

# Direct Seeded Flooded Rice in the Tropics

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# Concepts for a new plant type for direct seeded flooded tropical rice

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Direct seeded flooded rice is gradually replacing transplanted rice in many rice-growing areas of the tropics. Current high-yielding cultivars were bred for transplanted rice culture: little is known about the yield potential and plant type requirements for direct seeded flooded rice. Several field experiments in the Philippines were used to analyze the growth characteristics and yield potential of semidwarf IR rices when direct seeded. Simulation aided data interpretation and generated concepts for plant types with improved yield potential. Compared with transplanted rice, the same varieties when direct seeded required greater N inputs to produce the same yield. The absence of transplanting shock and a dense plant population caused excessive leaf and tiller production, followed by N dilution and premature senescence through foliar N deficiency. Maximum grain yields were 9 t/ha. Simulation indicated that yield potential can theoretically be increased 25% through modified assimilate partitioning between leaves and stems and by enhancing the vertical N concentration gradient within the foliage. Even greater yield improvements are predicted for plant types with a prolonged ripening period and sustained high foliar N concentrations. Components of a new plant type concept for greater resource use efficiency and yield potential include a) enhanced foliar growth during crop establishment, in combination with reduced tillering; b) less foliar growth and enhanced assimilate export from leaves to stems during late vegetative and reproductive growth, along with sustained high foliar N concentration; c) a steeper slope of the vertical N concentration gradient in the leaf canopy, with more N present in the uppermost stratum; d) expanded capacity of stems to store assimilates; and e) improved reproductive sink capacity, with a prolonged ripening period.

For centuries, in many regions of Asia, flooded rice has been understood as almost synonymous with transplanted rice. Now the availability of improved weed control technologies; the development of new, fast-establishing, early-maturing rices; and rising prices for labor in some rural rice-growing areas are motivating many farmers to shift from transplanting to direct seeding (De Datta 1986, Erguiza et al 1990).

Virtually all modern, high-yielding tropical lowland rice cultivars, however, were selected and bred for transplanted rice culture. Until recently, little information existed on how these cultivars performed when seeded directly and grown in dense populations, as is the case in broadcast seeded rice culture (the most popular direct seeding practice among farmers).

Studies using semidwarf IR cultivars indicate that direct seeded flooded rice culture results in crop growth dynamics profoundly different from those resulting from transplanted rice culture (Dingkuhn et al 1990a,b,c; Schnier et al 1990a,b). Early production of a large vegetative biomass, leaf area, and tiller number is characteristic of direct seeded flooded rice.

Its greater vegetative growth, compared with that of transplanted rice, is only partly due to a denser plant population, and thus more light interception during crop establishment. An equally important factor is the absence of transplanting shock, with a consequent absence of an initial lag-phase of growth (Dingkuhn et al 1990c). The resulting abundance of vegetative biomass impedes the yield formation process through nitrogen dilution and high maintenance respiration (Dingkuhn et al 1990a).

The design of new, high-yielding, resource use-efficient cultivars for direct seeded rice culture requires new knowledge on how the biological growth potential of rice can be translated into improved yields. Modern high-yielding rices have attained a yield plateau that is proving difficult to surmount using current plant types (Akita 1989, Tanaka et al 1966).

In the study reported here, we compared the growth dynamics and yield components of transplanted and direct seeded flooded rice as measured in field observations. Simulation helped explain the crop dynamics observed and generated predictions on how modified plant types would perform in a range of nutritional environments. The objective was to identify and quantify changes in plant characteristics that would raise the grain yield potential of direct seeded flooded rice at given N input levels, and of tropical irrigated rice in general.

## Materials and methods

Improved, lowland-adapted, semidwarf indica rices IR58, IR64, IR72, and IR29723 were grown in various field experiments during the 1986, 1987, 1988, and 1989 dry seasons (January-May) in two locations in the Philippines. One site was the IRRI experimental farm at Los Baños, Laguna; the other, the Maligaya Rice Research and Training Center (MRRTC) farm in Muñoz, Nueva Ecija.

All experiments used different plant establishment practices and sequential observations of plant dry matter accumulation (DM), N uptake and its distribution within the plant, leaf area index (LAI), tiller number, tissue death, and canopy CO<sub>2</sub> exchange rate (CER) throughout the growing seasons. The crops were transplanted using 20-d-old seedlings or direct seeded using pregerminated seed. Direct seeding treatments were broadcast seeding, dibble seeding at the same planting density and geometry as in transplanted, row seeding, or broadcast seeding with subsequent introduction of rows.

Treatments were laid out in factorial randomized complete block designs with four replications (experiment 1 had three replications).

Population densities averaged 100 (transplanted and dibble-seeded rice), 180 (row seeded), and 250 (broadcast seeded) plants/m<sup>2</sup>, with 4 plants/hill in transplanted and dibble-seeded rice. Spacing was 0.2 m between hills in transplanted and dibble-seeded rice and 0.25 m between rows in row seeded rice. Plots were kept flooded at 0.05 m water depth to 2 wk before maturity, then drained and allowed to dry.

CER was measured with a nondestructive, mobile, depletion system that enclosed a 0.6- × 0.6-m field area for less than 1 min per measurement. Gas exchange of single leaves was measured porometrically using an open system. (For details of the gas exchange measurement techniques, see Dingkuhn et al 1990c for canopy-based observations and Dingkuhn et al 1990e for leaf-level observations.) Sequential destructive sampling in each plot for leaf area, DM, N content, and tiller number was based on a 0.6- × 0.4-m area during vegetative growth and on a 0.4- × 0.4-m area during reproductive growth. Yield at maturity was determined from a 7.2-m<sup>2</sup> area. Plants from two hills or an equivalent ground area were collected from each corner of the yield sample area, for a combined sample of 0.32-m<sup>2</sup>/plot to determine yield components.

The experiments conducted were the following (for further details, see the references cited):

- Experiment 1: 1986 dry season, IRRI site, IR64 rice (Dingkuhn et al 1990c); crop establishment by transplanting and dibble seeding. Whole-season dynamics of DM, N uptake, LAI, tiller number, and CER. Diurnal observations on CER and evapotranspiration and response of CER to light.
- Experiment 2: 1986 dry season, IRRI site, IR64 rice; crop establishment by transplanting; different N rates and timing (Ingram et al 1990). Whole-season dynamics of DM, N uptake, LAI, tiller number, CER, and diurnal patterns of CER.
- Experiment 3: 1987 dry season, MRRTC site, IR64 rice; crop establishment by transplanting, dibble seeding, row seeding, and broadcast; different N rates, methods, and timing (Schnier et al 1990b). Whole-season dynamics of DM, N uptake, LAI, tiller number, CER, and diurnal patterns of CER.
- Experiment 4: 1988 dry season, MRRTC site, IR64 rice; crop establishment by transplanting and row seeding; 0, 30, 60, 90, 120, 150 kg N/ha (Schnier et al 1990a, Dingkuhn et al 1990a). Whole-season dynamics of DM, N uptake, LAI, tiller number, tiller death, and CER. Fertilizer N was applied using the liquid band placement technique (Schnier et al 1988); that suppressed N volatilization losses and made applied N almost quantitatively available to the plant.
- Experiment 5: 1988 dry season, MRRTC site, IR58, IR64, and IR27923 rice; crop establishment by transplanting, broadcast and broadcast with rows; different rates and timing of N (Dingkuhn et al 1990b). Whole-season dynamics of DM, N uptake, LAI, tiller number, tiller death, and CER.
- Experiment 6: 1989 dry season, MRRTC site, IR72 rice; crop establishment by transplanting, dibble seeding, and broadcast; different rates and timing of N (Dingkuhn et al 1990d,e). Whole-season dynamics of DM, N uptake, LAI, tiller

number, tiller death, and CER, with emphasis on the flowering stage. Study of canopy stratification. Single-leaf gas exchange measurements at flowering.

