

Possibility of Increasing Yield Potential of Rice by Reducing Panicle Height in the Canopy.

I. Effects of Panicles on Light Interception and Canopy Photosynthesis

T. L. Setter^{AB}, E. A. Conocono^A, J. A. Egdane^A and M. J. Kropff^A

^AInternational Rice Research Institute, PO Box 933, Manila, Philippines.

^BCorresponding author, facsimile: +63 2 891 1292.

Abstract. A new rice (*Oryza sativa* L.) plant type is proposed which is aimed at greater light interception by the leaves during grain filling and reduced susceptibility to lodging. This plant type is based on lowering panicle height in the canopy so that leaves are able to intercept more radiation. Panicle height of four cultivars with high yield potential ranged from 80 to 95% of canopy height at 14 days after flowering (DAF). Harvested panicle area index of two of these which were two tropical cultivars amounted to 0.45–0.57 m² m⁻², while the leaves above the panicles intercepted only 4–12% incident radiation at midday in these cultivars at 14 DAF. The potential impact of lowering panicle height in the canopy on canopy photosynthesis was evaluated by panicle removal. When panicles were removed, the irradiance at the bottom of the panicle layer of the canopy increased from 52 to 80%. At 11 DAF, net canopy photosynthesis of two cultivars similarly increased by 42–52% following removal of panicles. Increases in canopy photosynthesis were mainly due to increased light interception by leaves within the canopy since there were little or no changes in canopy dark respiration or in net leaf photosynthesis rates at the same irradiance following panicle removal. Optimum panicle height in the canopy and the effect of different panicle area index is further examined using a physiological model for light competition, INTERCOM. Reduced panicle height in the canopy is discussed in terms of considerations for and impacts of lowering panicle height in the canopy on canopy photosynthesis and yield of rice.

Introduction

Increases in yield potential of rice have resulted in nearly a doubling in productivity during the 1960s and 1970s. This has largely resulted from changes in morphology from tall, very leafy, traditional cultivars to the semi-dwarf cultivars with erect leaves such as IR8 (Chandler 1969). Although selections were based on short stature, lodging resistance and efficient partitioning between grain and straw (Takeda 1984), breeders were unintentionally selecting for improved canopy architecture, light penetration and other favourable agronomic characteristics (reviewed by Peng *et al.* 1994). Subsequently, additional improvements were incorporated in relation to tolerance to pests and diseases with the development of IR36 in 1976; this was once the most widely used rice cultivar in the world, accounting for over 11 million hectares of sown rice (Plucknett *et al.* 1987). There has been little progress in increasing yield potential of rice since the 1970s (Kropff *et al.* 1994). While current emphasis on rice breeding at the International Rice Research Institute focuses on the potential for developing hybrid rice and tropical japonicas (Peng *et al.* 1994), there are less

immediate prospects for the inbred indica rice cultivars (reviewed by Setter *et al.* 1994). This is at least partly due to the uncertainty about which morphological or physiological traits limit yield potential of modern high yielding rice cultivars.

Light is well known to limit crop canopy photosynthesis of rice at a high leaf area index (LAI), even at irradiation levels approaching full sunlight (Penning de Vries *et al.* 1989; Kropff 1993). At a high LAI, erect leaves allow deeper penetration and more even distribution of light in the canopy. The importance of this is demonstrated in past increases in yield of rice where leaves were left erect or made droopy by attaching lead beads; plants with erect leaves had up to 80% increases in canopy photosynthesis (at approx. 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR) and 35% increases in grain yield (Tanaka *et al.* 1969).

The importance of leaf angles and light distribution within a canopy is supported by simulation with crop models. Crop photosynthesis of a canopy with erect leaves was about 20% higher than that of a canopy with perfectly horizontal leaves at a LAI of 10 (van Keulen 1976).

Simulation with other models demonstrates that a combination of erect upper leaves and horizontal lower leaves gives the optimum structure for crop photosynthesis (Duncan 1971), although this depends on LAI (Kropff 1993).

More recent research in Japan indicates that there may be additional potential for increases in crop photosynthesis by selection for leaves with a V-shape rather than flat architecture (Sasahara *et al.* 1992). The V-shaped leaves are thought to enable greater canopy photosynthetic capacity due to several factors including decreased mutual shading and greater light penetration into the canopy. Photosynthetic rates of single leaves were reported to be almost the same as for a reference cultivar and the parents, i.e. the increased yield was presumably related to an improved canopy structure rather than to the leaf structure. In comparing cultivars which differ in such leaf structure, it will be necessary to evaluate canopy photosynthesis rates to conclude that this architecture will be an important factor to select for in future programs aimed at increasing yield potential.

While light penetration into the canopy is greatly enhanced in modern high yielding cultivars with erect leaves, the most important time of carbon assimilation for grain filling is after flowering. This is because approximately 75% of carbon for grain filling in rice comes from carbohydrate accumulated before flowering, while only about 25% comes from accumulated carbohydrate at flowering (based on ^{14}C assimilation, Cock and Yoshida 1972). One of the major obstructions to light interception by leaves during grain filling is the developing panicles, especially in cultivars where the panicle is high in the canopy; this applies to the majority of commercial rice cultivars. The contribution of panicles to canopy photosynthesis is examined in the Discussion.

In a crop of 6 t ha^{-1} the panicle area represents 0.6–0.9 $\text{m}^2 \text{ m}^{-2}$ based on the surface area of harvested panicles (Kropff 1993; Kropff *et al.* 1994). A detailed model of interplant competition for light capture, INTERCOM (Kropff 1993), was used to evaluate the effects of light interception by panicles on canopy photosynthesis. The INTERCOM model predicted that panicles in the top 10 cm of a rice canopy with a LAI = 4 would reduce canopy photosynthesis by 25% based on the light they intercepted, while panicles positioned 20 cm below the top of the leaves would reduce canopy photosynthesis by only 10% relative to canopies without panicles (Kropff 1993; Kropff *et al.* 1994). These values assume no gross photosynthesis by panicles and are based on a yield of only 6 t ha^{-1} during the wet season. At 10 t ha^{-1} yield levels, panicle area indices of about 1.2 have been measured (Kropff and Cassman, pers. comm.). In areas where rice grain yield approaches 15 t ha^{-1} such as the Yunnan Province, China (Gaoqun Yang, pers.

comm.) and Yanco, Australia (L. Lewin, pers. comm.) panicle area indices would be even greater, and a large reduction in canopy photosynthesis would be expected.

Experiments presented here are aimed at quantifying the light interception of panicles and by leaves above and below the panicles in full-grown plants in the field. Experiments to evaluate the effects of panicles on light interception and leaf and canopy photosynthesis were conducted mainly with two modern high yielding cultivars, IR36 and IR72, in treatments with and without panicle removal. Effects are then used to evaluate the optimum panicle height in a rice canopy using the INTERCOM model.

