QUANTITATIVE UNDERSTANDING OF THE IRRIGATED RICE ECOSYSTEM AND YIELD POTENTIAL

M.J. Kropff, K.G. Cassman, and H.H. van Laar

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A systems simulation approach is used to evaluate the physiological basis and crop management requirements for achieving rice yields higher than present yield frontiers in tropical environments. A general crop simulation model is parameterized for rice and used to evaluate yield differences between varieties grown with different N management and in different environments to understand the physiological basis of the system. The model explains accurately variations in productivity on the basis of differences in radiation, temperature, leaf N content, and leaf area index (LAI) throughout the growing season. The model predicts that higher N inputs could raise dry season yields from the current 7 t/ha to more than 9 t/ha. The simulations suggest that the yield potential of current short-duration varieties is similar to the yield potential of the first semidwarf variety, IR8. For yields above 10 t/ha, a simplified yield formation model predicts that leaf senescence must be delayed, the grain-filling period must be longer, and there must be more grains per m^2. Theoretically, 15 t/ha could be obtained in a tropical environment with a growth duration of 134 d, a grain-filling period of about 40 d, high LAI, and high leaf N concentration. The simulation model confirms these figures. F_1 hybrids show advantages in several physiological traits that are required for raising yield potential. Optimum crop management is crucial for realizing higher yield potentials. A rice crop would need at least 300 kg of N in aboveground biomass for a 15 t/ha yield with normal N concentration in the grains. Much of this N has to be taken up late in the growing season to meet the N requirements of a larger sink and a longer grain-filling period and to support the extended active leaf area duration due to delayed senescence.

One of IRRI's major objectives is to develop varieties with a yield potential of 15 t/ha in a tropical environment. This requires major genetic changes in the rice plant and improved management. Current breeding programs aim to improve the plant characteristics that are thought necessary for improved yield potential. Ecophysiological models have been used to design these plant types (Dingkuhn et al 1991, Penning de Vries 1991).

Rice breeding programs that focus on raising yield potential above 10 t/ha have problems when experiments cannot be conducted under optimum conditions. A simulation model for rice growth was developed to understand these conditions. Its performance was assessed using data from different environments and N management treatments. The model was used to determine the management requirements that would allow current varieties to express their full yield potential.

An ecophysiological model was used to determine more detailed physiological traits and crop management requirements that could lead to a major increase in yield potential, based on indications of the genetic variability of these traits. The possible role of hybrid rice in achieving increased yield potential is discussed.

Increasing the yield potential of rice: a simple concept

Yield potential can be defined as the yield of a crop when growth is not limited by shortages of water and nutrients, pests, diseases, or weeds. The determinants of potential growth and production are light, temperature, and varietal characteristics. Thus, yield potential must be defined for a specific environment.

Recent efforts have focused on obtaining a yield potential of 15 t/ha by improving the rice plant type (IRRI 1989). Several plant traits that improve yield potential have been identified. Penning de Vries (1991) analyzed the possibility of genetic improvement for a wide range of processes and concluded that there was some scope for increased assimilate production and that the grain-filling duration had to be lengthened. He emphasized that N uptake after flowering was important to maintain growth for a longer period. Dingkuhn et al (1991) emphasized a modified partitioning of assimilates between leaves and stems. However, the plant they modeled would not produce leaves after panicle initiation (PI), which would require major genetic changes and result in leaf area duration problems. This section discusses a simple framework of yield potential in rice, largely based on the work of Yoshida (1981), and insights obtained from systems approaches in agriculture.

The driving forces in crop yield formation are well-known. In the first place, both a source of carbohydrates are needed for yield formation. The source is formed by chlorophyll-containing tissue, mainly in the leaves. Stems, leaf sheaths, and the panicle contribute a small amount to canopy photosynthesis. The amount of dry matter stored in the grains comes from allocated stem reserves produced in the vegetative phase and from assimilates produced in the grain-filling period. Grain production is therefore determined by three components — the amount of stem reserves allocated to the grains, the rate of dry matter production in the grain-filling period, and the length of the grain-filling period (or growth rate duration).

Climate and N supply environment largely determine these components. Temperature affects the length of the vegetative period, thereby influencing the amount of stem reserves that can be translocated to the panicles, and the length of the grain-filling period. Radiation determines the growth rate of the crop. The growth rate at a given radiation level depends on the leaf area index (LAI) of the crop and the leaf N

concentration. Based on this analysis, a very simple model for grain yield can be defined.

$$Y = S + G \times D$$

where Y is grain yield, S is the net amount of stem reserves allocated, G is the average growth rate per day during the grain-filling period, and D is the length of the grain-filling period. Yoshida (1981) concluded that the contribution of stem reserves could account for about 2-2.5 t grains/ha. The rest must come from growth during the grain-filling period. For 10 t/ha, achieved in the 1960s with IR8 at IRRI, the grain-filling duration was 30 d, of which 25 d comprised 'effective' or linear-phase grain filling. These numbers give an estimated growth rate of $(10000 - 2000) \times 0.86$ (14% moisture) $/10 = 230$ kg/ha per d, or 275 kg/ha per d during the linear grain-filling period. This is a reasonable estimate; rice in tropical environments with a high LAI and a high leaf N content can produce 300-350 kg dry matter/ha per d.

This simple model for yield formation indicates that yields above 10 t/ha should come from increased allocation of stem reserves, a longer grain-filling period, or from an increased growth rate during grain filling. Increasing stem reserves beyond 2.5 t dry matter/ha is not realistic if we want to keep the vegetative period as short as possible, and because a sturdy stem and a high LAI are needed. For a grain yield of 15 t/ha, about 13 t dry matter/ha is needed. Assuming an average growth rate of 275 kg/ha per d during effective grain filling and an allocation of 2.5 t/ha dry matter grain from stem reserves, 38 d of effective grain filling and 43 d of total grain filling would be needed to produce the remaining 10.5 t/ha. Basically, this indicates that a variety that performs in tropical environments the same way current varieties perform at higher latitudes (where temperatures are lower) must be developed.

To achieve such yields, a proper sink is required. With a 1000-grain weight of 28 g, about 360 panicles/m², and 100 grains/panicle, a yield of 10 t/ha was obtained with IR8 in the 1960s (Yoshida 1981). A 15 t/ha yield requires about 150 grains/panicle with the same number of panicles/m², or 60,000 spikelets/m² with a normal number of unfilled spikelets.

Yield potential of current varieties

The yield potentials of rice varieties released in the past few decades have not been compared directly due to disease problems and declining yields at several experimental stations. The decline in yield on the IRRI experimental farm was first reported by Evans and De Datta (1979). Recent analysis of long-term experiments clearly shows a continuous decline in yield of fertilized and nonfertilized crops. Yields at IRRI in the 1960s reached 10 t/ha with 120 kg of N from fertilizer. Nowadays, top yields are 5-7 t/ha in the dry season (DS). In the minus-N plots (control), DS yield has declined from 6 to 3-4 t/ha.