For the simulation research, we developed a crop growth model L3QT. Its name reflects the fact that it simulates growth under N shortage (i.e., crop production level 3, de Wit 1986) with quarter-day integration intervals, and that it includes tiller formation. The major part of this model (L1Q + TIL described by Penning de Vries et al 1989) simulates processes of photosynthesis, respiration, partitioning, and phenological development from early establishment to maturity, and distinguishes among leaves (blades), stems, roots, panicles, and tiller number. L3QT accounts for changes in weather that occur continuously, particularly changes in solar radiation and temperature. As much as possible, these processes are described at a physiological level.

When L3QT was evaluated for rice crops under optimal growth conditions (Herrera-Reyes and Penning de Vries 1990), it was found to simulate rice growth rates quite well, provided that accurate initial values are supplied. The model also includes physiological responses to crop N status and permits detailed photosynthesis calculations.

Differences in L3QT from previously documented models are described below. Water stress is supposed not to occur in an irrigated crop and was therefore not simulated in this study. The crop parameters used are those for rice variety IR64.

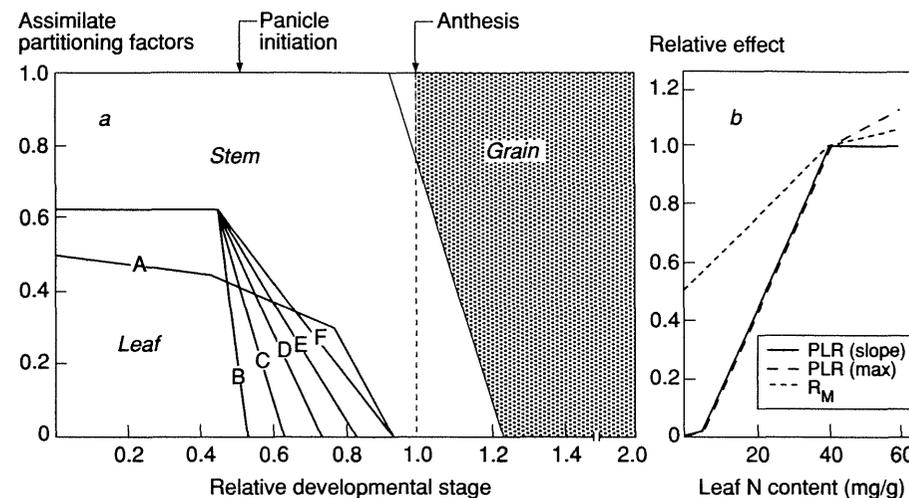
In L3QT, the foliage is explicitly subdivided into three horizontal strata of equal area but different N concentrations. Leaf N concentration affects the rate of several processes (Fig. 1b).

■ **Leaf photosynthesis.** The leaf gross photosynthesis radiation response curve is quantified by two parameters: the initial slope (quantum efficiency) at low light levels and the maximum photosynthesis rate at high light levels. The maximum rate is almost proportional to N concentration (Penning de Vries et al 1990, Dingkuhn et al 1990e). Quantum efficiency is supposedly related to this concentration at low N levels. This assumption, supported by observations (Dingkuhn, unpubl. data), was necessary to simulate low rates of CER measured in field crops with low N. Crop production is relatively sensitive to these parameters.

■ **Maintenance respiration.** The rate is related to leaf N concentration, but only half as much maximum leaf photosynthesis depends on N (Penning de Vries et al 1990). Maintenance respiration of the other organs is related to N concentration in the same way. Relationships between dark respiration and canopy N content were established by Ingram et al (1990).

■ **Senescence and loss of leaves.** Following Van Keulen and Seligman's (1987) findings in wheat crops, we related the rate of death of leaves in a given stratum to their N concentration. The amounts of green and dead leaves are calculated separately for each stratum, with leaf death proceeding successively from the lower to the upper layer.

Total N content of the leaves is an input in L3QT because there is not yet a model that can reliably simulate that variable. Another reason is that this study focused on crop



1. a) Patterns of assimilate partitioning among the foliage, stems, and grains used in growth simulation. Pattern A is the actual partitioning in IR64 rice. Patterns B to F are hypothetical. Root assimilate allocation is controlled separately. b) Relationships between leaf N concentration and gross photosynthesis (PLR) (maximum rate and the initial slope of light response) and maintenance respiration ( $R_M$ ). At 40 mg N/g, the initial slope is 0.4 kg CO<sub>2</sub>/ha per h (J/m<sup>2</sup> per s), the maximum rate is 66 kg CO<sub>2</sub>/ha per h, and  $R_M$  is 0.02 kg glucose/kg.

responses to certain N content in the canopy, not on ways to realize N uptake. In our experiments, N content of the green leaves was determined by sequential sampling throughout the season. L3QT determines average leaf N concentration by dividing N content by leaf weight. We preferred to use N content rather than N concentration as the input because quantity is a more stable feature than concentration.

Vertical distribution of N in the foliage was empirically measured for only one developmental stage, season, and variety (Dingkuhn et al 1990e). But our model shows it to be essential in understanding growth dynamics. In L3QT, the foliar N concentration of the central stratum equals the average, that of the lower layer is lower by a certain value, and that of the upper layer higher by the same value. This value was 10 mg N/g (1%) or less if it would decrease N concentration in the lower layer below the minimum 0.4%, in line with findings in experiment 6 (Dingkuhn et al 1990e). Total amount of N in the leaves is not affected by the gradient.

We found that L1Q's feedback of glucose levels on photosynthesis was too strong under conditions that allowed rapid growth, and eliminated it. The state variable weight of "storage organ" was redefined as "weight of grains," since the assimilating function includes formation of the empty panicle (under stem formation). Where not explicitly stated, grain yields were expressed at zero moisture.

Most crop parameters for IR64 were taken from Penning de Vries et al (1989) and Herrera-Reyes and Penning de Vries (1990). The pattern of assimilate partitioning

between leaves and stems followed pattern A in Figure 1, which best approximated the data for IR64 across crop establishment methods and N rates. It has been reported to be independent of crop N level (van Heemst 1986); this was confirmed in our experiments. The pattern of partitioning between roots and shoots was derived from observations by Diekmann (IRRI, pers. comm.). The fraction of stem reserves mobilized for grain growth was raised to 40% to simulate the significant weight loss of stems after flowering. The rates of phenological development were adjusted slightly to match the dates of flowering and maturity in our experiments.

Differences among crop establishment methods have no consequence for the structure of L3QT, and are only expressed in the initial values for crop weight and the pattern of crop N content.

To verify L3QT and evaluate the growth and yield formation processes, data from experiment 4 were used. Simulation started at 27 d after seeding (DAS) for direct seeded treatments and 21 d after transplanting (DT) for transplanted treatments. Initial dry weights of the various plant parts were used as inputs.

Meteorological data recorded at the experimental sites were used as inputs for model verification. For the extrapolations, 10-yr historic data for the IRRI farm were used (1979-88). This permitted us to determine both the average and standard deviation of growth dynamics and yield for our hypothetical crops in the dry and wet seasons.