Materials and Methods

Plant Material and Growth Conditions

Two modern high yielding cultivars of rice (*Oryza sativa* L.), IR72 and IR36, which are adapted to tropical environments, were used in experiments in 1994. Two additional cultivars from temperate environments in Australia, Amaroo and YRL 39, were also used in one experiment. Plants were grown during the dry season in the field at the Central Research Farm of the International Rice Research Institute (latitude $14^{\circ}13' \text{N}$, longitude $121^{\circ}15' \text{E}$). Fertiliser (180 kg N ha^{-1}) was applied (as urea) in a triple split basally, at mid-tillering and at panicle initiation. Seedlings were transplanted at $5 \times 5 \text{ cm}$ spacing with one plant per hill. Canopy height was measured as the height from the ground to the highest point in the canopy, whether due to leaves or panicles, under natural conditions. Panicle height was measured as the height from the ground to the top of the panicle.

Daily minimum and maximum temperatures with standard error of the mean (\pm s.e.m.) were 24.1 ± 1.0 and $32.9 \pm 0.6^{\circ}\text{C}$ respectively; global radiation during grain filling was $24.8 \pm 3.8 \text{ MJ m}^{-2} \text{ day}^{-1}$ with 9.7 ± 1.4 bright sunshine hours each day. In several instances, variations in rainfall or in irradiance of up to $1800 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PAR in the field prevented measurements from being taken all at identical times.

Leaf and Canopy Photosynthesis and Respiration

Leaf and canopy photosynthesis were measured using a LI-COR 6200 portable photosynthesis system (LI-COR, Nebraska, USA) between 0930 and 1600 hours at the irradiance stated in the tables and figures. Canopy photosynthesis was measured using a canopy frame $80 \times 80 \text{ cm}$ and 130 cm high covered with Mylar film (Hilcor Plastics, Whittier, CA, USA; 0.1 mm thickness) and built with a removable top to facilitate manipulations and gas equilibration of the canopy. Gas circulation within the canopy was provided using four 120 mm diameter, battery powered fans (Panflo model FBH12G12L, Matsushita Electric, Japan). The portable photosynthesis system was used as a gas analyser by placing the opened leaf chamber inside the canopy frame during measurements. Rapid gas mixing within the chamber was indicated by injecting approximately 100 mL CO_2 into the chamber and attaining a new CO_2 equilibrium within 10 s after injection. Canopy photosynthesis was measured several times for each replicate over 15 s intervals; measurements commenced and ended when chamber CO_2 was approximately 320 and 300 ppm respectively (cf. Dingkuhn *et al.* 1990).

For treatments where panicles were excised at the peduncle, the canopy was allowed to equilibrate for approximately 2 h after panicle excision before photosynthesis or respiration was measured. This was because of large fluctuations in flag leaf and canopy photosynthesis and dark respiration which occurred over 30 min after panicle excision in tropical conditions and over 60 min after panicle excision in temperate conditions in Australia (Setter, Egdane, Williams, Lewin and Conocono, pers. comm.). Single leaf photosynthesis measurements were made by exposure of the leaf perpendicular to the sun using a 0.25 L leaf chamber (LI-COR).

Leaf and canopy respiration were measured by placing leaves or canopies in the dark for at least 5–10 min before measuring the rate of CO₂ production. A double shade was erected for respiration measurements. This was particularly necessary for canopy respiration so that canopy temperatures were never more than 1–3°C above ambient. There was a significant increase in flag leaf respiration of two- to five-fold during the first 2 min following transfer of the plants to darkness (cf. Thomas *et al.* 1993 for cotton), and this appeared to be related to the leaf photosynthesis rate immediately prior to dark treatments. However, 5–10 min after transfer to darkness the leaf respiration rates were not significantly different for the next 30–60 min (data not shown); therefore, 5–10 min dark pretreatments were used for routine measurements of respiration.

Light Interception

Light interception (PAR) was measured with a Sunfleck ceptometer with a 80 cm long quantum sensor bar (model SF-80, Decagon Devices Inc., Washington, USA). The percentage light interception was calculated relative to incident radiation: (1) by the canopy, (2) by leaves above the panicles, and (3) by leaves and panicles within the panicle layer of the canopy as below:

- (1) $100 (\text{PAR above canopy} - \text{PAR at bottom of canopy}) / (\text{PAR above canopy})$;
- (2) $100 (\text{PAR above canopy} - \text{PAR at top of panicles}) / (\text{PAR above canopy})$; and
- (3) $100 (\text{PAR at top of panicles} - \text{PAR at bottom of panicles}) / (\text{PAR above canopy})$.

The 'top' and the 'bottom' of panicles are defined here as the highest and the lowest point of any part of the panicles in the canopy, while the 'panicle layer of the canopy' is the layer of the canopy ranging from the top to the bottom of panicles. The percentage light interception specifically by panicles with the height of the bottom of panicles x cm above the ground was calculated by:

- (4) $100 (\text{PAR at } x \text{ cm after panicle excision} - \text{PAR at } x \text{ cm before panicle excision}) / (\text{PAR at } x \text{ cm after panicle excision})$.

At least three samples were measured in three to four replicate plots for light interception measurements of each cultivar.

Leaf and Panicle Area

Leaf or panicle area was measured using an area meter (LI-COR, model 3100) using four to eight replicates. Panicle area was measured using freshly harvested panicles and also by aerial photography of panicles in the crop. Panicles needed to be closed up, i.e. with one layer of spikelets, during measurements with the area meter at least partly since the meter underestimated or did not

quantify the rachis area; closed, open and dissected panicles gave 100, 92 and 52% surface areas respectively (LSD [$P = 0.05$] = 9.9). For aerial photography, 0.5–1.0 m² of the rice crop was photographed from a height of approximately 1.5 m perpendicularly above the canopy. Photographs were enlarged to 200 × 250 mm and a transparency was used to shade panicle area. Shaded areas on transparencies were then measured in an area meter and values were calibrated relative to the size of the plot in the photograph. There were three to four replicates for each harvest and cultivar.