It is hypothesized that this yield decline is partly due to a change in the N supply environment, which reduces growth rates in the vegetative and grain-filling periods, through early leaf senescence and low photosynthesis rates. The rate of leaf photosynthesis at light saturation is linearly related to leaf N concentration (Van Keulen and

Seligman 1987), so the lower leaf N concentration could explain the reduction in growth rate. However, ecophysiological models and detailed data are needed to analyze the effect of different leaf N concentrations on yield.

To analyze the yield potential of varieties released by IRRI in the past 28 yr, a field experiment was conducted in the 1991 wet season (WS) with different N regimes, including a late N treatment. All the relevant growth parameters were carefully measured to allow data analysis with a simulation model.

The monoculture version of the model for crop-weed interactions, INTERCOM, was used (Kropff and Spitters 1992, Kropff and van Laar 1993). INTERCOM is based on the model SUCROS (Spitters et al 1989). (The MACROS module for potential rice production [Penning de Vries et al 1989] was not used because it greatly overestimated LAI and was calibrated to current yield levels by photosynthesis parameters.) Experimental data were first analyzed with LAI as input, since the carbon balance of the model is well-developed and validated (Kropff 1990, Spitters et al 1989, Kropff and Goudriaan 1989), so inaccuracy in the simulation of leaf area development could not confound conclusions made in the first analysis.

The ecophysiological model

The general structure of the model is presented in Figure 1. Under favorable growth conditions, crop growth rate is determined mainly by light and temperature. From the LAI of the species and the vertical distribution of leaf area, the light profile within the canopy is calculated. On the basis of single leaf photosynthesis, which depends on N concentration, the photosynthesis profile for the full canopy is obtained from the light and N profiles in the canopy. Integration over the height of the canopy and over the day gives the daily assimilation rate. After subtracting respiration requirements and accounting for losses due to conversion of carbohydrates into structural dry matter, the
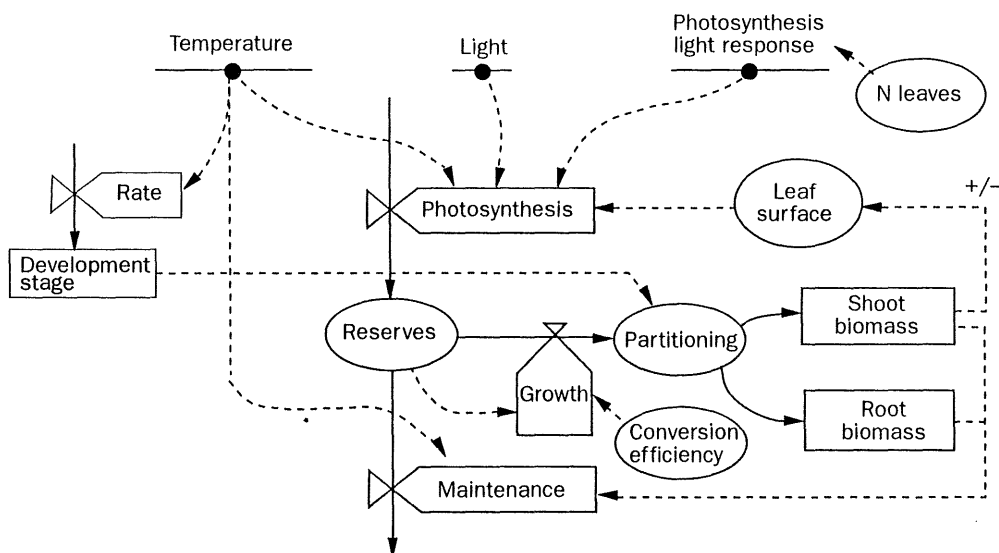
1. A schematic representation of the model. Boxes are state variables, valves are rate variables, circles are intermediate variables. Solid lines are flows of material, dotted lines are flows of information.

net daily growth rate in kg/ha per d is obtained. The dry matter produced is partitioned among the various plant organs. The development rate is tracked in the model as a function of ambient mean daily air temperature.

Before the canopy closes, leaf area development is calculated from mean daily temperature. The LAI can be simulated or experimental values can be used in the model. When the canopy closes, the increase in leaf area is obtained from the increase in leaf weight. Calculation of the net daily growth rates combines the increase in dry weight of leaves, stems, and grains, based on a partitioning coefficient that depends on the stage of development.

The model requires the following information: geographical latitude, standard daily weather data, plant density, date of crop emergence or transplanting, and parameter values that describe the morphological and physiological characteristics of the plant species. The time step of integration is 1 d.

The maximum rate of CO_2 assimilation at high radiation levels (the asymptote, A_m) depends on leaf N concentration (Fig. 2). The relationship between A_m and leaf N concentration is linear and shows little variation across environments and species (Van Keulen and Seligman 1987, Cook and Evans 1983, Fig. 3). The relationship given in Figure 3 was used in the model. It is important to note that N concentration is expressed on a per leaf area basis and not as a percentage of dry weight. This is because the maximum rate of CO_2 assimilation is expressed on a per area basis and depends on the amount of chlorophyll per unit of leaf area instead of weight. The total daily rate of CO_2 assimilation of the species is obtained by integrating the instantaneous rates of CO_2 assimilation over the LAI and over the day.

The effect of the profile of N concentration in the leaf canopy was taken into account.
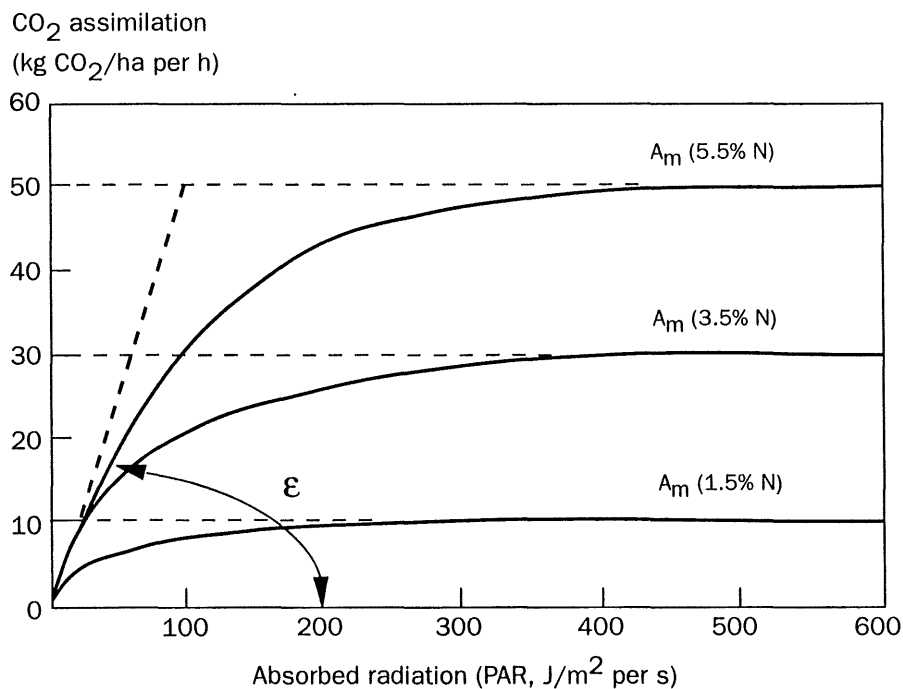
2. The CO_2 assimilation-light response curve of single leaves calculated for three N concentrations.

