Journal of Agricultural Science (2002), **138**, 269–279. © 2002 *Cambridge University Press*
DOI: 10.1017/S0021859601001903 *Printed in the United Kingdom*

Relationship between tillering and leaf area index: quantifying critical leaf area index for tillering in rice

X. ZHONG[1], S. PENG[2]*, J. E. SHEEHY[2], R. M. VISPERAS[2] AND H. LIU[3]

[1] *Rice Research Institute, Guangdong Academy of Agricultural Sciences, Guangzhou 510640, China*
[2] *Crop, Soil and Water Sciences Division, International Rice Research Institute (IRRI), DAPO Box 7777, Metro Manila, Philippines*
[3] *South China Institute of Botany, The Chinese Academy of Sciences, Guangzhou 510650, China*

(*Revised MS received 24 October 2001*)

SUMMARY

A field study was conducted at the International Rice Research Institute (IRRI), Philippines during the dry seasons of 1997 and 1998 under irrigated conditions. The objectives of this study were to quantify the critical leaf area index (LAI_c) at which tillering stops based on the relationship between tillering rate and LAI, and to determine the effect of nitrogen (N) on LAI_c in irrigated rice (*Oryza sativa* L.) crop. Results showed that the relative tillering rate (RTR) decreased exponentially as LAI increased at a given N input level. The coefficient of determination for the equation quantifying the RTR-LAI relationship ranged from 0·87 to 0·99. The relationship between RTR and LAI was affected by N input level, but not by planting density. The N input level had a significant effect on LAI_c with a high N input level causing an increase in LAI_c. Tillering stopped at LAI of 3·36 to 4·11 when N was not limiting. Under N limited conditions LAI_c reduced to as low as 0·98. Transplanting spacing and number of seedlings per hill had little effect on LAI_c. Results from this study suggest that LAI and plant N status are two major factors that influence tiller production in rice crops. The possibility that LAI influences tillering by changing light intensity and/or light quality at the base of the canopy where tiller buds and young tillers are located is discussed.

INTRODUCTION

Tillering plays an important role in determining rice grain yield since it is closely related to panicle number per unit ground area. Too few tillers result in too few panicles; but excess tillers cause high tiller abortion, small panicles, poor grain filling and a consequent reduction in grain yield (Peng *et al.* 1994). Optimization of tiller production by regulating tillering through in-season crop management is essential for achieving high rice yield (Jiang 1994; Su *et al.* 1996).

Increasing leaf area index (LAI) causes increased shading and tiller mortality and is associated with reduced tillering rate in rice crops (Lei & Wang 1961; Tanaka *et al.* 1966; Yoshida & Hayakawa 1970; Graf *et al.* 1990). In a rice simulation model, Graf *et al.* (1990) assumed that tillering slowed down as LAI increased and finally stopped at a LAI of 1·8. Their model successfully described tillering patterns. Blum *et al.* (1990) observed that wheat plants experiencing mild water stress produced more tillers after re-watering than non-stressed control plants. They speculated that this was due to the lower LAI in the stressed treatments. S. Peng (unpublished data) obtained similar results in a nitrogen (N)-stressed rice crop. Simon & Lemaire (1987) studied the relationship between tillering and LAI during sward establishment of perennial ryegrass and Italian ryegrass with different seedling densities and N application rates. They also determined the relationship between tillering and LAI on established swards of tall fescue during winter and early spring after different dates of last cut in the autumn. In both cases, tillering rate slowed down as soon as LAI reached a value of 3 and terminated rapidly at higher LAI.

Although it is well accepted that increasing LAI decreases tillering rate, this negative effect has not been quantified previously in a rice crop. The rice tillering models developed through mechanistic approaches simulate the tiller number per unit ground area based on carbohydrate supply or crop growth rate (Zhong *et al.* 1999). The direct effect of LAI and the interactive effect of N and LAI on tillering were not considered in those tillering models. Quantifying the relationship between tillering rate and LAI may

* To whom all correspondence should be addressed. Email: s.peng@cgiar.org

https://doi.org/10.1017/S0021859601001903 Published online by Cambridge University Press

help improve the predictability of the tillering models. Furthermore, describing the quantitative relationship between tillering rate and LAI will determine the critical LAI (LAI_c) at which tillering stops. In this study, we measured the tiller and leaf area production of three rice cultivars grown under a wide range of planting density and N input levels. The objectives of the study were (1) to quantify the relationship between tillering rate and LAI, (2) to determine LAI_c based on the relationship between tillering rate and LAI and (3) to determine the effect of N on LAI_c.

MATERIALS AND METHODS

Two field experiments were conducted during the dry seasons from January to May in 1997 (Experiment 1) and 1998 (Experiment 2) at the International Rice Research Institute (IRRI) farm, Los Baños, Laguna, Philippines (14° 11′ N, 120° 56′ E, elevation 21 m).

In Experiment 1, a randomized split-split-plot design with four replicates was used. Transplanting spacing (30×20, 20×20, 14×20 and 10×20 cm) was the main plot treatment and seedling number per hill (one, three and six seedlings/hill) was the subplot treatment. Two indica rice cultivars, IR72 and IR64, were arranged in sub-subplots. Each sub-subplot was 4 m long and 3 m wide. The lowest planting density of this study (30×20 cm with 1 seedling per hill) is often used in hybrid rice production because of the high cost of hybrid seeds, whereas the highest planting density (10×20 cm with six seedlings per hill) is close to the plant density of direct-seeded rice. Fourteen-day-old seedlings were transplanted on 22 January. 180 kg N/ha was applied to all treatments. The soil was Andaqueptic Haplaquoll with a pH 6·5, 16·9 g/kg of organic C, 1·5 g/kg of total N, 16·0 mg/kg of available P, 1·3 $cmol_c$/kg of exchangeable K and 39·9 $cmol_c$/kg of cation exchange capacity.