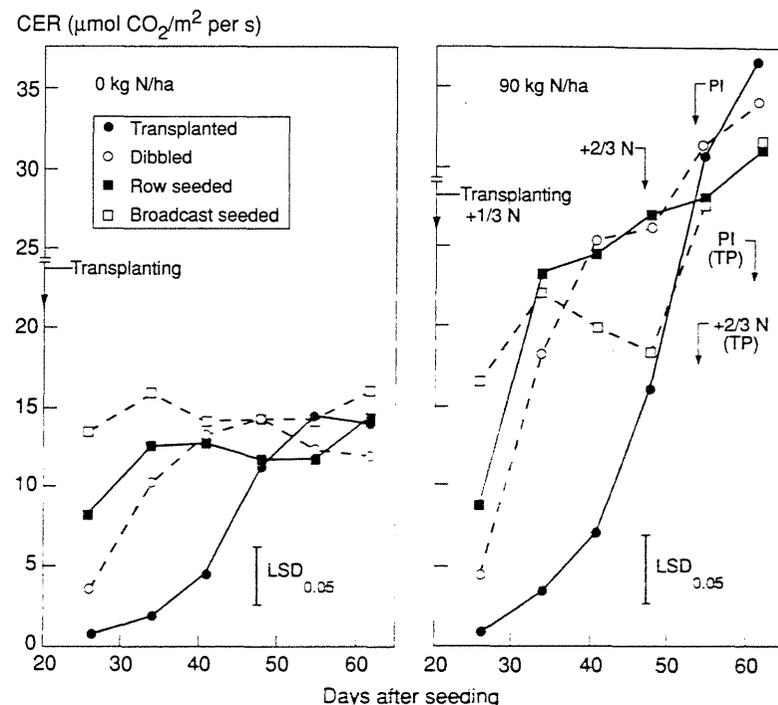
## Results and discussion

### Field observations

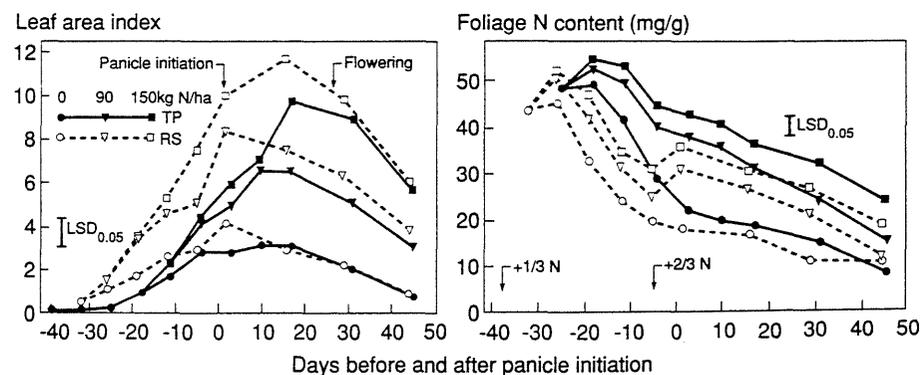
*Growth and yield analyses of broadcast-seeded, row-seeded, dibble-seeded, and transplanted rice.* Crop growth is a function of a population's cumulative assimilation of CO<sub>2</sub>. For medium-duration (110-124 d) cultivar IR64, CER was measured during all growth stages in all treatments (Fig. 2). Differences among planting methods were small at panicle initiation (PI) but highly significant during the first 45 d of growth.

Broadcast-seeded rice had the highest initial CER, due to its great population density, followed by row-seeded rice. Dibble rice, which had the same population density and geometry as transplanted rice, had significantly higher CER than transplanted rice. This difference was attributed to the growth inhibition caused by transplanting shock (Dingkuhn et al 1990c). Application of N fertilizer increased CER for all planting methods but did not eliminate the basic differences caused by transplanting shock. Consequently, direct seeded rice had a substantial growth advantage over transplanted rice during vegetative growth, resulting in greater biomass (data not presented) and leaf area (Fig. 3).

The initial growth advantage of dibble-seeded, row-seeded, and broadcast-seeded rice over transplanted rice carried over into the subsequent growth stages, generating a higher LAI under any fertilizer regime. The proliferation of foliage, however, was associated with a rapid decrease in foliar N content, due to the dilution of absorbed N in the plant tissues shown at the right in Figure 3.



2. Effect of planting method and N fertilizer application on canopy CO<sub>2</sub> assimilation rates (CER) during the vegetative growth phase of IR64 rice, Experiment 3, Muñoz, Nueva Ecija, Philippines, 1987 dry season. PI = panicle initiation.



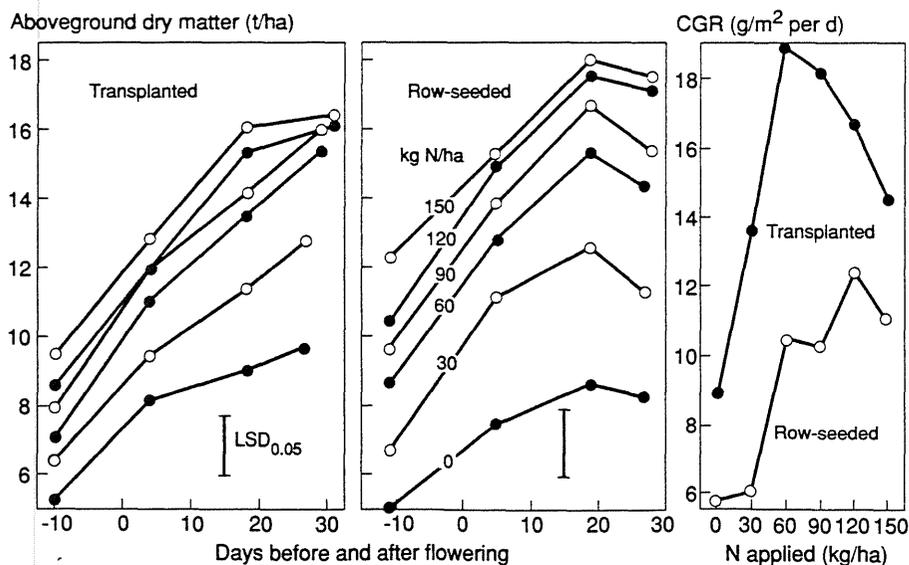
3. Effect of N fertilizer application on leaf area index and foliage N concentration of transplanted (TP) and row-seeded (RS) IR64 rice, Experiment 4, Muñoz, Nueva Ecija, Philippines, 1988 dry season.

Low foliar N concentration during reproductive growth of dibble-seeded, row-seeded, and broadcast-seeded rice depressed CER (Schnier et al 1990a, Dingkuhn et al 1990a) and resulted in low crop growth rates (CGR) during ripening (Fig. 4). The CGR at flowering and thereafter is an important determinant of grain yield and harvest index (HI) (Akita 1989; Dingkuhn et al 1990b,d,e).

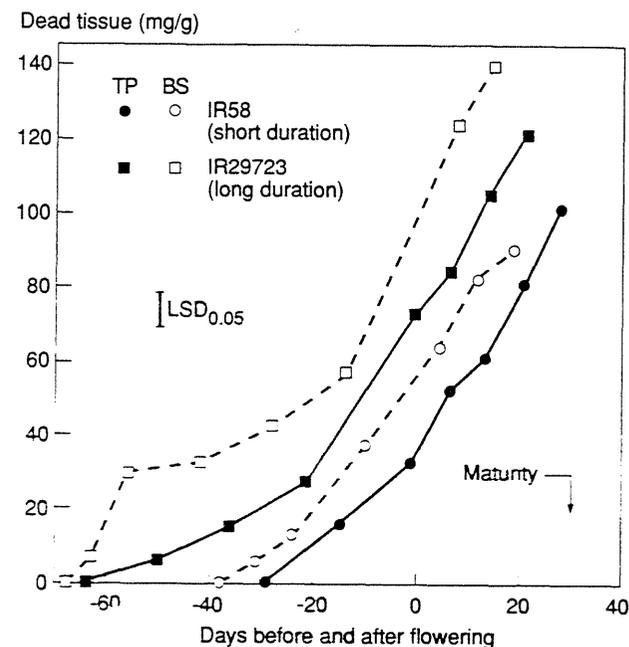
CGR during ripening responded to N fertilizer rate in an optimum-shaped function. To reach maximal CGR, higher N rates were required by row-seeded than by transplanted rice.