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Rate of net CO_2 assimilation (mg/m^2 per s)
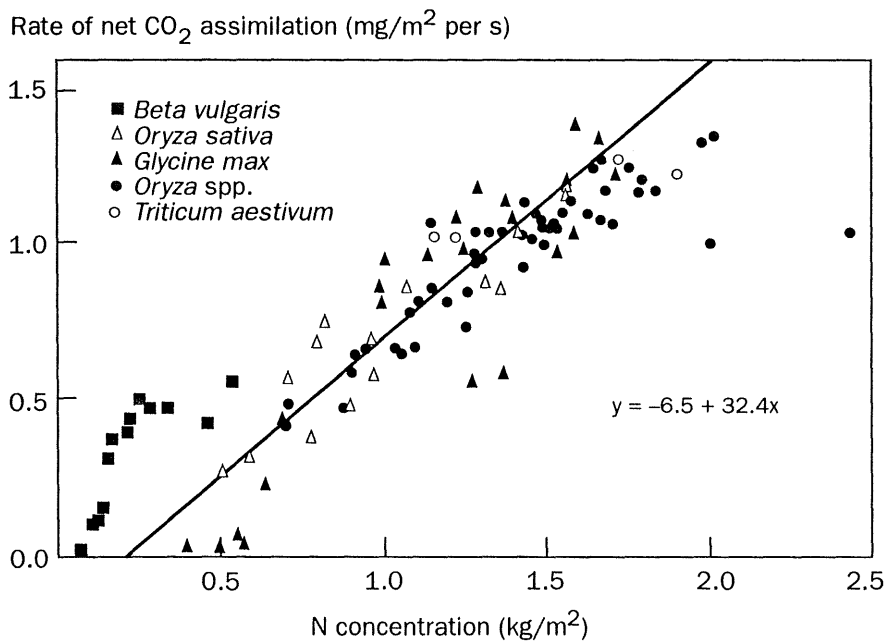
3. The relation between the maximum rate of CO_2 assimilation of single leaves and the leaf N concentration on a per area basis (kg/m^2) (Redrawn after van Keulen and Seligman 1987)
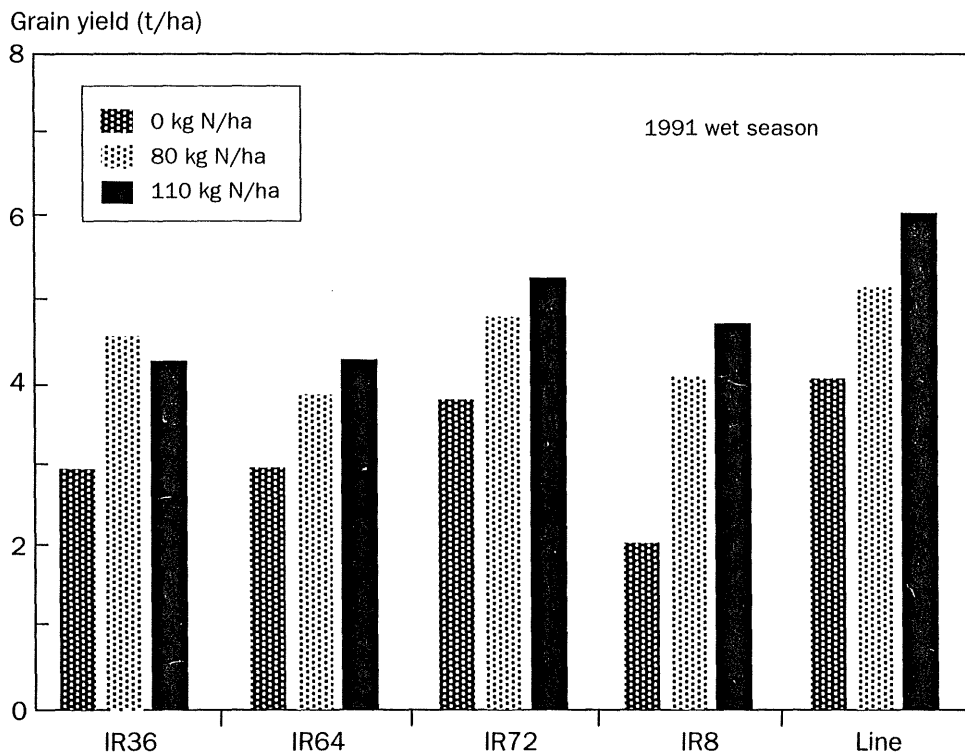
Grain yield (t/ha)

4. Grain yields of five rice varieties at three N application levels in the 1991 wet season (WS) at IRRI, Los Baños, Philippines.

Experimental design

Four improved, semidwarf indica rice varieties released since 1964—IR8, IR36, IR64, and IR72—and IR58109-113-3-3-2 (a new line) were grown on the IRRI experimental farm during 1991 WS. All varieties were transplanted on 13 Jul. Three N management treatments were applied: 0 N, the standard recommendation (80 kg N/ha in two splits before PI), and an alternative N management treatment with 110 kg N (80 kg N in two splits before PI and 30 kg N at flowering). Treatments were laid out in four replicates in a split-plot design, with N treatments as the main plots and varieties as subplots. Samples were taken from 14 hills at intervals, and LAI and organ dry weights were measured.

Experimental results

For all varieties, applying N increased yield (Fig. 4). The extra, late-season N application (30 kg N) raised yields in most varieties, with a maximum increase of 0.9 t/ha. The data for IR8 and IR36 are confounded because disease infections occurred in some treatments. At 110 kg of N, senescence was delayed by several days in the new line, and N concentration was higher during the grain-filling period (Fig. 5). In the 80 kg N treatment, total plant N decreased after flowering, indicating that soil N supply was deficient during grain filling.

Several important effects of late N application are evident in the three-quadrant analysis of the N response (Fig. 6). The recovery, or the slope, of the relation between N uptake and N supply increased greatly with late N, indicating that the additional 30 kg of N at flowering was taken up at a very high efficiency. This contrasts with conclusions from previous experimental and simulation studies which showed that no N could be taken up after flowering and that no benefit was to be expected at these yield levels (Penning de Vries et al 1990).