Modelling

The subroutines for instantaneous light competition of the ecophysiological simulation model INTERCOM were used to quantify the relationship between panicle height and canopy photosynthesis. The model and its evaluation have been described in detail by Kropff (1993). This model is based on the underlying physiological processes of competition for the limited resources of light and water between the species or organs, and the way these utilise the amounts taken up for dry matter production. The absorbed radiation is calculated in relation to plant height on the basis of (leaf) area of the competing species or organs and the distribution of the area over the height of the canopy. The profile of CO₂ assimilation in the canopy is calculated using the photosynthetic CO₂ assimilation for individual leaves. In this study, the panicles were treated as a second species. The key parameters in the canopy photosynthesis model are the light extinction coefficients and the parameters indicating the distribution of the leaf or panicle area over the height of the canopy. The variables used in the model are latitude (14°), Julian day (100), hour of the day (1200 hours) and incident radiation (2050 μmol m⁻² s⁻¹ (PAR)), measured LAI and panicle area index (PAI), the height of the top and the bottom of the panicles and leaves in the canopy, and the light response characteristics of leaves taken from Kropff *et al.* (1993). For panicles, the light response characteristics were assumed either half or zero relative to leaves. The INTERCOM model calculates the fluxes of direct and diffuse PAR and the angle of the direct sun beams. This is important for precise calculations of light penetration in the canopy. The INTERCOM model was used here rather than ORYZA1 (Kropff *et al.* 1993) since the latter does not simulate the competition for light among two or more different species or organs (see Discussion in Kropff 1993).

For Fig. 4, the simulations are based on calculated light extinction coefficients (k) of 0.9 for panicles and 0.4 for leaves. These k values are calculated using data for light absorption at different heights in the canopy before and after panicle removal using formulae derived from Beer's Law (Appendix 1).

Results

Plant, Panicle Height and Area and Light Interception of Panicles

Canopy height of IR72 was about 5 cm greater than IR36 at flowering; however, there was a 13 cm difference in panicle height between these two cultivars, being 75 ± 1 and 62 ± 1 cm respectively at 7–10 days after flowering (DAF).

Differences in panicle height between cultivars persisted to 14 DAF (Table 1). Panicles were 86 and 80% of the height of canopies for IR72 and IR36 respectively (calculated from Table 1). Differences in panicle height were not due to differences in panicle length, since panicle length in both IR72 and IR36 was about 20 cm (Table 1). The highest relative panicle height in the canopy was observed for an Australian rice cultivar, Amaroo, with a panicle height of 64 ± 1 cm which was 95% of canopy height. Another Australian cultivar, YRL 39, had panicles which were 82 ± 1 cm high and 83% of canopy height (at 14 DAF).

For yields of about 7 t ha^{-1} (Table 1), the harvested panicle area increased from zero prior to emergence to 0.45 and $0.6 \text{ m}^2 \text{ m}^{-2}$ for IR72 and IR36 respectively within 7–10 DAF (Fig. 1). A harvested panicle area of $0.51 \pm 0.04 \text{ m}^2 \text{ m}^{-2}$ for Amaroo at 14 DAF was similar to values for IR72 and IR36. Panicle area based on aerial photography was usually less than half of the values for harvested panicle area, and values were more variable within treatments (Fig. 1). For IR72, which had panicles high in the canopy, there was an increase in panicle area with time as measured by aerial photography (Fig. 1).

Light interception by the leaves above the panicles at 14 DAF was only 4 and 12% of incident radiation for IR72 and IR36 respectively, while light interception within the layer that the panicles occupied was 65–81% of incident radiation for both cultivars (Table 1). Light interception in the panicle layer was 81 and 65% for IR72 and IR36 respectively, relative to the irradiance above the canopy (Table 1). Similar values occurred for light interception by these different layers at 7, 10 and 20 DAF for IR72, and at 10 and 19 DAF

for IR36 (data not shown). In another experiment where irradiance was measured at the bottom of panicles of IR72 and IR36 at 19–20 DAF, when panicles were removed the irradiance at that height increased by $52 \pm 10\%$ and $80 \pm 19\%$ respectively. The increase in irradiance in the canopy following panicle removal was also used to estimate light interception by panicles of IR72 and IR36, which accounted for 35 ± 3 and $37 \pm 6\%$ of light absorbance in the panicle layer of the canopy. The light extinction coefficients for panicles and leaves of IR72 were approximately 0.9 and 0.4 respectively (Table 2).

Leaf and Canopy Photosynthesis

When panicles were excised and removed there was a short-term fluctuation in net canopy photosynthesis over 15–30 min, and this also occurred for net leaf photosynthesis of single flag leaves. This fluctuation in net flag leaf photosynthesis was at least partly the result of transient changes in leaf respiration (data not shown); hence all measurements after panicle excision were made about 2 h after excision.

Net canopy photosynthesis of IR72 and IR36 on a ground surface area basis with time during flowering is shown in Fig. 2A and B, respectively. When panicles were removed in both IR72 and IR36 at two different times during grain filling, there were always large increases in net canopy photosynthesis relative to canopies with panicles. Net canopy photosynthesis for IR72 and IR36 without panicles increased 52 and 42% respectively at 11 DAF, and about 75% for both IR72 and IR36 at 15–19 DAF (Fig. 2). In contrast, the effects of panicle removal on canopy dark

Table 1. Canopy height, panicle height and length, stratified LAI, light interception, panicles m^{-2} and grain yield (\pm s.e.m.) of IR72 and IR36 rice cultivars

All data are for 14 days after flowering except for panicles m^{-2} and grain yield, which were measured at maturity. Light interception within the layer of the canopy occupied by the panicles is expressed as a percentage of irradiance above the canopy

Measurement	Cultivars	
	IR72	IR36
Canopy height (cm)	77 ± 1	73 ± 2
Panicle height (cm)	66 ± 1	58 ± 2
Panicle length (cm)	19.0 ± 0.6	20.2 ± 0.6
Stratified LAI (%; $\text{m}^2 \text{ m}^{-2}$)		
Total	100 (6.5 ± 0.8)	100 (6.5 ± 0.3)
Above panicles	19 ± 1	18 ± 4
Within panicle level	41 ± 9	46 ± 2
Below panicles	40 ± 12	36 ± 4
Light interception (%)		
By canopy	95 ± 2	91 ± 5
By leaves above panicles	4 ± 1	12 ± 1
Within panicle layer	81 ± 6	65 ± 5
Panicles m^{-2} (at maturity)	599 ± 50	777 ± 28
Grain yield (t ha^{-1} ; at maturity)	6.6 ± 0.3	7.2 ± 0.6

respiration for both cultivars was relatively small (Fig. 2A and B), and there were no effects on net photosynthesis of individual flag leaves when panicles were either retained or removed (Fig. 3). During flag leaf photosynthesis measurements in Fig. 3, irradiance ranged from 1650 to 2250 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (PAR), and there were no significant differences in irradiance between any two measurements for plants with or without panicles.

Modelling

Simulation modelling demonstrated that panicle height in the canopy can have a large effect on gross canopy photosynthesis, reducing rates by as much as 45% at a harvested PAI of 1.1 with no panicle photosynthesis. These results are relative to plants with no panicles, i.e. with panicle height at 0% of canopy height (Fig. 4). Two variables, PAI and panicle photosynthesis, are also evaluated in the simulations. Doubling the PAI from 0.55 measured here to a value of 1.1 as observed in other experiments resulted in a 25% reduction in gross canopy photosynthesis for panicles at the top of the canopy (100% of canopy height, Fig. 4). However, at PAI = 1.1, lowering panicle height to 70% of canopy height increased rates of gross canopy photosynthesis to rates of a canopy at PAI = 0.55 with panicles at 100% of canopy height (assuming no panicle photosynthesis, Fig. 4). There were moderate beneficial effects of panicle photosynthesis when evaluated at the high rate of 50% panicle photosynthesis relative to leaf photosynthesis on a ground area basis, and these effects increased with increasing panicle height in the canopy and increasing PAI (Fig. 4).