In Experiment 2, IR72 and IR68284H (the latter being a hybrid) were used. Within each cultivar, a randomized split-plot design with four replicates was used with N treatment (0, 60, 120 and 180 kg/ha) forming the main plot treatment and transplanting spacing (30×20, 20×20 and 10×20 cm) forming the subplot treatment. Subplot size was 5 m long and 4 m wide. Fourteen-day-old seedlings were transplanted on 16 January with three seedlings per hill. The soil had a pH 7·0, 22·9 g/kg of organic C, 2·0 g/kg of total N, 7·3 mg/kg of available P, 1·2 $cmol_c$/kg of exchangeable K and 43·3 $cmol_c$/kg of cation exchange capacity.

In both experiments, pre-germinated seeds were sown on seedling trays to produce uniform seedlings. Nitrogen in the form of urea was applied before transplanting (basal), at mid tillering and panicle initiation in three equal splits. The mid tillering stage was defined as the midpoint between transplanting and panicle initiation. Basal N was applied and incorporated into the soil one day before transplanting. In all plots, phosphorus (30 kg P/ha as single superphosphate), potassium (40 kg K/ha as KCl), and zinc (5 kg Zn/ha as zinc sulphate heptahydrate) were applied one day before transplanting. Fields were flooded at one day after transplanting (DAT). Irrigation water was maintained at 5 to 10 cm deep until 7 days before maturity, when the field was drained. Weeds, diseases and insects were controlled as necessary.

In Experiment 1, plant samples were taken at 15, 22, 29, 36, 43, 50, 57 and 70 DAT (flowering) for IR72, or at 16, 23, 30, 37, 40, 47, 56 and 68 DAT (flowering) for IR64. Sampling area was 0·32 to 0·36 m^2 until panicle initiation and 0·20 to 0·24 m^2 thereafter, depending on transplanting spacing. In Experiment 2, plant samples were taken in 0·48 to 0·50 m^2 area at 14, 24, 33, 41, 55 DAT and flowering for IR72, and at 14, 25, 34, 48, 62 DAT and flowering for IR68284H. Flowering date ranged from 66 to 69 DAT for IR72 and from 74 to 76 DAT for IR68284H, depending on N levels. Samples were taken immediately before N application if N was applied on the sampling day. For each plant sample, number of tillers was counted first. Tillers with at least one visible leaf were counted as a tiller. In this study, main stem or mother tiller was counted as one tiller and was included in total tiller number. Leaf area was measured with a leaf area meter (LI-3000, LI-COR, Lincoln, Nebraska, USA) and expressed as LAI.

Mean tiller number per m^2 of the four replications was obtained and relative tillering rate (RTR) was calculated using the harvest-interval method (Yoshida & Hayakawa 1970):

$$RTR = [\log_e(n_2) - \log_e(n_1)]/(t_2 - t_1), \qquad (1)$$

where n_1 and n_2 were tiller number per m^2 at time t_1 and t_2 in DAT, respectively. The tiller number was the total number of tillers excluding the dead tillers. The precision of the estimation of RTR by Eqn 1 depends on the duration of the time interval, t_2–t_1, and the rate of change in tiller number during that interval. The smaller the interval, the more precise the approximation is. In this experiment, most sampling time intervals were less than 10 days, which were short enough to guarantee precise approximation.

The relationship between RTR and LAI was quantified by fitting data to the following equation and the values of parameters were estimated using the nonlinear optimization package PROCNLIN of the Statistical Analysis Systems Institute (SAS 1987).

$$RTR = \alpha[\exp(-\gamma LAI) - \beta], \qquad (2)$$

where α, β and γ are parameters. The parameter γ defines the slope at which RTR decreases exponentially as LAI increases and represents the sen-

https://doi.org/10.1017/S0021859601001903 Published online by Cambridge University Press