The low CGR during ripening of row-seeded rice was probably due to high biomass, and thus, to maintenance respiration (Dingkuhn et al 1990a), in combination with low foliar N concentration (Fig. 3), and reduced CO<sub>2</sub> assimilation rates (Yoshida 1981, Dingkuhn et al 1990e).

Another characteristic of direct seeded rice was phenologically early onset of senescence and, thus, tissue death (Fig. 5). Tissue death during the reproductive growth phase of monocarpic crops is usually associated with the transfer of carbohydrates, N, and P from the vegetative tissues to the reproductive organs (Biswas and Choudhuri 1980, Yoshida 1981). A substantial increase in necrotic tissue, however, occurred from 25 to 65 d before flowering, depending on cultivar and planting method. Senescence was observed phenologically earlier in a broadcast-seeded crop than in a transplanted crop, and earlier in a long-duration (IR58) than in a short-duration cultivar (IR29723). Preflowering senescence of medium-duration IR64 was intermediate (data not presented).



4. Effect of N fertilizer rate in transplanted and row-seeded IR64 rice on dry matter accumulation during ripening phase and crop growth rates (CGR) between flowering and maturity. Experiment 4, Muñoz, Nueva Ecija, Philippines, 1988 dry season.

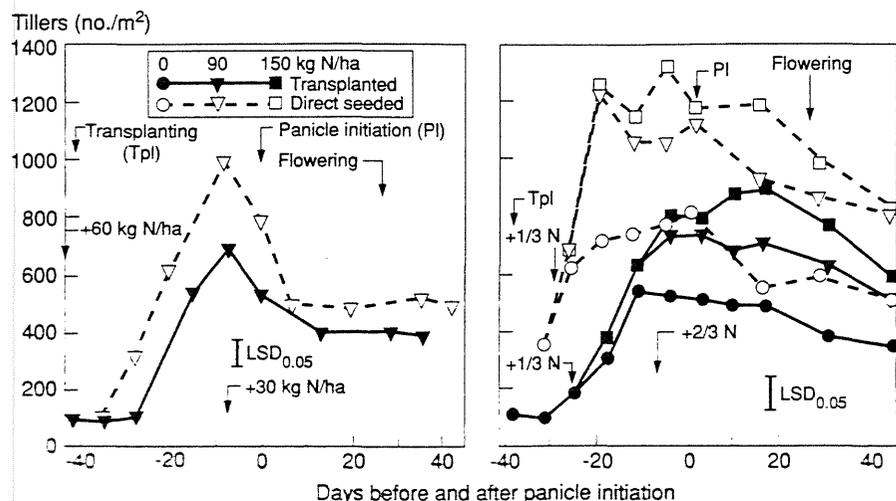


5. Relative accumulation of dead shoot tissue during the reproductive growth phases of transplanted (TP) and broadcast seeded (BS) IR58 and IR29723 rice fertilized with 90 kgN/ha. Experiment 5, Muñoz, Nueva Ecija, Philippines, 1988 dry season.

Senescence was delayed by high N rates (Dingkuhn et al 1990a) and late season foliar N application (Dingkuhn et al 1990d,e; data not presented), indicating that pre-ripening senescence is influenced by the N status of photosynthesizing tissues. Considering that direct seeded rice absorbed as much or higher amounts of N as did transplanted rice (Schnier et al 1990a,b), and that it had consistently lower foliar N concentration, we conclude that, when directly seeded, IR64 and similar rice cultivars have a tendency to develop foliar N deficiency. This N deficiency, in turn, results in low CER and CGR, and in early onset of senescence.

The patterns of tiller production and abortion across time (Fig. 6) were associated with planting method and N fertilizer regime in a manner similar to those of LAI shown in Figure 3. Phenologically, tillering began earlier in dibbled than in transplanted rice; this resulted in higher tiller number/area throughout the season. Tiller production was excessive, and thus was followed by a distinct abortion phase, particularly in direct seeded treatments.

Schnier et al (1990b) and Dingkuhn et al (1990b) showed that tiller production and abortion are linearly related to relative growth rate (RGR) throughout vegetative and early reproductive growth. Relative growth rates are generally high during initial growth, enabling high tillering rates during the establishment phase of direct seeded rice. On the other hand, this early period of high tillering potential in transplanted rice



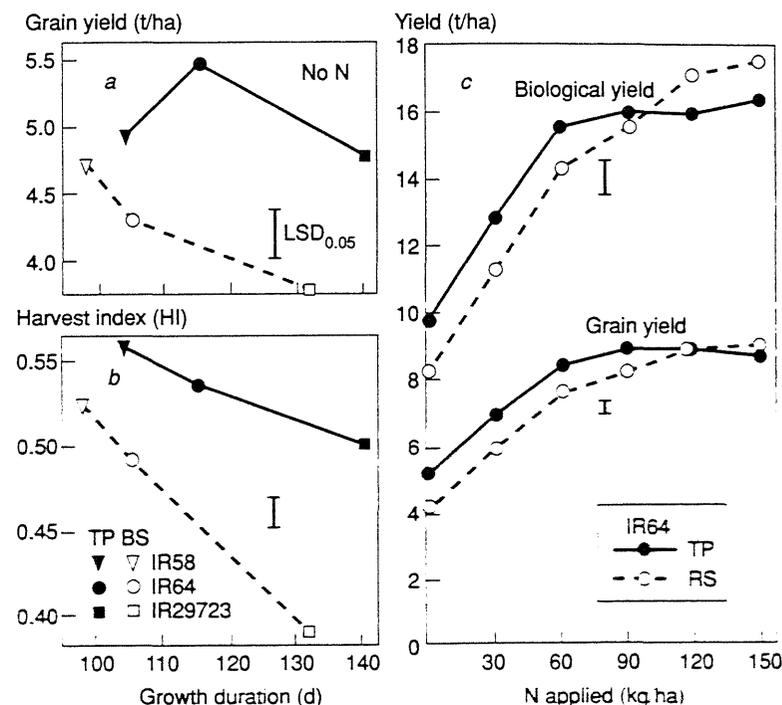
6. Tiller number of transplanted and direct seeded IR64 rice. Left: Transplanted and hill-wise dibbled rice having the same initial population (100 plants/m<sup>2</sup>) and planting geometry. Experiment 1. IRRIL 1986 dry season. Right: Transplanted (100 plants/m<sup>2</sup>) and row seeded rice (180 plants/m<sup>2</sup>) fertilized with 0, 90, and 150 kg N/ha. Experiment 4, Muñoz, Nueva Ecija, Philippines. 1988 dry season.

falls into a growth lag caused by transplanting shock. Consequently, transplanting shock not only delays, but also reduces tiller production.