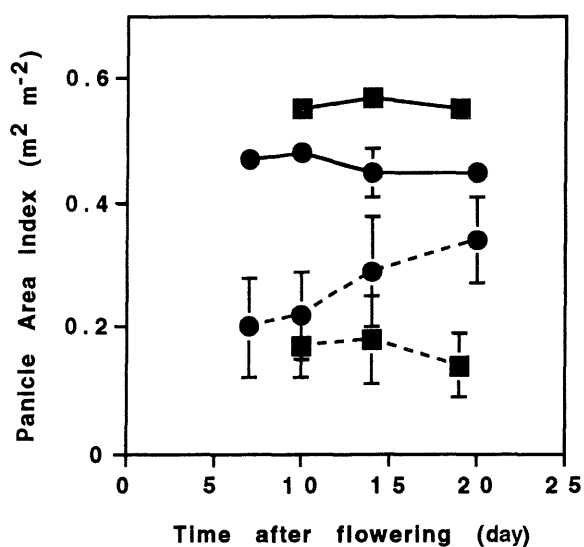


Fig. 1. Panicle area index (\pm s.e.m.) based on surface area of harvested panicles or on area of panicles measured from aerial photographs. Harvested panicle area (—●—); panicle area from aerial photography (---○---); IR72 (—■—); IR36 (---□---).

The simulations in Fig. 4 are plotted using light extinction coefficients (k) at 0.4 for leaves and 0.9 for panicles. The k value for panicles is calculated using data for light absorption at heights in the canopy before and after removal of panicles (Table 2 and Appendix 1). The simulated relationship between panicle height in the canopy and the percentage gross canopy photosynthesis at PAI = 0.55 is consistent with the one data point measured for IR72 (symbol in Fig. 4). This point is based on: (a) panicle height of about 85% of canopy height (calculated from Table 1), and (b) a gross canopy photosynthesis rate at this panicle height of 83% (calculated from Fig. 2A at 15 DAF) and relative to plants without panicles (the latter would simulate panicle height of zero).

Discussion

The current new plant type for rice under development at the International Rice Research Institute is aimed at increasing yield potential of tropical rice from present levels of about 10 t ha^{-1} to 13–15 t ha^{-1} (reviewed by Peng *et al.* 1994). This new plant type incorporates traits including increased sink (panicle) size, reduced tiller number, increased stem size for greater tolerance to lodging (see Concluding Remarks), and increased harvest index (Fig. 5A; see also Peng *et al.* 1994). This multiple-traits approach to increasing yield potential has advantages, and preliminary field experiments have been promising. Beyond this, future increases in rice yield potential towards 15 t ha^{-1} or more could come from any one of several possibilities including a greater sink size, increased grain-filling duration and greater 'stay green' characteristics of leaves (see reviews by Bennett *et al.* 1994; Kropff *et al.* 1994; Setter *et al.* 1994).

Future approaches to increasing yield potential will all have the same weaknesses using the traditional rice plant architecture (Fig. 5B). This is because, in the typical rice plant with panicles high in the canopy: (a) most of the leaves that supply panicles with carbohydrates are beneath the panicles, and consequently at low irradiance; and (b) the plant is susceptible to lodging due to the high centre of gravity (Fig. 5B). Both these problems would be alleviated using a new plant type with reduced panicle height in the canopy (Fig. 5C). This plant type would have advantages for its own sake in improving current high-tillering cultivars in tropical and temperate ecosystems, as well as for enhancing future increases in yield potential. For example, the application of high levels of nitrogen is often limited in current genotypes due to the susceptibility to lodging at high yield levels.

Panicle Area, Light Interception and Canopy Photosynthesis

The data presented here demonstrate that harvested PAI may amount to 0.5 or more for a rice crop grown under tropical conditions (Fig. 1) at yields of about 7 t ha^{-1} .

Table 2. Irradiance in a IR72 rice canopy before and after panicle removal and estimation of light extinction coefficient (*k*) for panicles

Irradiance was measured at 20 DAF. Light extinction coefficients (*k*) were calculated (Appendix 1) assuming $LAI_{\text{panicle layer}} = 2.5$ (from Table 1) and $PAI = 0.45$ (Fig. 1)

Location in canopy	Irradiance ($\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR)	<i>k</i>
Above canopy	2265	
Above panicles	1982	
Bottom of panicle layer		
With panicles	530 (100)	
Without panicles	808 (152)	
Calculated (<i>k</i>) in the panicle layer		
Panicles		0.94
Leaves		0.36

In another treatment at 10×10 cm plant spacings, IR72 had significantly greater harvested PAI of $0.58 \pm 0.1 \text{ m}^2 \text{ m}^{-2}$ with $7.5 \pm 0.6 \text{ t ha}^{-1}$ grain yield, relative to values of 0.45 for 5×5 cm spacings used here (Fig. 1). Values up to 1.2 for the harvested PAI of IR72 have been obtained in other experiments at 20×20 cm spacings particularly at high nitrogen supply (data not shown). Measurements of panicle area are undoubtedly underestimated using the area of panicles from aerial photographs due partly to the overlapping or droopy panicles in the canopy; they may also be underestimated from the tendency for panicles to spread out during measurements with the area meter. The greater values of harvested PAI are more meaningful here since

these are relevant to interception of vertical as well as reflected light in the panicle layer of the canopy. The extent that panicles cover the surface area of the canopy may be even greater for rice grown in temperate, high yield potential areas like Australia and China where yields may already approach 15 t ha^{-1} . Simulation of the effects of increased panicle area on canopy photosynthesis supports the importance of this factor to canopy photosynthesis. With a doubling of PAI from 0.55 to 1.10 the canopy photosynthesis was simulated to decrease from about 80 to 55% for panicles at the top of the canopy (relative to a canopy with panicle height equivalent to 0% of canopy height, Fig. 4).