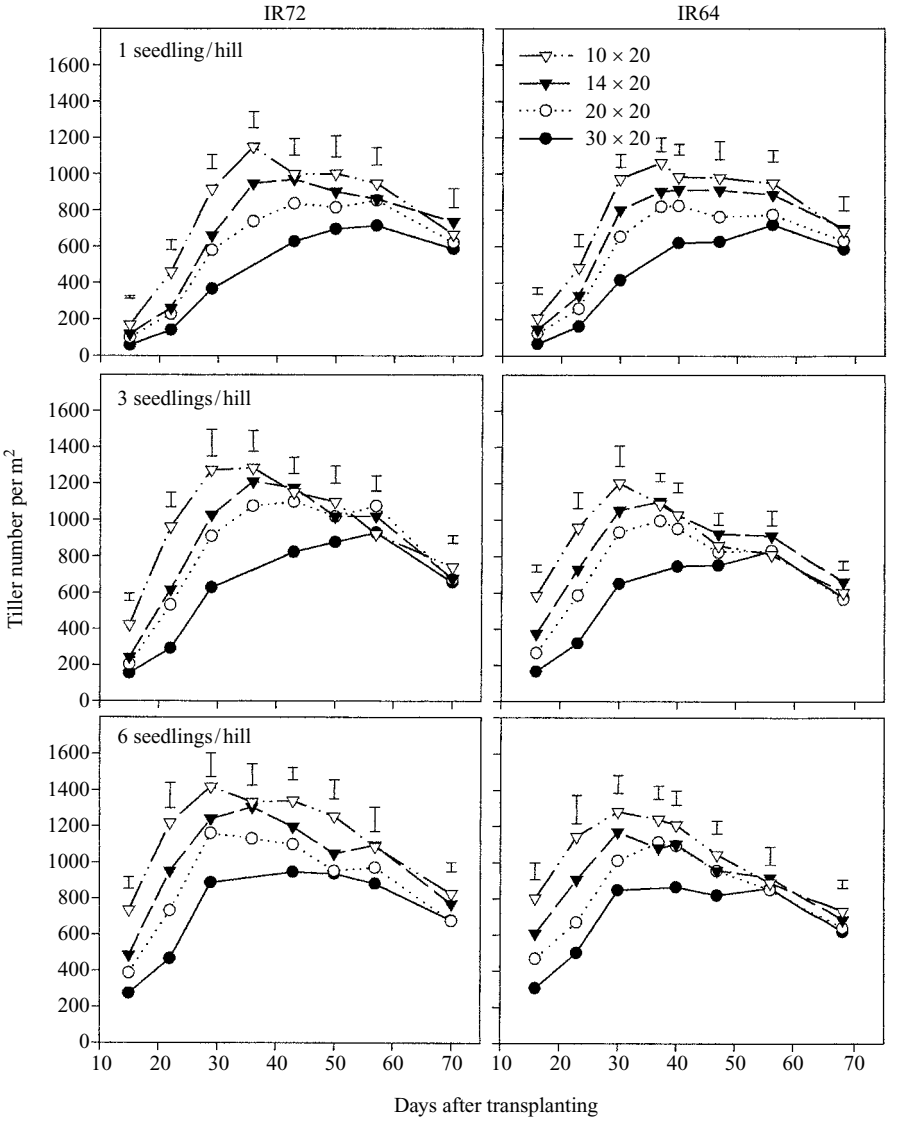


Fig. 1. Changes in tiller number (including main stem or mother tiller) per m² of IR72 and IR64 rice grown under different transplanting spacings (30×20, 20×20, 14×20 and 10×20 cm) and number of seedlings per hill (one, three and six seedlings/hill) at the International Rice Research Institute (IRRI), Philippines during the dry season of 1997. Nitrogen fertilizer at 180 kg/ha was applied for all treatments. Vertical bars represent standard error (D.F. = 9).

sitivity of tillering rate to LAI. When LAI approaches zero, RTR has its maximum:

$$\mathrm{RTR}_{\max} = \alpha(1-\beta). \quad (3)$$

When LAI (theoretically) approaches infinity, RTR has its minimum:

$$\mathrm{RTR}_{\min} = -\alpha\beta. \quad (4)$$

Comparing Eqns (3) and (4), we have:

$$\alpha = \mathrm{RTR}_{\max} - \mathrm{RTR}_{\min}, \quad (5)$$

and

$$\beta = \mathrm{RTR}_{\min}/(\mathrm{RTR}_{\min} - \mathrm{RTR}_{\max}). \quad (6)$$

The LAI_c was defined as the LAI at which RTR is equal to zero and was derived from the quantitative relationship between RTR and LAI (Eqn 2):

$$\mathrm{LAI}_c = -\log_e(\beta)/\gamma. \quad (7)$$

In order to test the significance of difference in LAI_c among treatments, the relationship between RTR and LAI was quantified and the LAI_c was obtained for each individual plot. Analysis of variance of the

https://doi.org/10.1017/S0021859601001903 Published online by Cambridge University Press

individual plot values then gave a pooled estimate of the standard error of mean (SE) for each parameter (SAS 1987).

RESULTS

Treatment effects on tillering and leaf area development

In all treatments, tiller number per m² increased to a maximum and then decreased (Figs 1 and 2). At a given date, tiller number increased as transplanting density, number of seedlings per hill and N input level increased. In 1997, maximum tiller number of the treatments ranged from 715 to 1418 per m² for IR72 and from 724 to 1330 per m² for IR64 (Fig. 1). When the number of transplanted seedlings per m² was the same, treatments with more hills per m² and fewer seedlings per hill had more tillers per m² than treatments with fewer hills per m² and more seedlings per hill. In 1998, the maximum tiller number of the