For all varieties, yield increased with higher N uptake, but the response curves indicate that the maximum yield level was not attained. Furthermore, the response curves suggest that the use of N for dry matter production is much more efficient in the new line, indicating a higher yield potential. The yield obtained with the new line was comparable with the best WS yields of IR8 in the 1960s. IR72 yielded somewhat below the new line, probably because of its small flag leaf and lower LAI. The distribution of LAI and N concentration in the leaf over height of the canopy shows that late N application mainly increased the N concentration in the flag leaf (Fig. 7).

Interpretation of experimental results using the ecophysiological model

The simulation model was used to analyze the data from the 1991 WS experiment. Leaf area index and measured leaf N concentration were put into the model. The simulation results were compared with the observed data (Fig. 8). Total biomass and panicle dry matter were simulated accurately by the model. The simulation predicted accurately
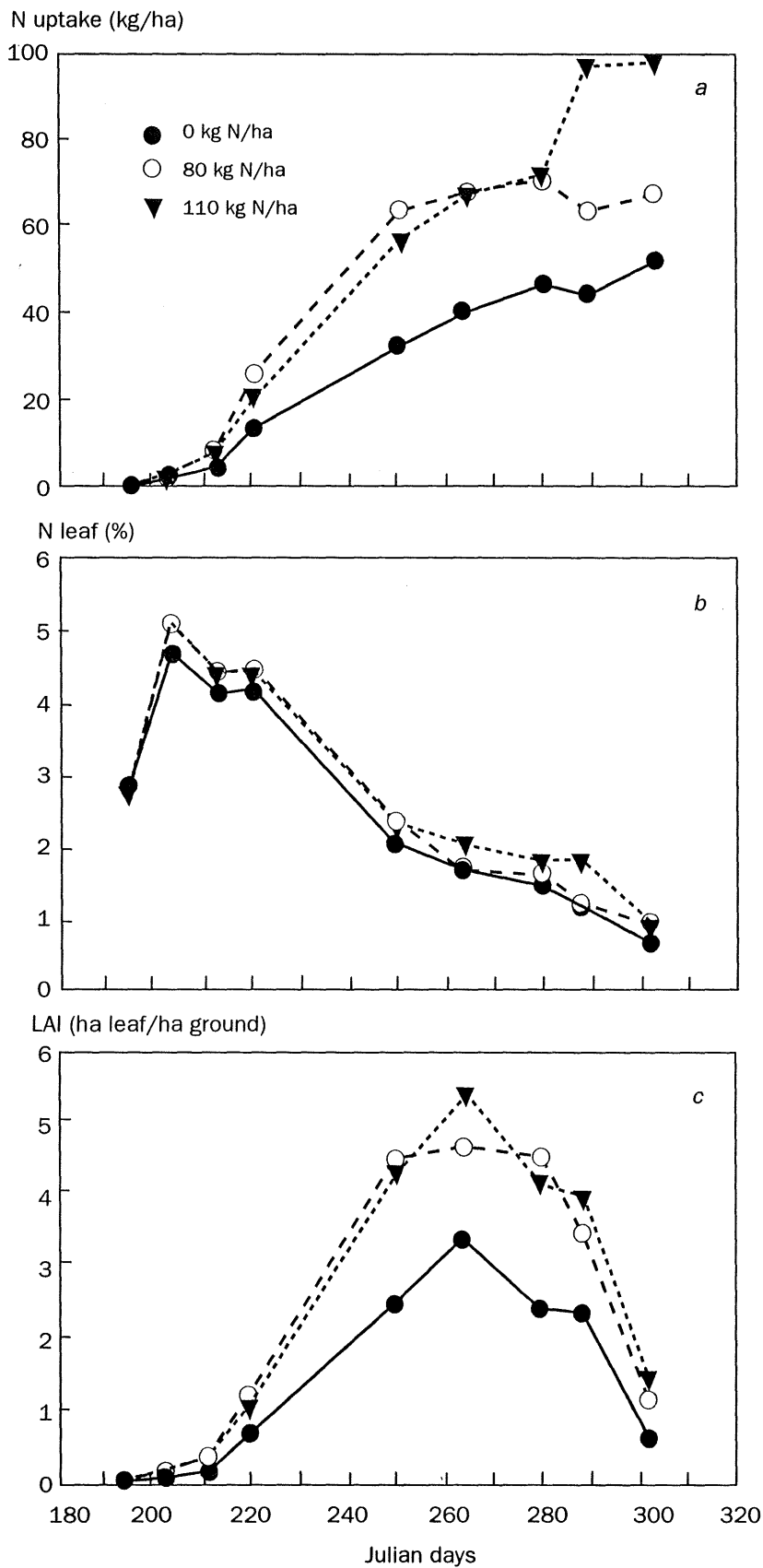
5. Measured results for IR58103-113-3-3-2 with three N treatments—0 kg N, 80 kg N, and 110 kg N—at IRRI, Los Baños, in the 1991 WS. (a) Time course of total N uptake, (b) Time course of average leaf N content, and (c) Time course of LAI.
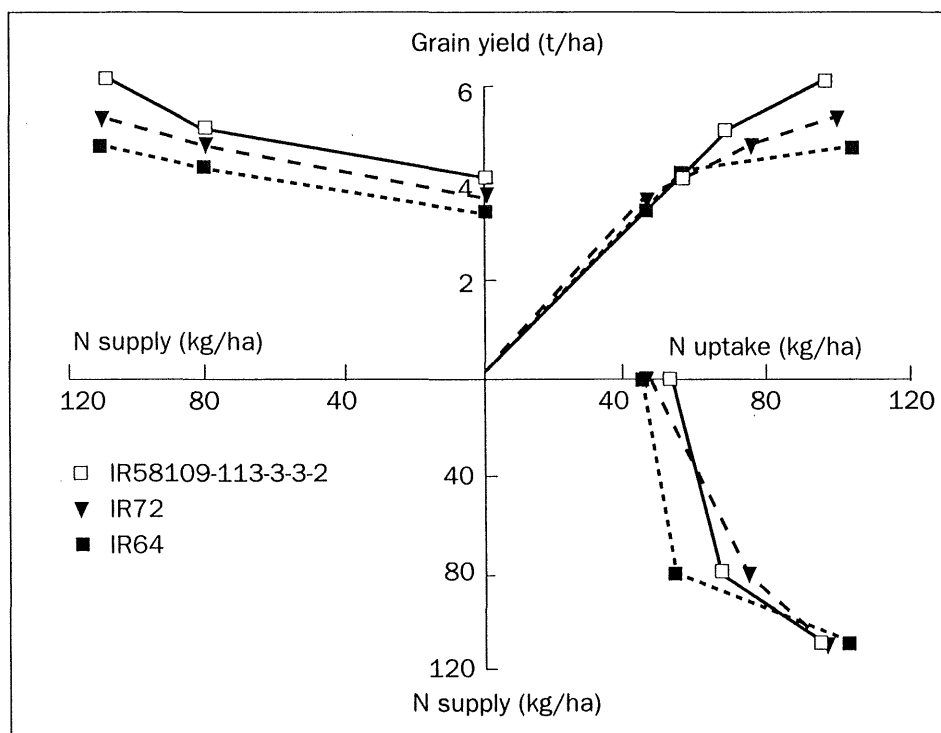
6. Three-quadrant relationships between grain yield, N uptake, and N supply for rice varieties IR58103-113-3-3-2, IR72, and IR64.

the enhanced growth rate of the crop during grain filling as a result of a higher leaf N content and LAI. Thus, the effects of late N application can be fully understood on the basis of differences in LAI and leaf N concentration.