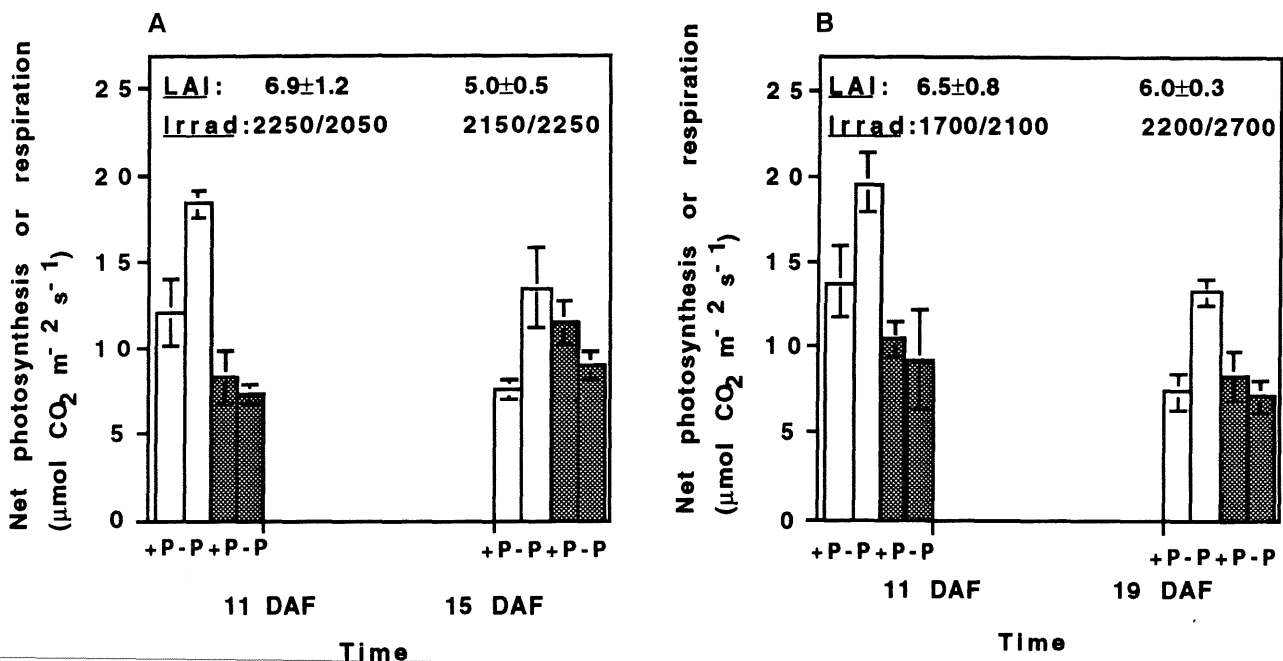


Fig. 2. Net canopy photosynthesis and dark respiration (\pm s.e.m.) of IR72 (A) and IR36 (B) in plants with panicles or with panicles removed. Net photosynthesis (open bars) and dark respiration (closed bars) are for canopies with panicles (+P) and with panicles removed (-P). LAI and irradiance in $\mu\text{mol m}^{-2} \text{s}^{-1}$ (PAR) are given above each time of sampling for +P/-P respectively.

The importance of panicles obstructing light available for leaves is supported by measurements here that found only 18% of total LAI above the panicles at 14 DAF (Table 1). Similarly, light interception by leaves above the panicles was small, but this showed a three-fold range (Table 1). Such low light interception values probably occurred because irradiance was measured at midday and leaves were erect; while cultivar differences in light interception by leaves above panicles (Table 1) were likely the result of more erect leaves for IR72 than for IR36.

The impact of completely eliminating light obstruction by panicles was evaluated by canopy photosynthesis measurements before and after panicle removal. Panicle removal resulted in large increases in net canopy photosynthesis measured in two cultivars over two times during grain filling (Fig. 2). These values are reasonable relative to the measurement that panicles plus leaves intercept 65–81% of the light within the panicle layer of the canopy (Table 1); and when panicles were removed the irradiance at the top of the peduncle increased by 52–80%. Calculations of irradiance in the canopy after panicle removal indicate that panicles account for about 40% of light absorbed in the panicle layer of the canopy. These

measurements would underestimate improved light penetration into the canopy because there would be an increased light absorption by leaves within the panicle layer of the canopy following panicle removal.

Simulation modelling predicted that a rice canopy without panicles would have about 25% greater net canopy photosynthesis relative to a canopy with panicles in the top 10–20 cm of the canopy (estimated for crops at 6 t ha⁻¹ yields by Kropff 1993; see also Fig. 4). This is consistent with measurements here, since the gross canopy photosynthesis of IR72 at 11 DAF with and without panicles was 20 and 26 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (calculated from Fig. 2 assuming respiration in the light is equivalent to dark respiration; see also Fig. 4). The mean net canopy photosynthesis rates (on a ground area basis) of 12–20 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Fig. 2) were lower than peak rates reported for rice of 30–50 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ at panicle initiation (IR54, Cruz *et al.* 1986; IR64, 60–70 days after seeding, Schnier *et al.* 1990 and Dingkuhn *et al.* 1990); however, they were similar to rates measured previously at anthesis (23 $\mu\text{mol m}^{-2} \text{ s}^{-1}$, IR72 at LAI = 5; Dingkuhn *et al.* 1992) or during grain filling (8–25 $\mu\text{mol m}^{-2} \text{ s}^{-1}$, IR72 at ≥ 88 days after seeding, Schnier *et al.* 1990).

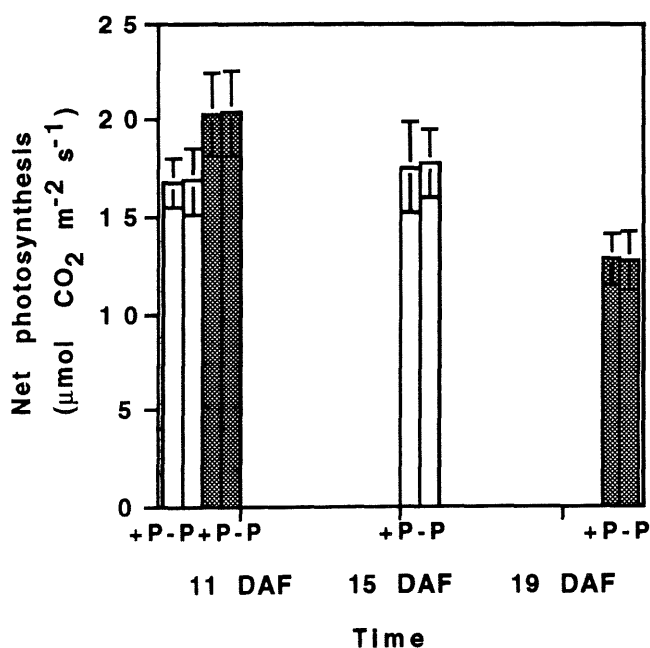


Fig. 3. Net leaf photosynthesis (\pm s.e.m.) of flag leaves of rice with or without removal of panicles during grain filling. IR72 (open bars), IR36 (closed bars); plants with panicles (+P) and with panicles excised (-P).