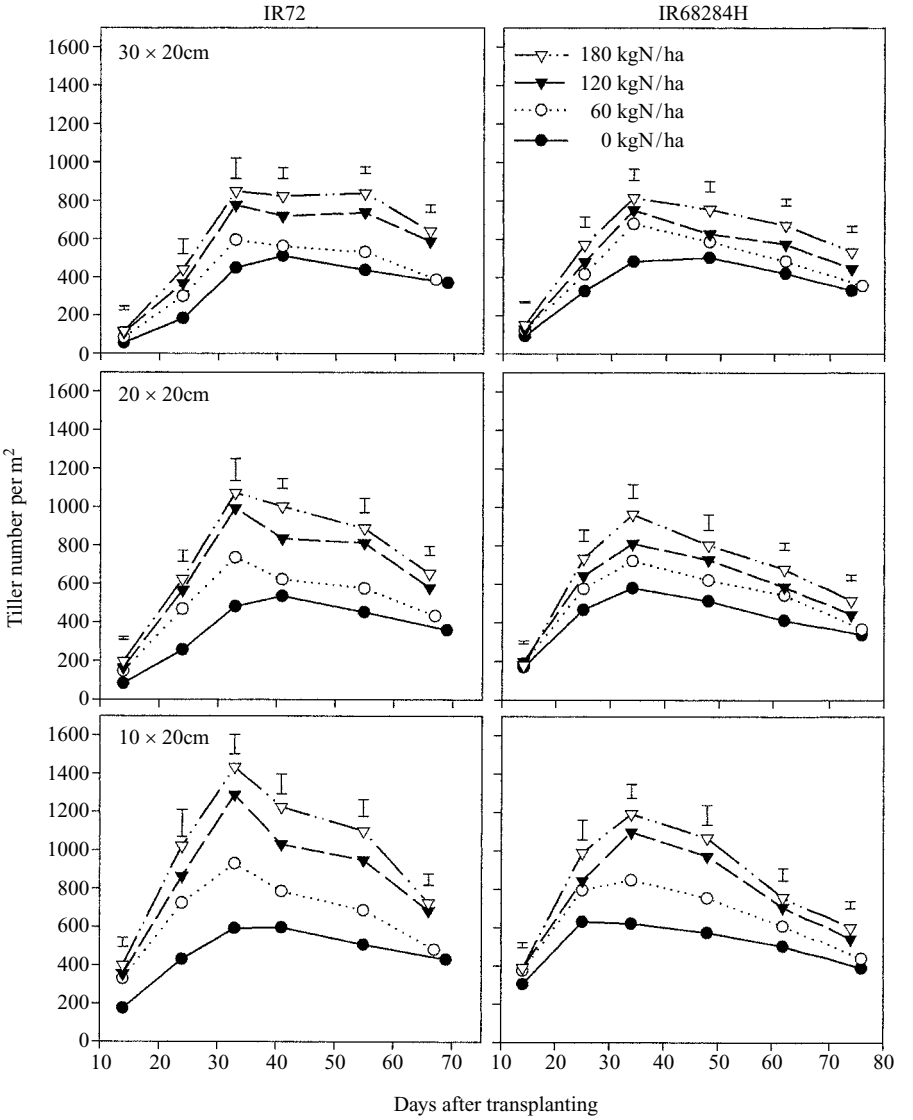


Fig. 2. Changes in tiller number (including main stem or mother tiller) per m² of IR72 and IR68284H rice grown under different nitrogen input levels (0, 60, 120 and 180 kg/ha) and transplanting spacings (30 × 20, 20 × 20 and 10 × 20 cm) at the International Rice Research Institute (IRRI), Philippines during the dry season of 1998. Three seedlings were transplanted per hill for all treatments. Vertical bars represent standard error (D.F. = 9).

https://doi.org/10.1017/S0021859601001903 Published online by Cambridge University Press