To test the model further, the relation between simulated and measured total biomass and yield was examined. The data used were from the 1991 WS experiment (as above), a 1988 experiment at IRRI with IR64, and experiments with IR64 and five N rate treatments in 1988 DS in Muñoz, Nueva Ecija, Philippines (Dingkuhn et al 1991) (Fig. 9). The results indicate that the model explains differences in biomass production and yield across N treatments, varieties, and environments.

Predicting DS yield potential of current varieties

The model was used to study the attainable yield of IR72 and the new line under DS conditions at IRRI (Table 1). Weather data from 1987 DS were used. With similar N concentrations in the leaves, yields of 7.0 and 8.2 t/ha were simulated. Yields of up to 9.3 t/ha were simulated by assuming a 20% higher N concentration in the leaves. These results indicate that the DS yield potential of current varieties is similar to that of IR8, and that present yields at IRRI are lower than this potential because of insufficient N uptake by the crop.
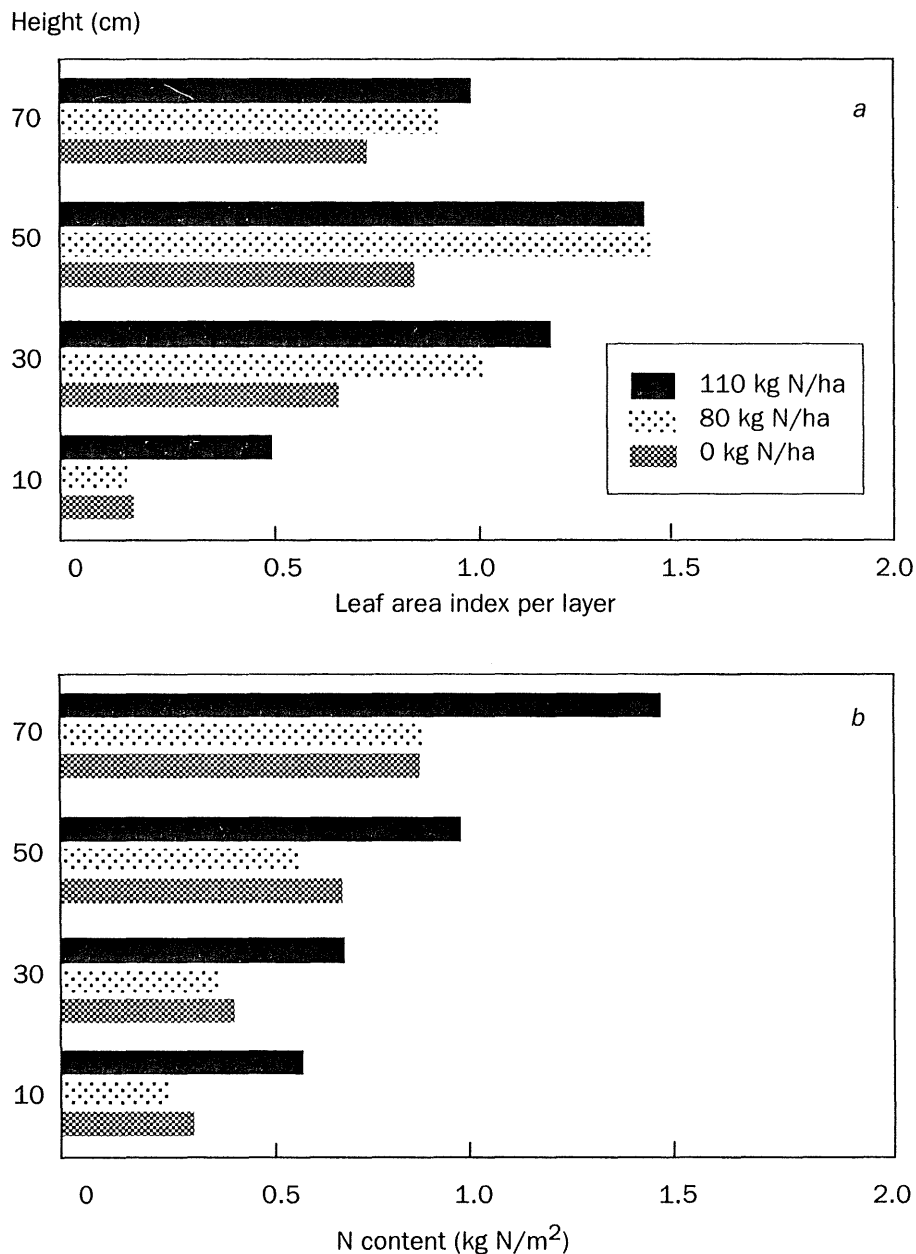
Height (cm)

7. Distribution of LAI (a) and leaf N concentration (b) over height of the canopy of IR58103-113-3-3-2 in the 1991 WS at three treatments, 0 N, 80 kg N/ha before PI, and 110 kg N/ha given as 80 kg in two splits before PI and 30 kg at flowering.

Increased yield potential

This section analyzes the three key processes of yield formation using the ecophysiological simulation model.

Increasing the amount of stem reserves and their allocation

Dingkuhn et al (1991) proposed raising stem reserves by increasing partitioning of assimilates from leaves to stems. They changed the dry matter allocation pattern in their