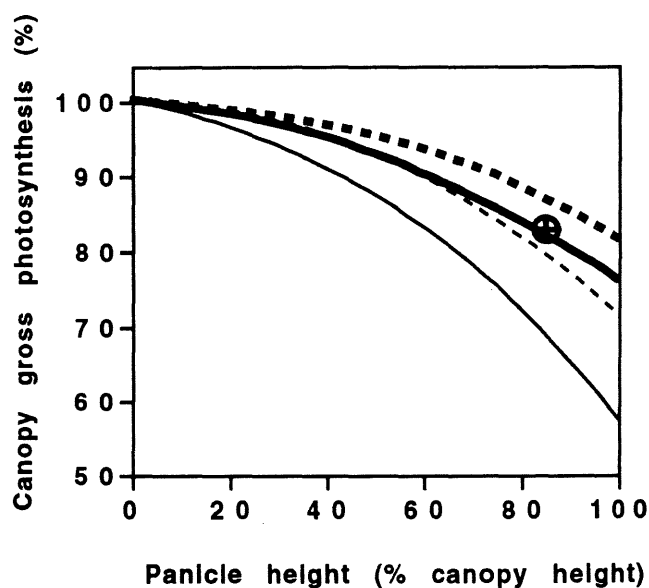


Fig. 4. Simulation of canopy gross photosynthesis at different panicle heights under conditions of different harvested panicle area index either with or without panicle photosynthesis. Curves, simulated data. Circle with cross, measured data at PAI = 0.55. Panicle photosynthesis is assumed zero (—, —) or 50% of leaf photosynthesis (- - -, - - -) on a ground surface area basis; harvested PAI = 1.10 (- - -, —) or 0.55 (- - -, —).

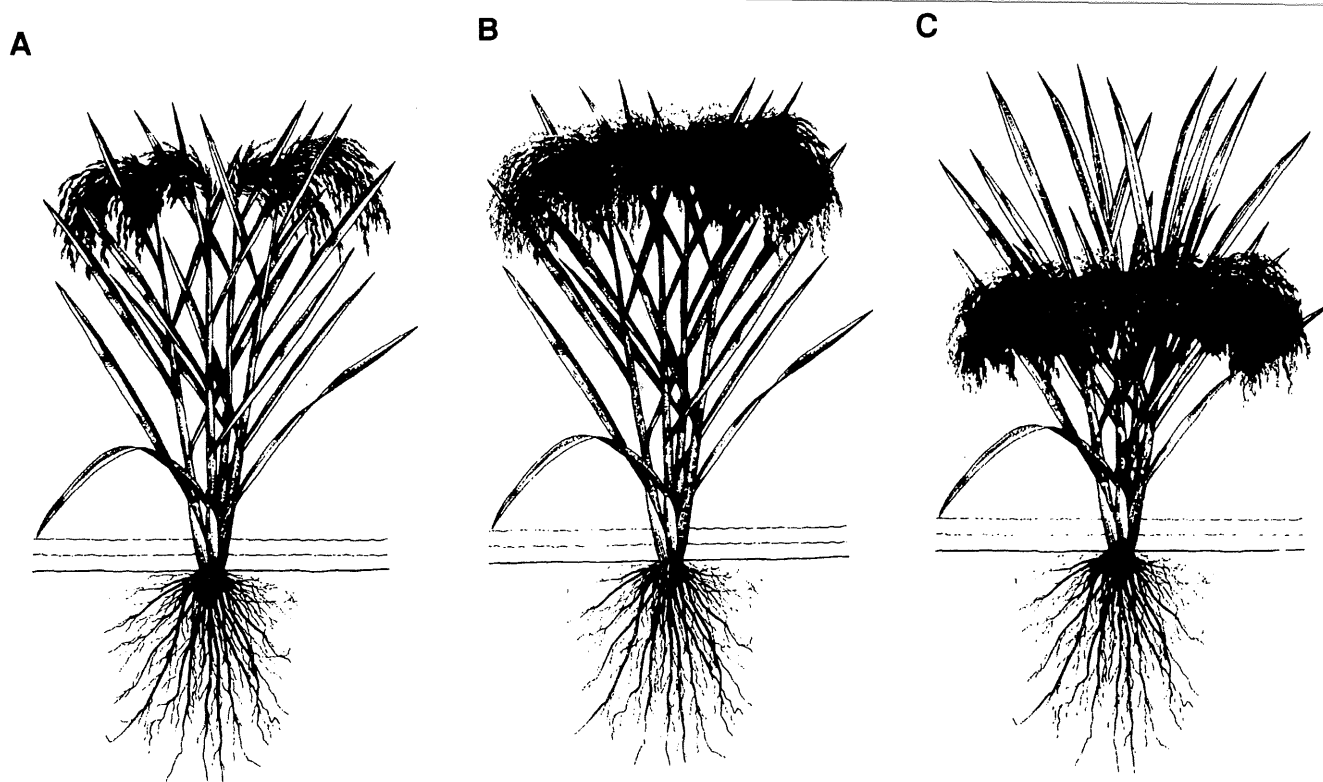


Fig. 5. Possible new plant types for irrigated rice demonstrating: (A) current new plant type aimed at 10 t ha^{-1} (IRRI, 1989), (B) the same plant type as (A) but with 15 t ha^{-1} or more, and (C) a new generation of plant type aimed at 15 t ha^{-1} incorporating greater light interception by leaves and resistance to lodging via a lower centre of gravity.

Excision of panicles would normally be expected to reduce rather than increase canopy photosynthesis because of the removal of a sink. This occurs for wheat where ear removal resulted in reduced translocation of ^{14}C assimilated from the flag leaf and a 40% reduction in photosynthetic rate within 3–24 h (King *et al.* 1967). Reductions in leaf photosynthesis following panicle excision did not occur in the rice cultivars used here since there were no significant effects of panicle excision on net leaf photosynthesis when measured at 2 h after excision (Fig. 3). The lack of any effects on leaf photosynthesis was also observed in other experiments with different cultivars even 24 h after panicle excision (data not shown). One reason for this difference between rice and wheat may be that rice is able to establish a carbohydrate sink in stems and possibly other tissues and thereby maintain high photosynthesis rates. When mobilisation of accumulated stem carbohydrates in wheat is estimated from stem dry weight losses less respiration (Rawson and Evans 1971), or from ^{14}C assimilated from single leaves (Wardlaw and Porter 1967), assimilates mobilised from stems accounted for only 3–13% of the final grain weight. Similar calculations for changes in stem dry weight of rice give values of 10–30% of stem carbohydrates

to grain weight (Yoshida 1981; Wei *et al.* 1982). Another contributing factor to the increases in net canopy photosynthesis of treatments here with removed panicles may be a reduction in canopy boundary layers in the canopy associated with a greater movement of air into and out of the canopy.