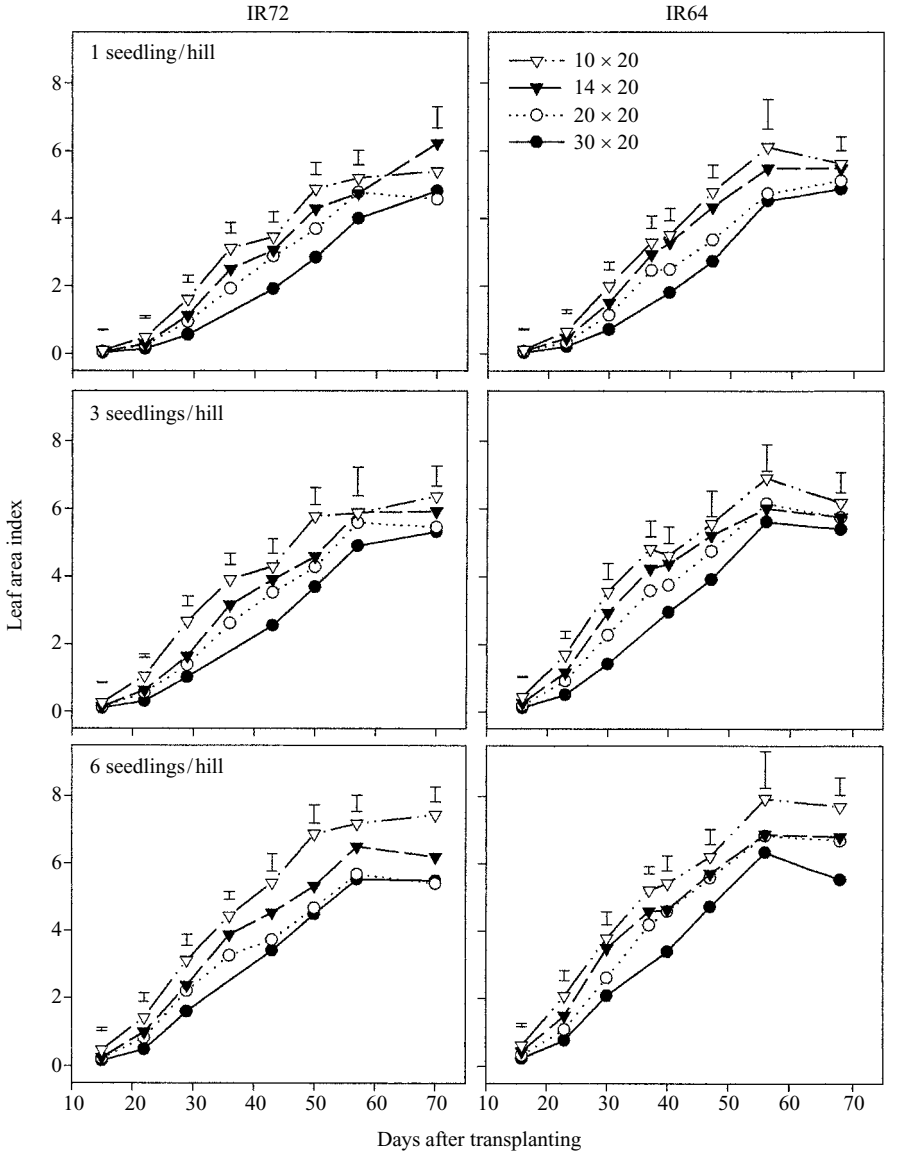


Fig. 3. Changes in leaf area index of IR72 and IR64 rice grown under different transplanting spacings (30 × 20, 20 × 20, 14 × 20 and 10 × 20 cm) and number of seedlings per hill (one, three and six seedlings/hill) at the International Rice Research Institute (IRRI), Philippines during the dry season of 1997. Nitrogen fertilizer at 180 kg/ha was applied for all treatments. Vertical bars represent standard error (D.F. = 9).

treatments ranged from 510 to 1434 per m² for IR72 and 518 to 1194 per m² for IR68284H (Fig. 2). IR72 produced more tillers than IR68284H except for zero-N treatment.

The date when the tiller number per m² reached maximum (defined as maximum tiller number stage hereafter) varied among treatments (Figs 1 and 2). In 1997, high planting density treatments achieved maximum tiller number earlier than lower planting density treatments (Fig. 1). In 1998, the planting density affected the maximum tiller number stage only in the zero-N treatments (Fig. 2). Nitrogen treatments had small and inconsistent effects on the maximum tiller number stage.

Higher planting density treatments produced greater leaf area per unit ground area (Figs 3 and 4). At a given planting density, leaf area increased as N input level increased. IR68284H had greater LAI than IR72

https://doi.org/10.1017/S0021859601001903 Published online by Cambridge University Press