Kg dry matter/ha
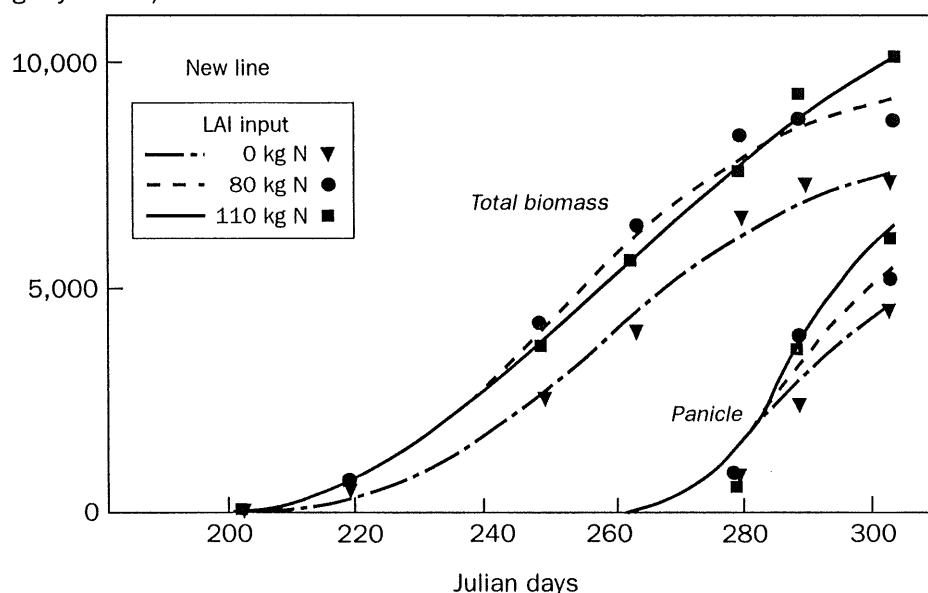
8. Simulated (lines) and observed (symbols) time course of total dry matter production and panicle dry weight for IR58103-113-3-3-2 in the 1991 WS.
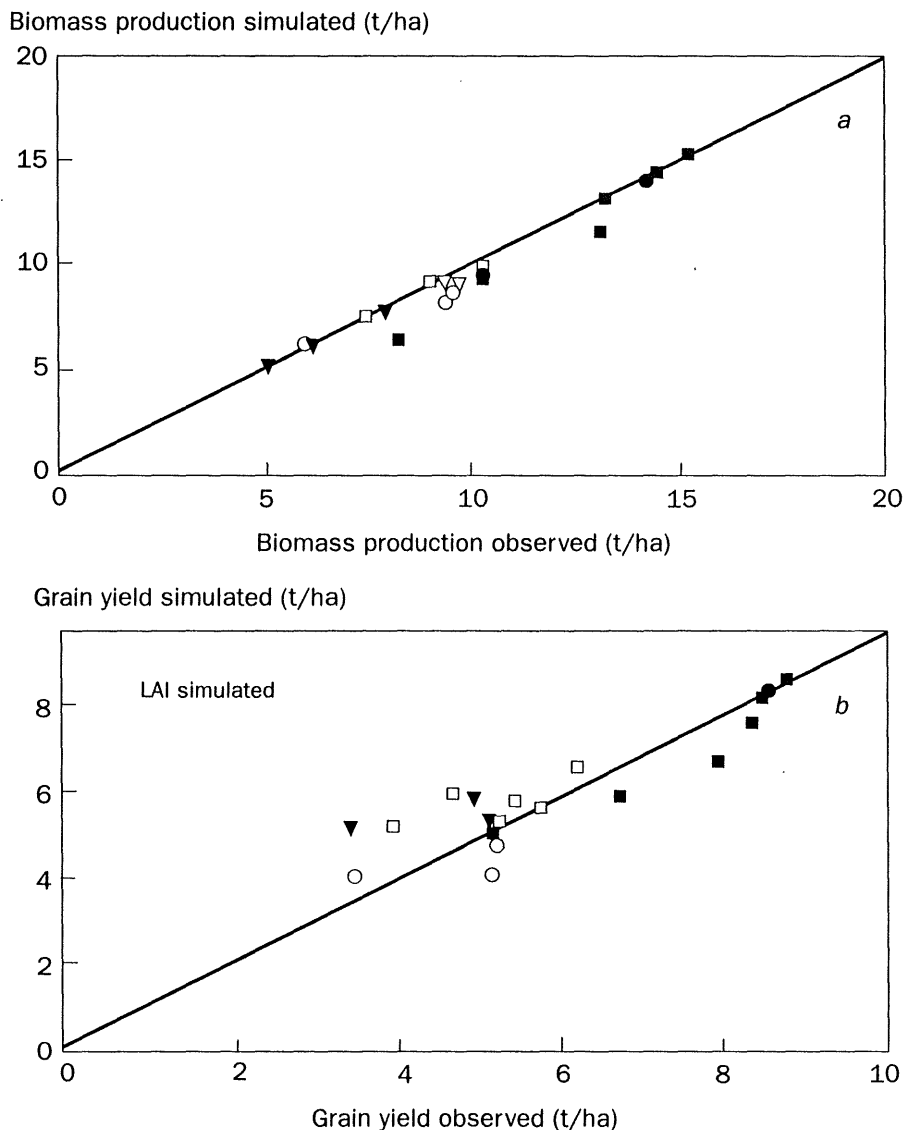
Table 1. Observed and simulated yields (t/ha) of IR72 and the new line for 1991 WS (IRRI, Los Baños, Philippines) and simulated effect of a change in season and higher leaf N content.

	IR72			New line		
	Yield duration (t/ha)	Total filling (d)	Grain (d)	Yield duration (t/ha)	Total filling (d)	Grain (d)
Observed						
1991 WS	5.7	94	28	6.1	108	23
Simulation results						
1. 1991 WS	5.6	94	28	6.3	109	23
2. 1987 DS	7.0	100	30	8.2	118	24
3. As 2 + N conc. 20% higher	7.9	100	30	9.3	118	24

simulation model and found that a yield increase of 25% was possible. However, in their model, the allocation of dry matter to leaf tissue stopped at PI, which is not realistic as several leaves, including the flag leaf, must still emerge and expand. Increasing the amount of stem reserves and efficiency of their allocation to the grain would probably have major consequences for lodging resistance.

Increasing the rate of dry matter production during grain filling

The superiority of higher yielding varieties only becomes apparent toward the end of the growing season. The maximum growth rate of closed canopies does not differ that much among C_3 crop species (Evans 1990). The maximum growth rate of hybrid rice is the same as that of inbred parents (Akita 1988).

Biomass production simulated (t/ha)

Biomass production observed (t/ha)

Grain yield simulated (t/ha)

Grain yield observed (t/ha)

9. Observed vs simulated total biomass (a) and yield (b) of five varieties at three N application levels in the 1991WS and IR64 in the 1988 dry season (DS) (Akita, unpubl. data) at IRRI's farm (Los Baños, Philippines) and IR64 in Muñoz (Philippines) in the 1988 DS.

In many crops, increased 'stay green' has been a major achievement of breeders over the past few decades (Evans 1990). The crops still had green leaves at maturity (C. T. de Wit and H. van Keulen, pers. commun.). For wheat, yield increases were based on lengthening the duration of photosynthetic activity by splitting N applications and improving crop protection (Spiertz and Vos 1985). Unfornately, no detailed complete data sets from that time are available. However, the effect of late N application in the 1991 WS experiments shows that late N can have the same effect in rice as it has in wheat.