The two cultivars used here had differences in panicle height which were 9 and 16 cm below the top of the canopy for IR72 and IR36 respectively (Table 1), yet there were relatively small differences in the effect of panicle removal on net canopy photosynthesis (Fig. 2). However, at 11 DAF the increase in net canopy photosynthesis following panicle removal was 52% for the high-panicle type IR72 and only 42% for the low-panicle type IR36 (Fig. 2A and B). An even smaller difference for canopies with and without panicles would be expected for IR36 at 11 DAF due to the differences in irradiance which occurred during measurements (Fig. 2B). Other effects that could be related to the similar values for cultivars include a similar percentage of LAI above panicles of 18% for both cultivars, and possible differences in panicle photosynthesis of these two cultivars. The latter potential is supported by simulation modelling (Fig. 4).

Genotypic differences in panicle photosynthesis and the importance to canopy photosynthesis during grain filling will be evaluated in detail elsewhere. However, such large increases in net canopy photosynthesis after panicle removal do not indicate a substantial contribution of panicles to net canopy photosynthesis. Contributions of panicles to gross photosynthesis of the canopy may be substantial. Panicle photosynthesis was estimated to contribute as much as 30% of the gross photosynthetically assimilated CO₂ of the flag leaf (Imaizumi *et al.* 1990). This is likely an upper limit since other leaves in the rice canopy will contribute to carbon assimilation of the canopy, and in experiments of Imaizumi and colleagues the carbon exchange of excised panicles was determined in panicles which were spread out to eliminate mutual shading. Gross and net photosynthesis of panicles evaluated in a different cultivar grown in the field were only 8 and 2% respectively of total shoot photosynthesis (Yoshida and Cock 1971), while Tsuno *et al.* (1975) concluded that panicle photosynthesis contributed only 5% to net photosynthesis relative to vigorously growing leaves (see also review by Yoshida 1972).

Determining Optimum Panicle Height in the Canopy

The modules of the INTERCOM model for instantaneous light competition of different tissues in the canopy were used to determine the relationship between panicle height and canopy photosynthesis. Simulation modelling predicts that panicle gross photosynthesis equivalent to 50% of the leaf photosynthesis on a ground area basis will increase canopy gross photosynthesis at most by about 10% at PAI of 0.55 (for panicles at top of canopy, Fig. 4). This simulated small effect occurs because carbon assimilation lost by the panicles when they are lower in the canopy is compensated for by gains in carbon assimilation by leaves. Future research will require more detailed determination of light extinction coefficients in different layers of the canopy as well as light response curves of panicles and leaves to assure the accuracy of these simulations. In any case, the optimum panicle height will be as close to the ground as possible. Evaluations in future will require determination of the minimum sheath and culm biomass necessary to sustain high yield potentials. In the field with 10–15 cm water depth and 20 cm long panicles, the minimum feasible panicle height would be more like 35–40 cm, i.e. at about half the height of most modern semi-dwarf cultivars. Such low panicle heights as shown in Fig. 5C may also need to be balanced with other considerations of suitable flag leaf lengths to remain erect and particularly the optimum LAI above panicles. It is interesting that at least some high yielding genotypes may already incorporate low panicle height in the canopy as a factor contributing to their high yield potential (Setter, Conocono and Egdane, unpublished data).

Concluding Remarks

The data presented here suggest that a reduction in panicle height in a rice canopy could have a large impact on increasing canopy photosynthesis during grain filling and hence subsequent yield. Important additional benefits would include increased resistance to lodging due to the lower centre of gravity (Setter *et al.* 1994); a quantitative evaluation of the impact of lowering panicle height in the canopy will be presented elsewhere (Setter, Laureles, Conocono and Egdane, unpublished data). This characteristic for increasing lodging tolerance may be preferable to selection for thicker stems. Borrell *et al.* (1991) reported that since panicle development in wheat is most rapid during stem elongation, there would be competition between the developing stem and the developing ear. Therefore increased stem size for tolerance to lodging could be at the expense of yield.

There are several concerns for lowering panicle height in some situations due to increased susceptibility to flooding and high water depths, diseases and rat damage. Hence plant types with low panicle heights may have the greatest impact on irrigated rice in high yielding environments where these factors can be controlled. In some cases, development of increased tolerance to diseases may be necessary for successful adaptation of low-panicle plant types. Further work is required to look at the implications of differences in instantaneous canopy photosynthesis for growth over the whole grain-filling duration. Two different approaches have recently supported the importance of panicle height to canopy photosynthesis and yield using isogenic lines differing in panicle height and by manipulation of panicle heights using growth regulators (Setter, Conocono and Egdane, unpublished data). These results will be presented in subsequent work.

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References

- Bennett, J., Brar, D. S., Khush, G. S., Huanh, N., and Setter, T. L.** (1994). Molecular approaches to yield potential. In 'Breaking the Yield Barrier: Proceedings of a Workshop on Rice Yield Potential in Favorable Environments'. (Ed. K. G. Cassman.) pp. 63–76. (IRRI: Los Baños.)
- Borrell, A. K., Incoll, L. D., and Dalling, M. J.** (1991). The influence of the *Rht*₁ and *Rht*₂ alleles on the growth of wheat stems and ears. *Annals of Botany* **67**, 103–110.
- Chandler, R. F. Jr** (1969). Plant morphology and stand geometry in relation to nitrogen. In 'Physiological Aspects of Crop Yield'. (Eds J. D. Eastin, F. A. Haskins, C. Y. Sullivan and C. H. M. Van Bavel.) pp. 265–285. (ASA: Madison.)