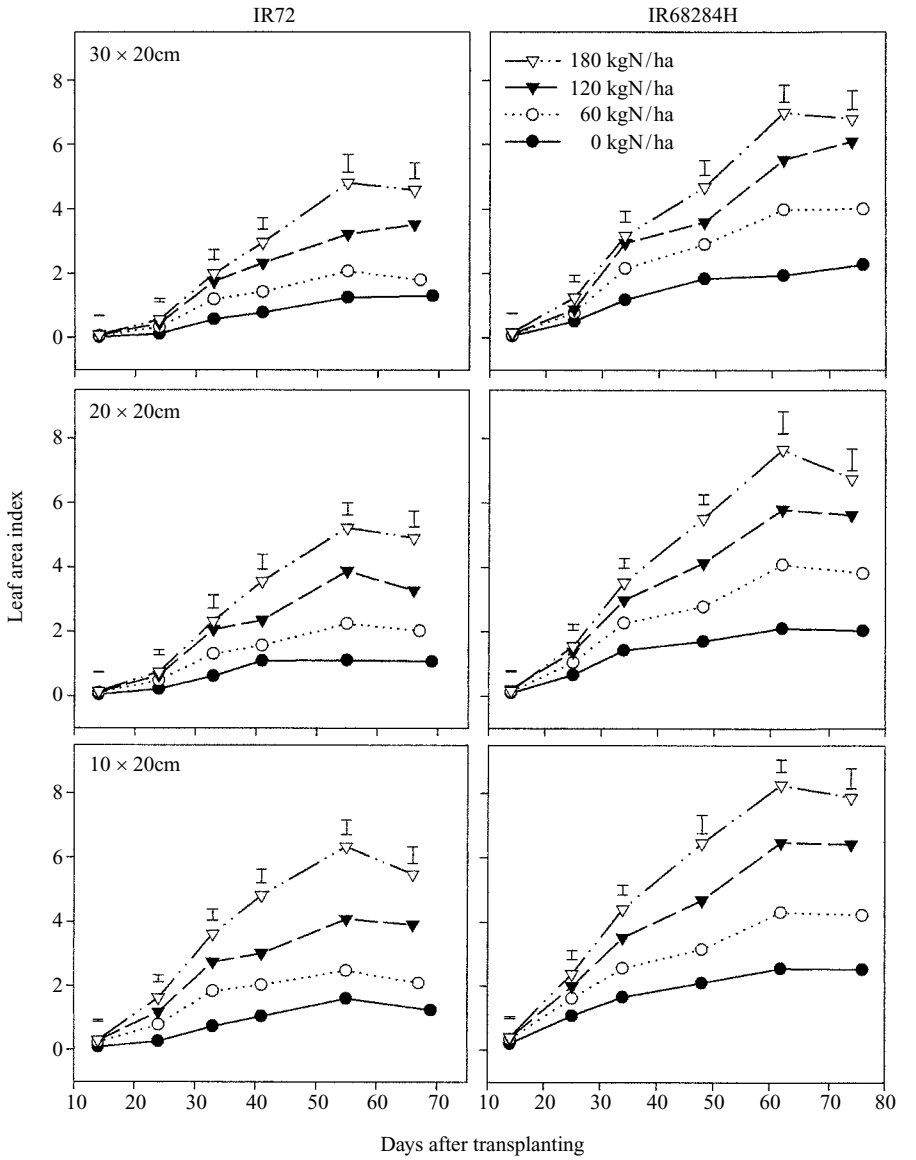


Fig. 4. Changes in leaf area index of IR72 and IR68284H rice grown under different nitrogen input levels (0, 60, 120 and 180 kg/ha) and transplanting spacings (30 × 20, 20 × 20 and 10 × 20 cm) at the International Rice Research Institute (IRRI), Philippines during the dry season of 1998. Three seedlings were transplanted per hill for all treatments. Vertical bars represent standard error (D.F. = 9).

at the same planting density and N input level. Maximum LAI was achieved from about 10 days before flowering to flowering, depending on cultivar, planting density and N input level. Maximum LAI of the treatments ranged from 4·6 to 7·4 for IR72 and from 4·9 to 7·9 for IR64 in 1997, and from 1·2 to 6·3 for IR72 and from 2·1 to 8·5 for IR68284H in 1998.

Relationship between tillering rate and LAI

RTR decreased exponentially as LAI increased (Fig. 5). Transplanting spacing and number of seedlings per hill had no consistent effect on this relationship in 1997 (Fig 5*a*, *b*). In 1998, different transplanting spacing had a similar relationship between RTR and

https://doi.org/10.1017/S0021859601001903 Published online by Cambridge University Press

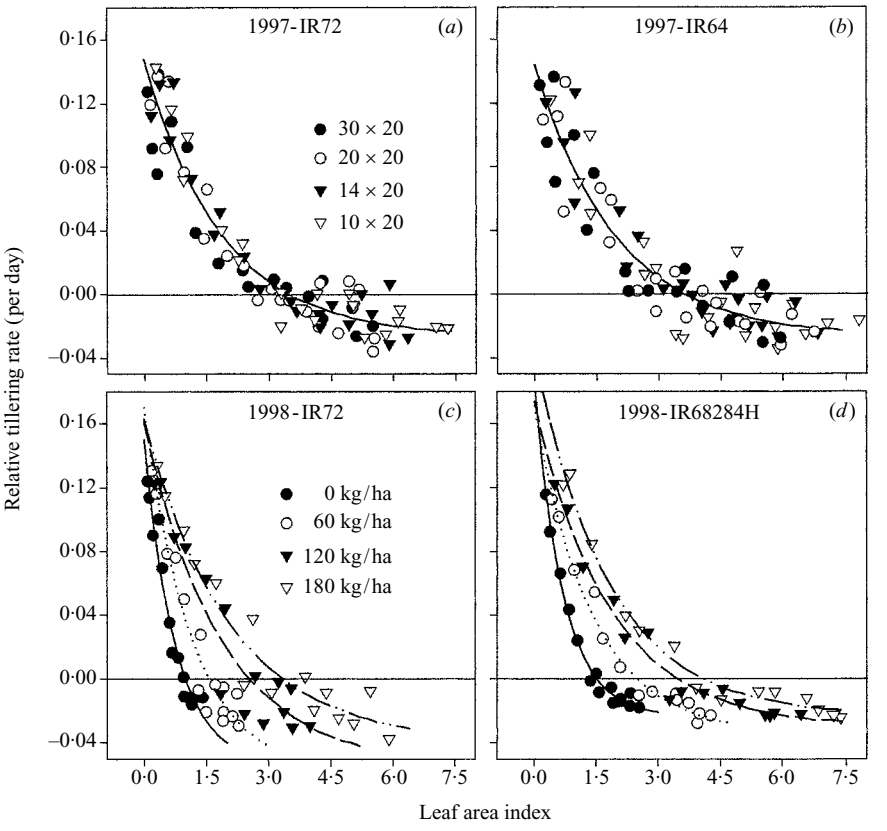


Fig. 5. Relationship between relative tillering rate (RTR) and leaf area index at different transplanting spacing and N input level. In 1997, 180 kg N/ha was applied for all treatments (*a* and *b*). In 1998, three transplanting spacings were 30 × 20, 20 × 20 and 10 × 20 cm for each N levels (*c* and *d*). Curves are plotted using the fitted equations, with coefficients of determination and values of parameters shown in Table 1. Horizontal lines show RTR = 0. Symbols are the same for *a* and *b*, and *c* and *d*, respectively.

LAI at a given N input level. However, N treatments had a significant effect on this relationship (Fig. 5*c*, *d*). At a certain LAI, the higher N input level resulted in a greater RTR. Although RTR decreased as tiller number per m² increased (Fig. 6), the relationship between RTR and LAI was much closer than that between RTR and tiller number per m².

The relationship between RTR and LAI was described quantitatively using Eqn 2. At a given N input level, Eqn 2 fitted the data of all tested cultivars well, with coefficient of determination ranging from 0·87 to 0·99 (Table 1). The high coefficient of determination suggests that the development stage did not have much effect on the relationship between the tillering rate and LAI. There was little difference in parameter values between IR72 and IR64 in 1997. In 1998, IR72 and IR68284H had similar values of α and γ, but IR72 had greater β values than IR68284H. Although no consistent differences in α and β were observed among N input levels, the value of γ decreased considerably as N input level increased.