As a result of the differences in tillering behavior, direct seeded rice in general had more panicles/area but fewer spikelets/panicle and, eventually, fewer grains/panicle (Schnier et al 1990a; Dingkuhn et al 1990d,e; data not presented). When N inputs were low, grain yields were lower in broadcast-seeded and row-seeded rice (Fig. 7) than in transplanted rice. However, with 120-150 kg N/ha, the differences in grain yield among planting methods disappeared. Direct seeded rice seems to require greater N resources than does transplanted rice, to escape the N deficiency during the late season that reduces yield. Potential yields, however, were not affected by crop establishment method.

Direct seeded rice consistently had a lower HI than transplanted rice (Dingkuhn et al 1990c, Schnier et al 1990a). The HI is positively associated with foliar N concentration and CGR at flowering (Dingkuhn et al 1990d,e; Akita 1989). As a general trend, differences in foliar N content, grain yield, and HI among planting methods were smallest for short-duration rice. The performance of direct seeded rice became increasingly inferior to that of transplanted rice as growth duration increased (Dingkuhn et al 1990b).

In summary, short-duration cultivar IR58 gave its highest yields when broadcast seeded and fertilized with 90 kg N/ha (Dingkuhn et al 1990b). For this cultivar, the vegetative growth phase in transplanted treatments (with productivity reduced by



7. a and b: Effect of growth duration on grain yield and harvest index of transplanted (TP) and broadcast-seeded (BS) rice. Experiment 5, Muñoz, Nueva Ecija, Philippines. 1988 dry season. c: Effect of fertilizer N rate on grain and biological yield of TP and row-seeded (RS) rice. Experiment 4, Muñoz, Nueva Ecija, Philippines, 1988 dry season.

transplanting shock) was too short to build up sufficient yield potential. However, dense populations resulted in superior vegetative growth and tillering, and, consequently, higher grain yields.

For medium-duration cultivar IR64, higher yields under direct seeding were achieved when the crop was dibbled and 2/3 of the N fertilizer band-placed at midseason (Schnier et al 1988, 1990b). This treatment combination resulted in relatively low tillering and high foliar N content, achieving high HI and grain yield. For long-duration cultivar IR29723, no treatment combination raised direct seeded grain yield above transplanted yield.

The current tropical semidwarf rice plant type gives maximal grain yields under transplanted culture if the vegetative growth phase is long enough to provide the necessary yield potential. Under direct seeded culture, high grain yields require greater N resources than they would with transplanting, and shorter growth duration to prevent vegetative overgrowth.

*Growth- and yield-limiting properties of the canopy at flowering.* The results presented in Figures 2-7 indicate that tiller and leaf area production are excessive in

direct seeded medium- and long-duration cultivars, while foliar N concentration is suboptimal during reproductive and ripening phases.

A canopy stratification study of broadcast-seeded and transplanted IR72 rice (experiment 6) at anthesis provided insights into limitations to yield. Grain yield was linearly correlated with CER at anthesis ( $r = 0.91^{**}$ ). Similarly, CER/productive tiller determined grain yield/panicle, with broadcast-seeded rice having a much lower CER/tiller and, thus, lower grain yield/panicle than transplanted rice.

Harvest index depended on N concentration in the flag leaf ( $r = 0.75^{**}$ ). The lower HI of broadcast-seeded rice, therefore, was probably partly caused by a lower flag leaf N concentration. Nitrogen limited leaf  $CO_2$  assimilation rates (CAR) for all leaf positions, including the flag leaf (which had the greatest N concentration). The contribution of lower leaf positions to yield was insignificant.

CER at anthesis was positively correlated with plant N uptake, N concentration, and CAR of the flag leaves, and negatively correlated with tiller number (Dingkuhn et al 1990e). A multiple, stepwise regression analysis of HI against various properties of the canopy at anthesis identified CER and N concentration of the flag leaf to be positively correlated with HI and LAI, and N concentration of the lower leaf positions to be negatively correlated with HI.

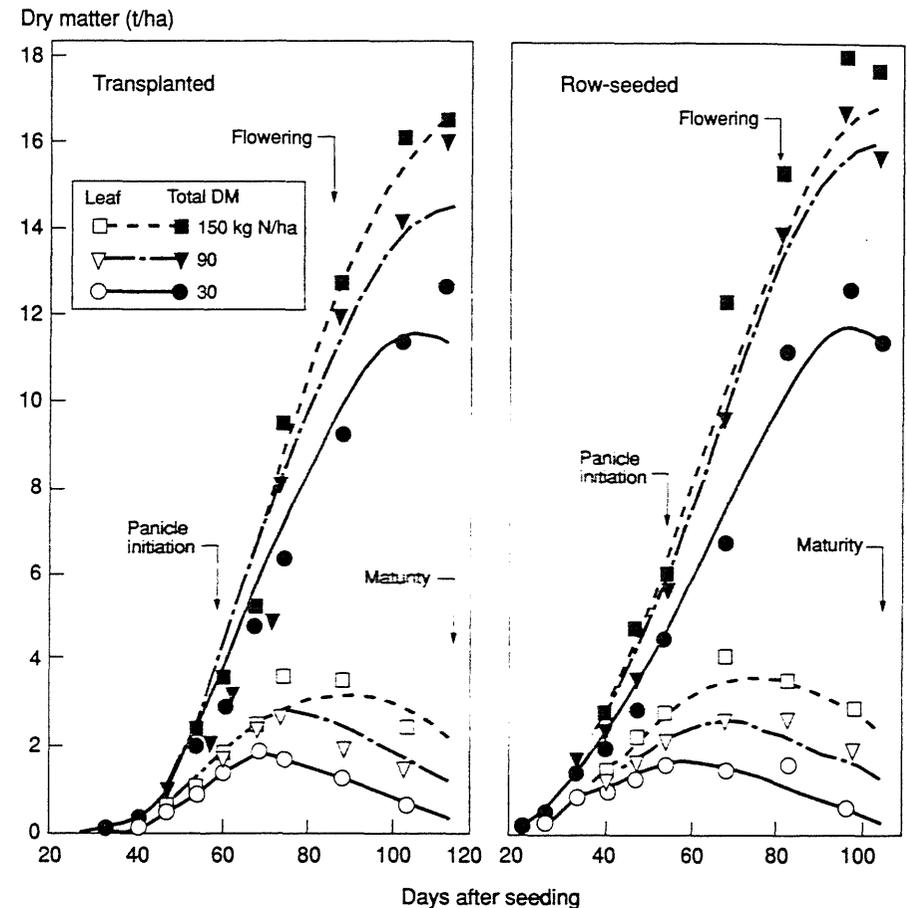
We conclude that to maximize HI and grain yields for broadcast-seeded rice, a moderate tiller number and LAI in combination with high foliar N concentration are required. Much of the foliar N should be located in a photosynthetically active form in the flag leaf, while N contained in the lowest leaf positions should be made available for growth of grain. In other words, spikelets should receive their N from the lower plant parts and their C from the uppermost leaves.

An additional source of carbohydrates for spikelet filling is the reserves located in the stem and leaf sheaths (Chaturvedi and Ingram 1990). If direct seeded rice plants are to allocate less dry matter to foliage while having high CER, an expanded reserve organ for assimilates produced prior to spikelet filling is needed.

The potential to further improve dry matter production and grain yield of irrigated rice does exist, particularly when the crop is direct seeded. The necessary changes in the architecture of the crop's canopy, however, are difficult to achieve through alternative cultural practices alone (Schnier et al 1990b; Dingkuhn et al 1990d,e).