- Cock, J. H., and Yoshida, S.** (1972). Accumulation of ^{14}C labelled carbohydrate before flowering and the subsequent redistribution and respiration in the rice plant. *Proceedings of the Crop Science Society of Japan* **41**, 226–234.
- Cruz, R. T., O'Toole, J. C., Dingkuhn, M., Yambao, E. B., Thangaraj, M., and De Datta, S. K.** (1986). Shoot and root responses to water deficits in rainfed lowland rice. *Australian Journal of Plant Physiology* **13**, 567–575.
- Dingkuhn, M., De Datta, S. K., Pamplona, R., Javellana, C., and Schnier, H. F.** (1992). Effect of late-season N fertilization on photosynthesis and yield of transplanted and direct seeded tropical flooded rice. II. A canopy stratification study. *Field Crops Research* **28**, 235–249.
- Dingkuhn, M., Schnier, H. F., De Datta, S. K., Wijanco, E., and Dörffling, K.** (1990). Diurnal and developmental changes in canopy gas exchange in relation to growth in transplanted and direct-seeded flooded rice. *Australian Journal of Plant Physiology* **17**, 119–134.
- Duncan, W. G.** (1971). Leaf angle, leaf area and canopy photosynthesis. *Crop Science* **11**, 482–485.
- Imaizumi, N., Usuda, H., Nakamoto, H., and Ishihara, K.** (1990). Changes in the rate of photosynthesis during grain filling and the enzymatic activities associated with the photosynthetic carbon metabolism of rice panicles. *Plant and Cell Physiology* **31**, 835–843.
- IRRI** (1989). 'IRRI Toward 2000 and Beyond.' (IRRI: Los Baños.) 66 pp.
- King, R. W., Wardlaw, I. F., and Evans, L. T.** (1967). Effects of assimilate utilisation on photosynthetic rate in wheat. *Planta* **77**, 261–276.
- Kropff, M. J.** (1993). Mechanisms of competition for light. In 'Modelling Crop-Weed Interactions'. (Eds M. J. Kropff and H. H. van Laar.) pp. 33–61. (CAB: Wallingford and IRRI: Los Baños.)
- Kropff, M. J., Cassman, K. G., Peng, S., Matthews, R. B., and Setter, T. L.** (1994). Quantitative understanding of rice yield potential. In 'Breaking the Yield Barrier: Proceedings of a Workshop on Rice Yield Potential in Favorable Environments'. (Ed. K. G. Cassman.) pp. 21–38. (IRRI: Los Baños.)
- Kropff, M. J., van Laar, H. H., and ten Berg, H. F. M.** (1993). 'ORYZA1. A Basic Model for Irrigated Rice Production.' (IRRI: Los Baños.) 89 pp.
- Peng, S., Khush, G. S., and Cassman, K. G.** (1994). Evolution of the new plant ideotype for increased yield potential. In 'Breaking the Yield Barrier: Proceedings of a Workshop on Rice Yield Potential in Favorable Environments'. (Ed. K. G. Cassman.) pp. 5–20. (IRRI: Los Baños.)
- Penning de Vries, F. W. T., Jansen, D. M., ten Berge, H. F. M., and Bakema, A.** (1989). Simulation of ecophysiological processes of growth of several annual crops. Simulation Monographs 29. (Pudoc: Wageningen and IRRI: Los Baños.) 271 pp.
- Plucknett, D. L., Smith, N. J. H., Williams, J. T., and Anishetty, N. M.** (1987). A case study in rice germplasm: IR36. In 'Gene Banks and the World's Food'. pp. 171–185. (Princeton University Press: Princeton.)
- Rawson, H. M., and Evans, L. T.** (1971). The contribution of stem reserves to grain development in a range of wheat cultivars of different height. *Australian Journal of Agricultural Research* **22**, 851–863.
- Sasahara, T., Takahashi, T., Kayaba, T., and Tsunoda, S.** (1992). A new strategy for increasing plant productivity and yield of rice. *International Rice Communication Newsletter (FAO)* **41**, 1–6.
- Schnier, H. F., Dingkuhn, M., De Datta, S. K., Mengel, K., and Faronilo, J. E.** (1990). Nitrogen fertilization of direct-seeded flooded vs transplanted rice. I. Nitrogen uptake, photosynthesis, growth and yield. *Crop Science* **30**, 1276–1284.
- Setter, T. L., Peng, S., Kirk, G. J. D., Virmani, S. S., Kropff, M. J., and Cassman, K. G.** (1994). Physiological considerations and heterosis to increase yield potential. In 'Breaking the Yield Barrier: Proceedings of a Workshop on Rice Yield Potential in Favorable Environments'. (Ed. K. G. Cassman.) pp. 39–62. (IRRI: Los Baños.)
- Takeda, T.** (1984). Physiological and ecological characteristics of higher yielding varieties of lowland rice. In 'International Crop Science Symposium'. Oct. 17–20. Fukuoka, Japan. pp. 1–14.
- Tanaka, T., Matsushima, S., Kojyo, S., and Nitta, H.** (1969). Analysis of yield determining process and its application to yield prediction and culture improvement of lowland rice. XC. On the relation between the plant type of rice plant community and the light curve of carbon assimilation. *Proceedings of the Crop Science Society of Japan* **38**, 287–293.
- Thomas, R. B., Reid, C. D., Ybema, R., and Strain, B. R.** (1993). Growth and maintenance components of leaf respiration of cotton grown in elevated carbon dioxide partial pressures. *Plant, Cell and Environment* **16**, 539–546.
- Tsuno, Y., Sato, T., Miyamoto, H., and Harada, N.** (1975). Studies on CO_2 uptake and CO_2 evolution in each part of crop plants. II. Photosynthetic activity in the leaf sheath and ear of rice plant. *Proceedings of the Crop Science Society of Japan* **44**, 287–292.
- van Keulen, H.** (1976). A calculation method for potential rice production. Contributions. *Central Research Institute for Agriculture, Bogor, Indonesia* **21**, 1–26.
- Wardlaw, I. F., and Porter, H. K.** (1967). The redistribution of stem sugars in wheat during grain development. *Australian Journal of Biological Sciences* **20**, 309–318.
- Wei, M.-L., Shen, M. C., Chen, C.-S., and Liu, D.-J.** (1982). Physiological studies of rice tillers. I. Partition of dry matter, nitrogen and total non structural carbohydrates during grain filling. *Proceedings of the National Science Council ROC (A)* **6**, 190–196.
- Yoshida, S.** (1972). Physiological aspects of grain yield. *Annual Review of Plant Physiology* **23**, 437–464.
- Yoshida, S.** (1981). 'Fundamentals of Rice Crop Science.' (IRRI: Los Baños.) 269 pp.
- Yoshida, S., and Cock, J. H.** (1971). Growth performance of an improved rice variety in the tropics. *International Rice Communication Newsletter (FAO)* **20**, 1–15.

Appendix 1

Light extinction coefficients for leaves (k_L) and panicles (k_p) within the panicle layer of the canopy were calculated based on Beer's Law (see also Kropff 1993):

$$I_{hb}/I_o = e^{-(k_p PAI + k_L LAI)} = (e^{-k_p PAI}) (e^{-k_L LAI}), \quad (1)$$

where, I_{hb} = irradiance at the bottom of the panicles before panicle excision and I_o = irradiance at the top of the panicles. In the case of only leaves in the panicle layer this was simplified:

$$I_{ha}/I_o = e^{-k_L LAI}, \quad (2)$$

where, I_{ha} = irradiance at the bottom of panicles after panicle excision.

Substituting in Eqn (1):

$$I_{hb}/I_o = (e^{-k_p PAI}) (I_{ha}/I_o), \quad (3)$$

$$\ln (I_{hb}/I_{ha}) = -(k_p PAI), \quad (4)$$

therefore,

$$k_p = \ln (I_{hb}/I_{ha}) / -PAI. \quad (5)$$

From Table 2 and Eqn (5):

$$k_p = \ln (530/808) / (-0.45) = 0.94,$$

and from Table 2 and Eqn (2):

$$k_L = \ln (808/1982) / (-2.5) = 0.36.$$

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