Critical LAI for tillering

The LAI_c was calculated using Eqn 7. In 1997, LAI_c averaged across planting density treatments was 3·47 for IR72 and 3·68 for IR64 (Table 2). Transplanting spacing and number of seedlings per hill had no significant effect on the LAI_c. In 1998, LAI_c ranged from 0·98 to 3·37 for IR72 and from 1·45 to 4·11 for IR68284H, depending on N input level (Table 3). The differences in LAI_c among N input levels were significant. The higher the N input level, the greater the LAI_c. Compared with N treatment, transplanting spacing had a relatively small influence on LAI_c (Table 3).

DISCUSSION

Several studies have stated that tillering rate is negatively associated with LAI (Lei & Wang 1961; Tanaka *et al.* 1966; Yoshida & Hayakawa 1970; Simon & Lemaire 1987). However, this negative relationship has not been quantified. In the current

https://doi.org/10.1017/S0021859601001903 Published online by Cambridge University Press

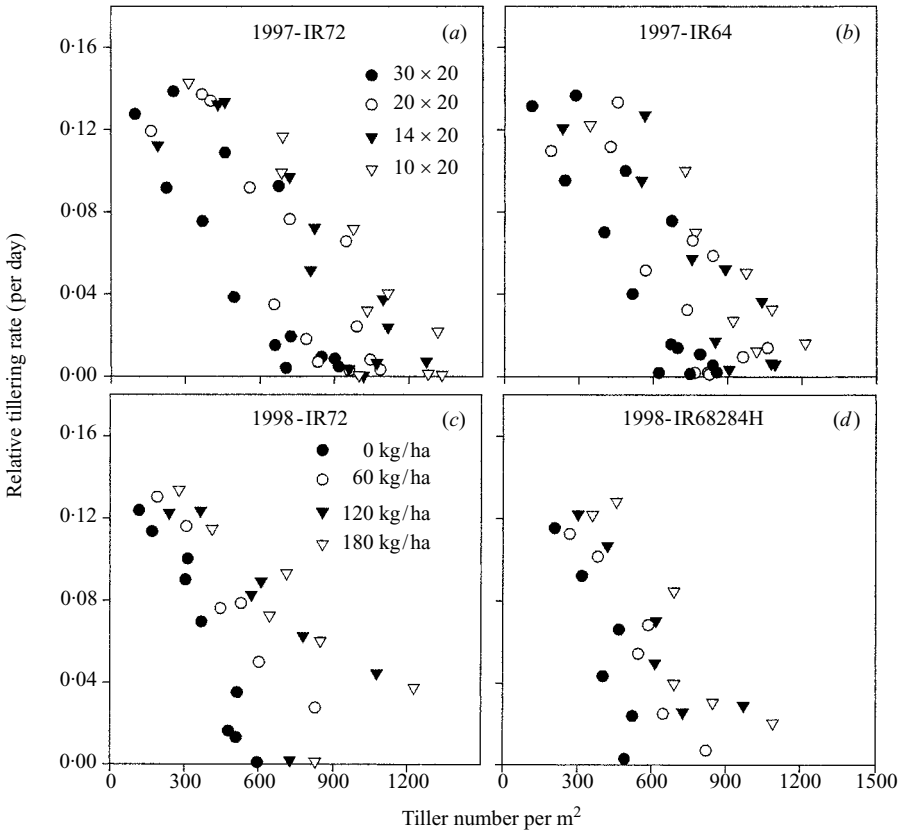


Fig. 6. Relationship between relative tillering rate and tiller number (including main stem or mother tiller) per m^2 at different N input levels. In 1997, 180 kg N/ha was applied for all treatments (*a* and *b*). In 1998, three transplanting spacings were 30×20, 20×20 and 10×20 cm for each N level (*c* and *d*). Symbols are the same for *a* and *b*, and for *c* and *d*, respectively.

Table 1. *Values of parameters in the equation between relative tillering rate* (*RTR*) *and leaf area index* (*LAI*). *The equation is* $RTR = \alpha[exp(-\gamma LAI) - \beta]$. *These values were derived from the data of two field experiments conducted at the International Rice Research Institute* (*IRRI*), *Philippines during the dry seasons of 1997 and 1998 under different planting density and nitrogen input level*

Year	Cultivar	N input (kg/ha)	Value of parameters			Coefficient of determination (r^2)
			α	β	γ	
1997	IR72	180	0·17	0·15	0·54	0·91
	IR64	180	0·17	0·16	0·51	0·87
	S.E. (D.F. = 36)		0·005	0·011	0·020	
1998	IR72	0	0·20	0·26	1·34	0·96
		60	0·23	0·26	0·87	0·94
		120	0·22	0·26	0·54	0·91
		180	0·20	0·20	0·49	0·95
	S.E. (D.F. = 9)		0·009	0·023	0·060	
	IR68284H	0	0·21	0·12	1·42	0·99
		60	0·21	0·17	0·72	0·98
		120	0·20	0·15	0·55	0·98
		180	0·23	0·10	0·56	0·99
	S.E. (D.F. = 9)		0·010	0·019	0·059	

https://doi.org/10.1017/S0021859601001903 Published online by Cambridge University Press

Table 2. *Critical leaf area index in which tillering stopped in different transplanting spacing and seedling number per hill for rice cv. IR72 and IR64 grown at the International Rice Research Institute (IRRI), Philippines during 1997 dry season*