### Simulation of rice genome modifications

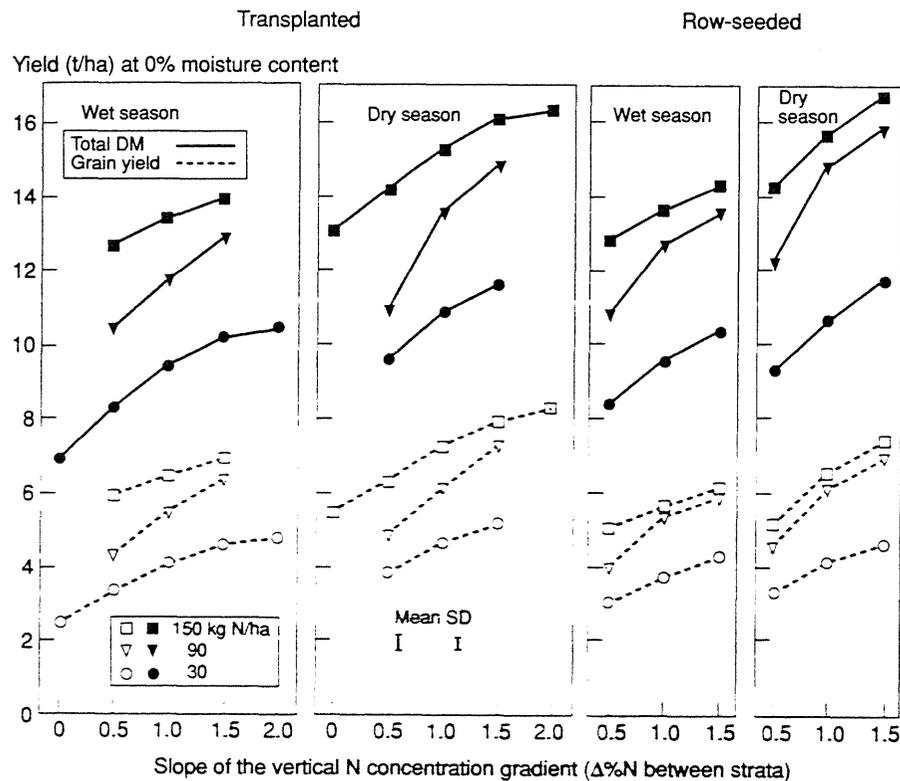
The performance of the L3QT model in computing crop growth and yield was evaluated by simulating all trials of experiment 4. Figure 8 shows measured and simulated growth curves for three levels of N. Intermediate growth parameters evaluated were average leaf N concentration, CER, leaf area dynamics, tillering, and HI (data not presented). The agreement of trends in all cases and of absolute values in most cases gave us the confidence to conclude that L3QT can be used to explore the benefits of different new plant type designs for yield and nitrogen use efficiency. We



8. Simulated (solid and dashed lines) and measured (points) dry matter accumulation aboveground and in the leaves of transplanted and row seeded IR64 rice fertilized with 30, 90, or 150 kg/ha. Experiment 4, Muñoz, Nueva Ecija, Philippines, 1988 dry season.

investigated several features; the most promising are presented here. Most of these features affect production, irrespective of crop establishment method.

*The N gradient.* The impact of modifying the vertical N concentration gradient in the foliage across three strata was investigated. Growth kinetics and dry matter yield were simulated for six N rates and two crop establishment methods (transplanting and row seeding), for constant gradients from 0 to 4% (differences between the upper and central and the central and lower strata of 0-2% N, with the upper layer having the highest concentration). Figure 9 shows the mean effects and standard deviation of these gradients on the biological and grain yields for transplanted and row-seeded IR64 rice crops, fertilized at three levels, in the wet and dry seasons. Nitrogen distribution



9. Simulated mean dry matter (DM) and grain yields for wet and dry seasons across 1979-88 for transplanted and row-seeded IR64 rice, fertilized with 30, 90, or 150 kg N/ha. The difference in foliar N concentration between the top and bottom strata was treated as a variable. Vertical bars indicate standard deviation. IIRRI, 1979-88.

appears to have a significant effect on both biological and grain yields; the effects are roughly similar in both crop establishment methods and across N regimes and seasons. This is in particular brought about by the higher productivity per amount of leaf N during the reproductive period.

A similar effect can be achieved by increasing the total amount of N in the crop, but this crude solution would require more fertilizer and would be less efficient. It is therefore suggested that increasing the vertical N gradient in the foliage offers an opportunity to increase yields at a constant level of N input. A canopy stratification study using IR72 rice (Dingkuhn et al 1990d,e) gave empirical support to these predictions: grain yields were correlated positively with flag leaf N content; N in the lower leaf strata had little or no impact.

The numerical value of the gradient might depend on the level of N applied to the crop. To test this, we determined the best fit of simulations to the experimental data.

When the N rate was low to moderate (30-90 kg N/ha) in row-seeded rice and low to high (30-150 kg N/ha) in transplanted rice, the best fit was for a difference of 1.0-1.25% N (Table 1). For zero N (controls), smaller gradients (0.5-0.75% N) gave the best fit. With high inputs (120-150 kg N/ha), steeper gradients (1.5-1.75% N) fitted the row-seeded treatments best.

This suggests that the vertical foliar N gradient depends on the N rate. Downward adjustment of the N concentration in the leaves that become shaded could be the mechanism that leads to a gradient. Optimizing the efficiency of absorbed N for crop production would result from the process.

Further studies are needed to determine the vertical foliar N concentration gradient in rice crops, and to establish its responsiveness to N inputs, development stage, LAI, and radiation levels. The distribution of N within leaf blade, and thus, the leaf angle, will affect the gradient as well. There may be significant differences among rice varieties.

We have not found reports on the significance of this aspect of photosynthesis and N distribution, but the topic invites further analysis by modeling and field research. No difference between strata makes the N concentration of layers equal. This case corresponds to a model in which the N concentration of all leaves equals the measured average value (e.g., Van Keulen and Seligman 1987). However, this can lead to a significant underestimation of crop yield. In our examples, underestimation amounted to about 1 t/ha (Fig. 9).

*Modifications in the leaf-stem ratio.* Because maximum leaf area in the row-seeded crop appeared to be excessive, we simulated the consequences of producing fewer leaves. The pattern of assimilate partitioning between leaves and stems is an important determinant of potential production (Potter and Jones 1977). In its basic version, L3QT uses a partitioning pattern where during early vegetative growth, new assimilates not partitioned to the root and not consumed by respiration processes are divided equally between foliage and stem (pattern A in Figure 1). The fraction consumed for leaf growth subsequently decreases to zero at booting. This is followed by activation of the reproductive sink, which then attracts all new assimilates and mobilizable reserves until either the sink is saturated or the source exhausted.

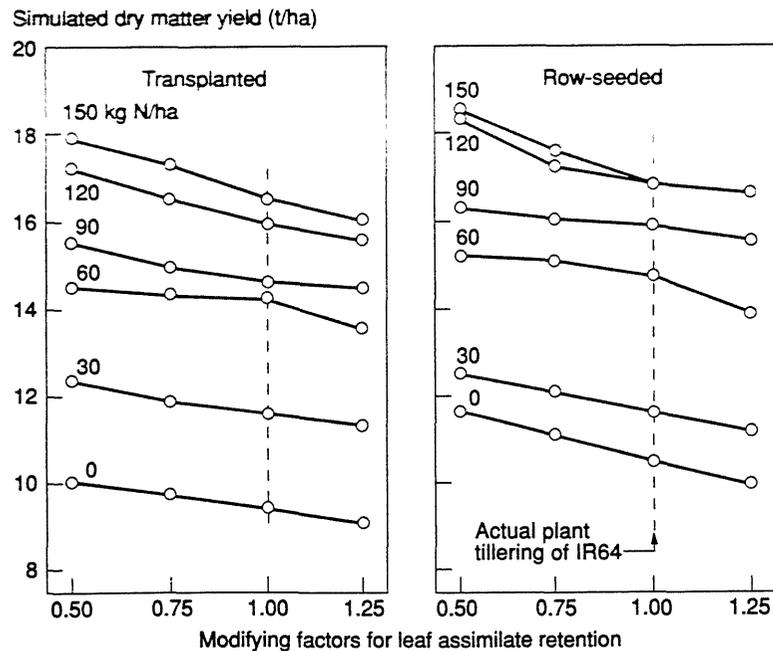
Table 1. Simulated vertical N concentration gradients between top and bottom strata in the foliage, giving the best fit to growth and yield of transplanted and row-seeded IR64 rice (experiment 4).