Penning de Vries (1991) discussed the possibility of increasing yield potential by improving physiological processes—for instance, by suppressing photorespiration
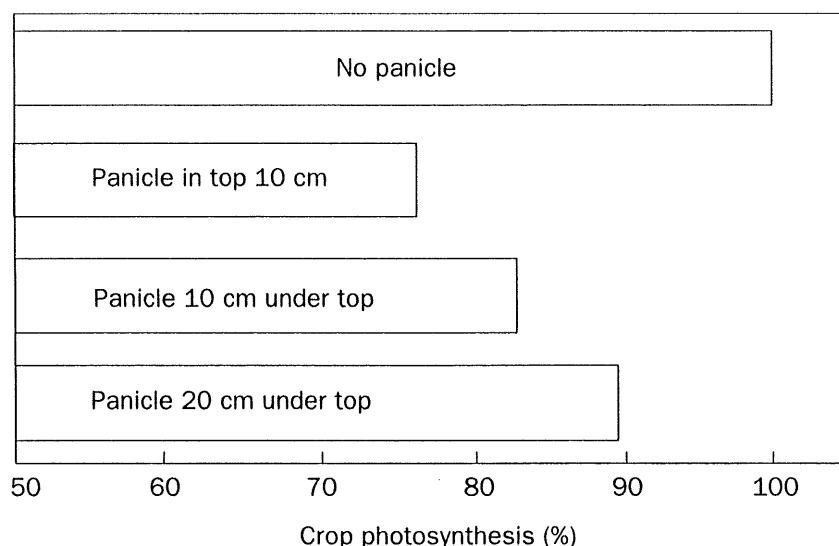
and reducing maintenance respiration. So far, there are no indications that photorespiration can be suppressed in C_3 plants. Indications that genetic variation in maintenance respiration is related to variation in yield were found by Spitters, de Visser, and Penning de Vries (Centre for Agrobiological Research, Wageningen, The Netherlands, pers. commun.), although the size of the effect was very small. An interesting option mentioned by Penning de Vries is the increase of CO_2 flow from the soil through the root aerenchyma to the leaves, providing extra CO_2 for photosynthesis. However, sound evidence that this mechanism contributes to photosynthesis has not yet been documented.

Dingkuhn et al (1991) suggested increasing the N gradient in the canopy. This fits very well with the conclusions of our study and the results of the 1991 experiment. However, leaf N concentration in the top of the canopy is more important than the gradient itself. Dingkuhn et al (1991) simulated yields of 11.5-13.5 t/ha with 48 d of grain filling, which is much longer than what we found, based on both the simple approach and the simulation study.

We observed that the position of the panicles in the canopy varies strongly between varieties. The effect of panicle position on light absorption by the leaves was studied with a detailed model for interplant competition for light capture (Kropff and Spitters 1992). In 1991 WS, the panicle area index (PAI) reached 0.6-0.9 m^2 panicle/m^2 ground. The model showed that panicles in the top 10 cm of the canopy reduced canopy photosynthesis (LAI=4) by 25%, whereas panicles 20 cm below the top reduced canopy photosynthesis by only 10% (Fig. 10). There is large genetic variability in panicle height and flag leaf size in the canopy. These traits may provide promising characteristic for modification by breeders.

Lengthening the grain-filling period with long green leaf area duration

The ecophysiological simulation model was used to evaluate the outcome of the simple calculations. The starting point was the simulated yield of 9.3 t/ha of the new line with

No panicle

Panicle in top 10 cm

Panicle 10 cm under top

Panicle 20 cm under top

50   60   70   80   90   100

Crop photosynthesis (%)

10. Simulated reduction in leaf canopy photosynthesis as a result of shading by panicles at different positions in the canopy.

Table 2. Simulated effect of a change in grain-filling duration in the new line using 1987 DS weather data, Los Baños, Philippines.

	Yield (t/ha)	Total duration (d)	Grain filling (d)
1. 1987 DS	8.2	118	24
2. As 1 + N conc. 20% higher	9.3	118	24
3. As 2. Grain-filling duration from 24 to 31 d	11.7	125	31
4. As 2. Grain-filling duration of 40 d	14.7	134	40

Los Baños weather data from 1987 DS, with 20% higher leaf N concentrations than was observed in the 1991 WS experiment (Table 1). The effect of a longer grain-filling duration was examined, based on the outcome of the simple conceptual analysis previously presented.

Lengthening the grain-filling period from 24 to 31 d increased panicle dry matter to 11.7 t/ha. A grain-filling duration of 40 d and a harvest index of 0.6 gave 14.7 t/ha (Table 2). This is very close to the 43 d calculated with the simple concept of grain filling and illustrates the relatively simple structure of the system. However, in these simulations, a substantial amount of green leaf area remained active for a long period. This requires thick, large, and green leaves (due to high N concentrations), that senesce slowly. Japonica varieties have these characteristics, and a hybrid developed recently between a tropical japonica and an indica variety shows similar visual characteristics (S.S. Virmani, IRRI, pers commun.). The question that remains to be answered is: What is the genetic variability in the length of the grain-filling period? Senadhira and Li (1989) studied the length of the grain-filling period of 21 rice cultivars at IRRI's experimental farm during the 1987 DS. The duration of grain filling ranged from 16 to 40 d. However, rate of grain filling was low in the long-duration varieties, giving lower panicle weights. Interpreting this data is hindered by the agronomic practices used in the study, one plant per hill at 30- × 20-cm spacing, and only 60 kg of N given as a basal application. Experiments to evaluate the length of the grain-filling duration in relation to growth and production of some of these lines at optimum N levels are now in progress.

Implications for crop management

Increasing yield potential from 10 to 15 t/ha will have major implications for crop management. Based on normal N concentrations in the plant organs, it was calculated that about 200 kg of N must be taken up by a crop yielding 10 t/ha, and 300 kg of N is required for 15 t/ha. Reducing the grain N content could be an option, but that would reduce grain quality and protein content. Normal rice soils can supply the crop with about 60 kg N/ha, so a substantial amount of N must be added to achieve potential yields. At a recovery of 50%, which is high for existing flooded rice ecosystems, large amounts of N fertilizer will be needed. Of course, the economical and environmental implications of such high inputs have to be studied in detail. Better N management,

including a multisplit application strategy that maintains adequate N supply throughout the season while minimizing N losses, is likely to be a prerequisite. At the foundation of such a strategy is the prediction and in-season reestimation of the minimum N uptake requirement (MNUR) (Cassman et al 1994). The simulation model could be helpful in estimating the MNUR throughout the growing season. However, processes related to N translocation and their relationship to the N status of the plant must be quantified accurately. A first setup for such a model is being developed.

