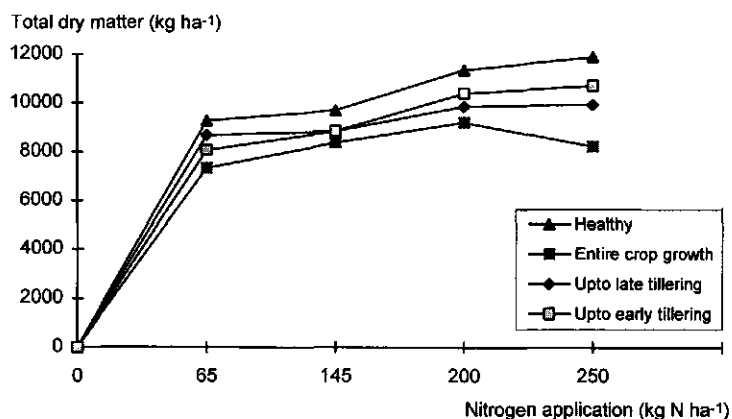


Figure 3b. Observed weights of total dry matter of cultivar Annada during 1995 dry season for healthy crop and different diseases epidemics, Field experiment 2.

Discussion

The effects of pests and diseases, in general, are more significant at the higher yield levels. A healthy crop, essential for high yields, is also a dense crop and provides favourable micro-meteorological conditions which may promote epidemiological development of many diseases and affect the yield loss-pest density relationship (Rabbinge & Bastiaans, 1989). Similarly, severity and incidence of bacterial leaf blight

disease varies depending upon cultivar susceptibility and nutritional status of the crop. Keeping this in view, different disease scenarios were created both at the field level and through simulation for cultivar Annada to understand the effect of the disease on rice growth and yield.

Simulation results showed highest yield losses at high N levels with early disease onset. With a decrease in N level, disease onset presumably gets delayed and severity may also get reduced. Therefore, yield losses may be lower at low N levels. Maximum yield loss through simulation was between 2400 and 4000 kg ha⁻¹. With decreasing leaf N content, total dry matter production generally was reduced and so was the effect of the disease.

The field experiments were designed to maintain the disease epidemics on the crop for different durations. The disease was initiated artificially at different development stages of crop growth in the first experiment. In the second experiment, it was initiated at the same time (early tillering stage) and maintenance of the epidemic ended in a phased manner, giving scope for natural spread of the disease. Occurrence of such varying levels of incidence and severity of the disease is common under farmers' field conditions. Thus, the information generated on the estimation of the effects of different levels of disease pressures for different durations on the crop may become a useful guide for rice cultivation. Earlier researchers (Gregory et al., 1978) have used successive inoculations to simulate disease increase over time. Similarly, long- and short-duration epidemics were also created by manipulating dates of inoculations to estimate yield loss due to stem rust of wheat (Romig & Calpouzos, 1970) and *Septoria glycine* on soybean cultivars (Young & Ross, 1978).

Observed effects of the disease in the first experiment indicate that reductions in grain yield and total dry matter were higher in early and late tillering inoculations at higher levels of N application. Though the disease was for a longer duration on the crop inoculated at early tillering stage, the differences in reduction between early and late tillering inoculations were negligible. It might be due to leaf area compensation for the infection when the crop was at early tillering stage (Teng, 1988; Reddy et al., 1994). The reductions were less marked in plots inoculated at flag leaf appearance since the disease on the crop was for a short duration. The crop grown at lower N levels suffered less in terms of grain yield and total dry matter production due to slow disease progress.

The results of the second experiment showed that losses were lower in the plots when the crop was left to natural disease spread after initial inoculations. It indicates that losses are higher when the disease progresses continuously on the crop especially grown at higher levels of N application. Higher levels of N favour increased leaf area formation, providing more substrate for the disease. Increased leaf area damage leads to increased losses. Grain yield and total dry matter production is generally lower at low N application. This slows down the disease progress and losses due to the disease also decrease. Thus, it would be more appropriate to grow the crop at moderate N levels.

This would help in delaying the disease onset with reduced severity and this would in turn increase production.

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