N applied (kg/ha)	Gradient (delta % N)	
	Transplanted	Row-seeded
0	1.5	1.0
30	2.0	2.0
60	2.5	2.5
90	2.5	2.5
120	2.5	3.0
150	2.5	3.5

Two types of modifications of assimilate partitioning were evaluated: modifying the leafiness of the crop by an overall reduction or increase of the assimilate fraction for leaves, and modifying leaf area dynamics by an increase in the fraction for leaves in young plants and a reduction later.

Simulation of an overall lower or higher fraction of assimilates for leaf growth (pattern A in Figure 1 multiplied by 0.5, 0.75, or 1.25) showed consistent but small effects on dry matter production (Fig. 10). The least leafy canopy gave the highest dry matter yields at all N rates and for all crop establishment methods. Reduced leaf production, with the resulting higher N concentration in the foliage, can be expected to moderately improve biological yields (transplanted rice, 6.0%; row-seeded rice, 7.3%). The benefit comes from greater CO<sub>2</sub> assimilation and reduced maintenance respiration during reproductive growth, which exceeds the loss brought about by a delayed establishment of full crop cover.

To approximate a leaf production pattern that would lead to maximum crop growth rates, partitioning patterns B to F in Figure 1a were tested for transplanted and row-seeded rice at low, medium, and high N levels. Partitioning patterns that enhanced leaf growth during early stages (until 45 DAS), with a subsequent sharp decline in



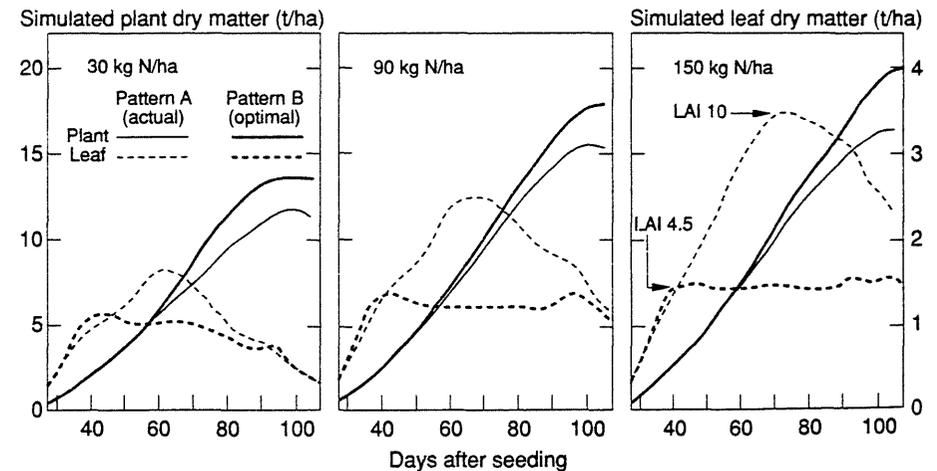
10. Simulated dry matter yields of transplanted and row-seeded flooded IR64 rice at various N rates, treating foliar assimilate retention for leaf growth as variable. Factor 1.0 left the pattern of foliar assimilate retention (pattern A in Fig. 1) unchanged. Factor 0.5 reduces relative leaf growth by 50% and enhances assimilate export accordingly.

Table 2. Simulated effects of assimilate partitioning patterns (A-F) on biological (BY) and grain (GY) yield of transplanted (TP) and row-seeded (RS) flooded rice (experiment 4).\*

	Yield (t/ha)											
	A		B		C		D		E		F	
	GY	BY	GY	BY	GY	BY	GY	BY	GY	BY	GY	BY
TP 30 N	5.2	11.4	5.4	11.2	<u>6.0</u>	<u>13.2</u>	5.8	12.7	5.7	12.6	5.3	12.8
TP 90 N	7.8	14.4	7.1	13.7	<u>8.5</u>	<u>16.9</u>	7.8	15.9	7.4	15.1	7.0	14.7
TP 150 N	8.1	16.5	7.8	14.9	<u>9.7</u>	<u>18.6</u>	9.5	18.5	8.7	17.4	8.1	16.6
RS 30 N	4.4	11.3	5.2	12.3	<u>5.3</u>	<u>13.1</u>	5.1	12.7	4.7	12.0	4.5	11.5
RS 90 N	6.9	15.8	<u>7.6</u>	<u>17.7</u>	7.2	17.5	7.0	16.7	6.9	16.0	6.9	15.8
RS 150 N	6.7	17.1	<u>8.1</u>	<u>19.9</u>	7.6	19.3	7.3	18.5	7.2	17.6	6.9	17.1

\*Pattern A represents the best fit to empirical IR64 data. Patterns B to F are hypothetical patterns, as shown in Figure 1a. Underlined results indicate the apparent optimal partitioning pattern for the treatment.

production of new leaves, increased grain yield by 10-25% (0.8-1.6 t/ha) (Table 2). Growth curves for the actual (A) and the optimized pattern (B for row-seeded, C for transplanted rice) of assimilate partitioning were significantly different (Fig. 11). The optimized patterns exhibited faster canopy establishment, followed by maintenance of a low to moderate leaf mass (1.0-1.6 t/ha, equivalent to a LAI of 2.9-4.6, depending on N rate) for much of the season. Foliar N concentration remained higher than that in the actual pattern throughout the reproductive phase and well into the ripening phase (data not presented); photosynthesis and dry matter production were particularly high during mid- and late season.



11. Simulated dry matter accumulation aboveground and in the leaves of row-seeded IR64 rice at three N rates. Simulation used assimilate partitioning pattern A (actual partitioning) and an optimized pattern (B for row-seeded rice, C for transplanted rice as shown in Figure 1a).

Such an improved partitioning pattern requires increased retention of assimilates in the foliage before PI, but a halt in leaf production once a moderate LAI is reached. The period with an increased rate of leaf production coincides with the main phase of tiller production. Reduced tillering, a desirable trait in cultivars adapted to direct seeding (Dingkuhn et al 1990a, Schnier et al 1990b), would free assimilates for leaf formation. Research is needed to determine whether the improved partitioning pattern is biologically possible.