Increasing yield potential and hybrid vigor
It is extremely important to analyze the physiological background of the so-called hybrid vigor, as it may be possible to obtain similar traits in conventionally bred lines

One physiological trait cited in hybrids was vigorous seedling growth, resulting in earlier canopy closure and better sink formation (Akita 1988). However, as soon as the canopy closed, no differences in photosynthesis, respiration, and growth rate were observed (Akita 1988, Yan Zhen De 1988). This fast early growth and leaf area development may help to produce high yield in short-duration varieties, but similar effects may be obtained by narrower spacing of the hills. An important advantage is improved partitioning of photosynthates to the grains, which may be due to the different lengths of the generative and vegetative phases. A better canopy structure was also reported by Yan Zhen De (1988) and Akita (1988). However, detailed physical information was not given.

Conclusions

Systems approaches at different levels of detail can help in the process of designing and testing varieties for specific environments. Simple approaches as discussed in this paper help to identify the most promising options. Detailed ecophysiological models can help in analyzing the physiological processes and predicting crop management requirements, such as the MNUR (Cassman et al 1994). These models can be used to analyze genotype-environment interactions and to interpret the results of multilocation trials (Dua et al 1990). However, one should be careful in using the detailed simulation models to define the effect of physiological traits, as compensation effects may confound conclusions. For example, in the model used in this study, the effect of shading by panicles was not included. The competition model showed that canopy photosynthesis was reduced by more than 15%. It may well be that the simplified way that the effect of a vertical N profile in the canopy was introduced compensated for this. It is important, therefore, that the components of these detailed models are tested with experimental data.

Leaf area development and dry matter partitioning are not simulated satisfactorily by the existing models. Empirical functions that cannot explain different allocation patterns across N treatments are used (de Wit and Penning de Vries 1985, Evans 1990, Thiyagarajan et al 1991).

A combination of longer grain-filling duration, more spikelets/m^2, and longer green leaf area duration are needed to obtain grain yields beyond 10 t/ha in tropical

environments. Multilocation trials, where a range of varieties is grown under optimum management and where the crop is sampled in detail, are needed to obtain further insights into the feasibility of raising the yield frontier in rice.

Acknowledgments

References cited

Akita S (1988) Physiological bases of heterosis in rice. Pages 67-77 in Hybrid rice. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Cassman K G, Kropff M J, Yan Zhen De (1994) A conceptual framework for nitrogen management of irrigated rice in high-yield environments.

Cook M G, Evans L T (1983) Nutrient responses of seedlings of wild and cultivated *Oryza* species. Field Crops Res. 6:205-218.

De Wit C T (1992) Resource use efficiency in agriculture. Agric. Sys. 40:125-151.

De Wit C T, Penning de Vries F W T, (1985) Predictive models in agricultural production. Philos. Trans. Royal Soc. London B 310:309-315.

Dingkuhn M, Penning de Vries F W T, De Datta S K, van Laar H H (1991) Concept for a new plant type for direct seeded flooded tropical rice. Pages 17-38 in Direct seeded flooded rice in the tropics. Selected papers from the International Rice Research Conference, 27-31 Aug 1990, Seoul, Korea. International Rice Research Institute, P.O. Box 933, Manila, Philippines.

Dua A B, Penning de Vries F W T, Seshu D V (1990) Simulation to support testing of rice varieties in international trials. Trans. Am. Soc. Agric. Eng. 33(4):1185-1194.

Evans L T (1990) Assimilation, allocation, explanation, extrapolation. Pages 77-87 in Theoretical production ecology: reflections and prospects. R. Rabbinge, J. Goudriaan, H. van Keulen, F. W. T. Penning de Vries, and H. H. van Laar, eds. Simulation Monograph 34. PUDOC, Wageningen, The Netherlands.

Evans L T, De Datta S K (1979) The relation between irradiance and grain yield of irrigated rice in the tropics, as influenced by cultivar, nitrogen fertilizer application and month of planting. Field Crops Res. 2:1-17.

IRRI—International Rice Research Institute (1989) IRRI towards 2000 and beyond. P.O. Box 933, Manila, Philippines. 66 p.

Kropff M J (1990) The effects of long-term open-air fumigation with SO_2 on a field crop of broad bean (*Vicia faba* L.). III. Quantitative analysis of damage components. New Phytol. 115:357-365.

Kropff M J, Goudriaan J, (1989) Modelling short term effects of sulphur dioxide. III. The effect of SO_2 on photosynthesis of leaf canopies. Neth. J. Plant Pathol. 95:265-280.

Kropff M J, Spitters C J T (1992) An eco-physiological model for interspecific competition, applied to the influence of *Chenopodium album* L. on sugar beet. I. Model description and parameterization. Weed Res. 32:437-450.

Kropff M J, van Laar H H, eds. (1993) Modelling crop-weed interactions. CAB-IRRI, P.O. Box 933, Manila, Philippines. 269 p.

Penning de Vries F W T (1991) Improving yields: designing and testing VHYVs. Pages 13-19 *in* Systems simulation at IRRI. IRRI Res. Pap. Ser. 151.

Peening de Vries F W T, Jansen D M, ten Berge H F M, Bakema A (1989) Simulation of ecophysiological processes of growth of several annual crops. Simulation Monograph 29. PUDOC, Wageningen, and International Rice Research Institute, P.O. Box 933, Manila, Philippines. 271 p.

Penning de Vries F W T, Van Keulen H, Alagos J C (1990) Nitrogen redistribution and potential production in rice. *In* International congress of plant physiology. S. K. Sinha, P. V. Lane, S. C. Bhargava, and A. K. Agrawal, eds. Society for Plant Physiology Biochemistry, Water Technology Center, Indian Agricultural Research Institute, India. 513 p.

Senadhira D, Li G F (1989) Variability in rice grain-filling duration, Int. Rice Res. Newsl. 14(1):8-9.

Spiertz J H J, Vos J (1985) Grain growth of wheat and its limitation by carbohydrate and nitrogen supply. Pages 129-141 *in* Wheat growth and modelling W. Day & R. K. Atkin, eds. NATO ASI Series. Series A: life science. Vol. 86. Plenum Press, New York.

Spitters C J T, van Keulen H, van Kraalingen D W G, (1989) A simple and universal crop growth simulator: SUCROS87. Simulation Monograph. PUDOC, Wageningen, The Netherlands. 147-181 p.

Thiyagarajan T M, Mohandass S, Palanisamy S, Abdul Kareem A (1991) Effect of nitrogen on growth and carbohydrate partitioning in rice. *In* Simulation and systems analysis for rice production (SARP). F. W. T. Penning de Vries, H. H. van Laar, and M. J. Kropff, eds. PUDOC, Wageningen, The Netherlands. 132-136 p.

Van Keulen H, Seligman N G (1987) Simulation of water use, nitrogen and growth of a spring wheat crop. Simulation Monograph. PUDOC, Wageningen, The Netherlands. 310 p.

Yan Zhen De (1988) Agronomic management of rice hybrids compared with conventional varieties. Pages 217-223 *in* Hybrid rice. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines.

Yoshida S (1981) Fundamentals of rice crop science. International Rice Research Institute, P.O. Box 933, Manila 1099, Philippines. 269 p.

Notes