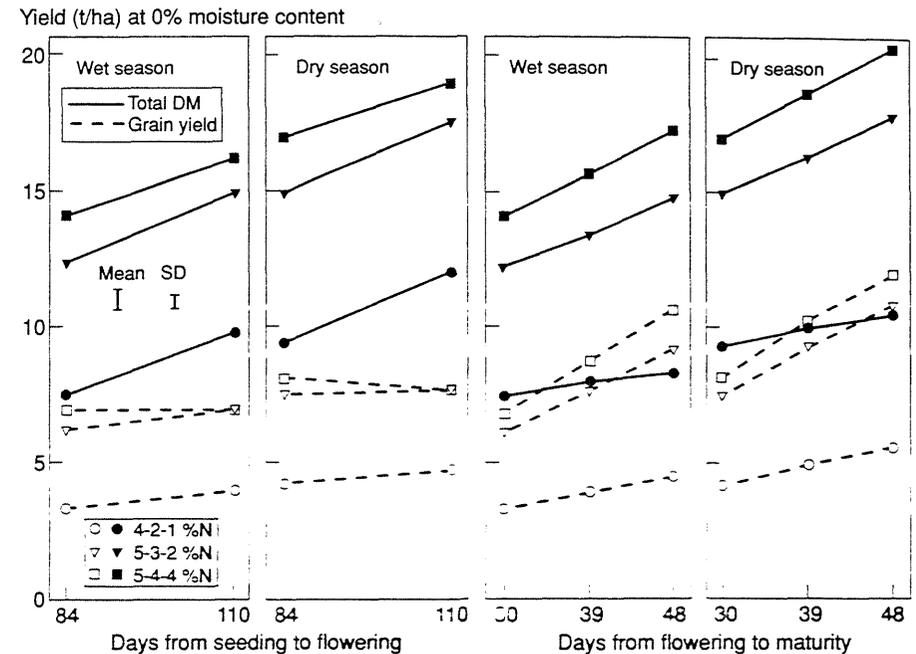
*Extended vegetative and ripening phases.* The durations of the vegetative and ripening phases of rice depend on genotype, temperature, and daylength (vegetative phase only). Most modern, high-yielding rices grown under tropical conditions are photoperiod-insensitive, have a growth duration of 100-130 d, and ripen 25-30 d after anthesis. Because temperatures are higher in the tropics, this ripening phase is short compared with that of rice and other cereals grown in the temperate zone (Penning de Vries et al 1989, Angus et al 1981). Because there is a maximum rate of grain growth, the short duration of ripening puts a relatively low ceiling on the potential yield of tropical rice. Lengthening that phase raises the ceiling. Temporary storage of assimilates in the stem can carry over some photosynthesis from before flowering to grain formation, so that a longer vegetative phase can be beneficial as well.

We simulated the effect of extending the vegetative and ripening phases by 30 and 60%. Growth patterns were compared in crops with rapidly declining average foliage N concentrations (4% N initially, 2% at flowering, and 1% at maturity), slowly declining concentrations (5, 3, and 2%, respectively), and consistently high concentrations (5, 4, and 4%, respectively). The first case resembles a crop fertilized with N at a moderate level; the second, a crop fertilized at a high rate. The last case shows the yield that would be attained if the foliage did not have to provide N to the grain.

Extending the duration from seeding to flowering by 30% (from 84 to 110 d) strongly enhanced biological yield but did not significantly affect grain yield (Fig. 12), and HI was consequently lower. Such results agree with field observations (Dingkuhn et al 1990b). The expected benefit from extra reserves was lost to increased maintenance respiration.

Extending the ripening phase from 30 to 39 or 48 d improved both biological and grain yields, provided that foliar N concentration remained high. Prolonging the ripening phase by 9 d improved simulated grain yield by up to 25%; prolonging it by 18 d improved yield by 50%, leading to top grain yields of 9.5-11.5 t/ha with 39 d ripening and 11.5-13.5 t/ha with 48 d ripening (expressed at 14% moisture). The HI increased to about 0.62. We suggest that more attention be given to prolonging the reproductive phase of tropical rice and to keeping foliar N concentration high.

A longer reproductive phase requires lengthening the period of spikelet filling. For our simulation runs, the sink capacity of the panicle was set to be nonlimiting. The maximum size of individual rice grains appears to be genetically fixed, with the maximum usually approached near maturity. An improved crop should therefore have an increased number of active spikelets filled in a staggered manner or at a slower rate. To a lesser degree, staggered filling is already realized in existing rice cultivars; they



12. Simulated mean effects of a hypothetical prolongation of the vegetative growth phase by 30% and the ripening phase by 30 or 60% on dry matter and grain yields in IR64 rice over 10 yr, (1979-88). Foliar N concentration was assumed to decrease from crop establishment through heading to maturity following the patterns 4-2-1, 5-3-2, or 5-4-4% N (wt/wt).

exhibit early maturation in distant spikelets and late maturation in proximal spikelets and spikelets of higher order (Dingkuhn, unpubl. results).

*Combined improvements.* If the suggested crop improvements were combined in a single simulation run, still higher yields would be predicted. However, we refrained from doing so because further discussion of the individual aspects is needed first, and because some improvements may be physiologically conflicting.

Most of the simulated yield increases are brought about by combining a longer duration of the green leaf area and sustained photosynthesis rate. Since the N concentration of the grain should not be affected, the increase in yield implies that grains require a proportional amount of extra N. However, most N in the grain is currently provided through translocation from the leaves, where it is needed for photosynthesis. To avoid self-destruction (Sinclair and de Wit 1975) and to realize a major increase in grain yield, it is imperative that alternative sources of N be utilized, such as reserves in stems (Penning de Vries et al 1990) or sustained uptake. Research on N redistribution mechanisms and their variability among rice cultivars is needed.

Another aspect of rice with an improved assimilate source during reproductive growth that needs attention is sink capacity. Although an improved N status between

PI and heading (which is one of the characteristics of the proposed plant types) usually also increases the number of spikelets initiated and differentiated (Dingkuhn et al 1990d), the potential sink size of current cultivars may not match the assimilate supply offered in new plant types. Larger panicles with more spikelets and a lower percentage of degenerated spikelets are required.

## Conclusions

Field experiments showed that modern, high-yielding semidwarf rices can yield up to 9 t/ha (at 14% moisture) under both transplanted and direct seeded flooded culture. A direct seeded crop, however, requires greater N input than a transplanted crop to achieve its maximum yield. This difference is associated with overproduction of vegetative material (leaves, tillers) in direct seeded rice during the period of linear growth, resulting in dilution of resorted N and, subsequently, foliar N deficiency. Consequently, direct seeded rice had lower growth rates during the ripening phase, and earlier senescence and lower HI than transplanted rice. The higher planting density of a row- or broadcast-seeded crop and the absence of transplanting shock accounted for these characteristics. Although alternative cultural practices can improve yield and fertilizer N efficiency, new plant types might be more effective.

Simulations indicate that changes in the canopy would enable both direct seeded and transplanted flooded rice to achieve higher yields. The beneficial effects, however, would be greater in direct seeded rice because, under transplanted culture, growth characteristics already show a certain resemblance with the projected optimum (lower tillering, less leaf area, higher foliar N concentration). Assuming that the absolute amount of N allocated to the foliage remains unchanged, the following modifications of N and assimilate partitioning would improve yields:

- prolong the ripening phase,
- maintain a high N concentration in the leaves,
- increase the slope of the vertical N gradient in the foliage,
- allocate more assimilates to leaf growth in young crops,
- reduce leaf growth during the late vegetative and reproductive phases, and
- expand the assimilate storage capacity of the stems.

With respect to broadcast-seeded rice, these improvements should be combined with the following plant characteristics:

- improved seedling anchorage,
- reduced tillering ability,
- longer life span and larger size of flag leaves, and
- larger panicles and higher sink capacity.

Simulation results indicate that the current yield barrier observed in modern tropical rices can theoretically be raised substantially, provided that it is possible to generate new plant types with modified N and assimilate partitioning patterns and/or a more productive and longer ripening phase. Grain yield increases from a combination of these changes would probably exceed 25%. The biological feasibility of the concepts

outlined, however, requires verification through physiological studies and analyses of the existing rice gene pool.

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## Notes

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