Treatment	IR72	IR64
Transplanting spacing (cm)		
30 × 20	3·60	3·65
20 × 20	3·36	3·56
14 × 20	3·54	3·92
10 × 20	3·36	3·59
S.E.(D.F. = 9)	0·178	0·200
Number of seedlings per hill		
1	3·53	3·42
3	3·36	3·73
6	3·51	3·92
S.E.(D.F. = 24)	0·090	0·134

Table 3. *Critical leaf area index in which tillering stopped in different N input level and transplanting spacing for rice cv. IR72 and IR68284H grown at the International Rice Research Institute (IRRI), Philippines during 1998 dry season*

Treatment	IR72	IR68284H
N input level (kg/ha)		
0	0·98	1·45
60	1·56	2·47
120	2·55	3·51
180	3·37	4·11
S.E. (D.F. = 9)	0·094	0·104
Transplanting spacing (cm)		
30 × 20	1·95	2·89
20 × 20	2·07	2·67
10 × 20	2·33	3·09
S.E. (D.F. = 24)	0·060	0·088

study, data from a wide range of planting densities and N input levels were used to quantify the relationship between tillering rate and LAI. Critical LAI in which tillering stopped was determined based on the relationship between tillering rate and LAI for each treatment. To our knowledge, this is the first report on the quantitative relationship between tillering rate and LAI and on the effect of N on LAI_c in rice crop.

When N was not limiting, LAI_c ranged from 3·36 to 4·11 across cultivar, season and planting density treatments. Critical light transmission ratio (LTR_c) at the base of the canopy is defined as LTR in which tillering stops. LTR_c can be calculated using the equation $LTR_c = \exp(-0{\cdot}5\ LAI_c)$, assuming a light extinction coefficient of 0·5. The LAI_c values of 3·36 to 4·11 correspond to the LTR_c values of 0·13 to 0·19. In other words, when light intensity at the base of the canopy dropped to 13–19% of incident radiation, tiller production stopped in the N-sufficient rice crop. In the N-deficient rice crop, LAI_c decreased and tillering stopped at a greater LTR at the base of the canopy. The concept of LAI_c and LTR_c was confirmed in another field experiment conducted at IRRI during the dry season of 1998. In that experiment, we transplanted three cultivars (IR72, IR64 and IR68284H) at an extremely low planting density (1 m × 1 m, 1 seedling/hill) with very high N input (300 kg/ha). Tillering continued even after flowering in all three cultivars (data not shown). This was because LAI during the entire growing season was smaller than LAI_c, and LTR at the base of the canopy never reached LTR_c.

Plant population biologists consider that tillering is regulated by the existing tiller number per unit ground area through the so-called 'self-thinning' mechanism (Brown & Rothery 1993). However, the present study showed that the relationship between tillering rate and LAI was much closer than between tillering rate and tiller number per m². This suggests that it was LAI, rather than tiller number, that determined when tillering stopped. The negative feedback of tiller number on tillering may work through LAI since high tiller number generally results in large LAI. The value of LAI_c could be used to predict the maximum tiller number stage and improve the predictability of tillering models. In several tillering models, maximum tiller number stage cannot be predicted and is commonly assigned arbitrarily at a certain growth stage such as panicle initiation or stem elongation (Graf *et al.* 1990; Gao *et al.* 1992; Miller *et al.* 1993).

There was a significant effect of N input on LAI_c. Tillering stopped at greater LAI in higher N input treatments. The values of LAI_c at high N input level in this study are comparable with those reported by Lei & Wang (1961) for rice (3·5 to 4·0) and Simon & Lemaire (1987) for ryegrass (about 3·0). However, a much lower LAI_c of 1·8 was reported by Graf *et al.* (1990), possibly because of the low N input (60 kg/ha) in their study. It was reported that tissue death of a rice plant depended on both LAI and tissue N concentration (Dingkuhn *et al.* 1991). Yamamoto *et al.* (1995) suggested that N input and LAI interactively affected tillering. In this study, seasonal average leaf N content of N input treatments at 0, 60 and 120 kg/ha was 20%, 15% and 5% lower than that at 180 kg N/ha, respectively. Therefore, LAI and plant N status are two major factors that influence tiller production in rice crop.

LAI probably affects tillering by attenuation of light intensity and/or by influencing light quality at the base of the canopy where tiller buds and young tillers are located. Shading inhibits tillering and

https://doi.org/10.1017/S0021859601001903 Published online by Cambridge University Press

enhances tiller mortality (Matsushima 1970; Honda 1977; Ong & Marshall 1979; McMaster *et al.* 1987; Yamamoto *et al.* 1995; Caton *et al.* 1997). Wang & Lei (1961) found that dead tillers were generally less than 60 cm tall and received very low light intensity. Number of panicles per unit ground area correlated positively with the intensity of solar radiation (Suzuki & Nakamura 1978). Light quality can be expressed as red/far-red ratio (R/FR). Light quality may have an independent effect on tillering. Lower R/FR caused slower tillering in ryegrass (Deregibus *et al.* 1983), wheat (Casal 1988) and barley (Davis & Simmons 1994). Under field conditions, the effects of light intensity and light quality on tillering are difficult to separate from each other because both light intensity and R/FR decrease exponentially as LAI increases (Morgan & Smith 1981). The effect of LAI on tillering rate quantified by Eqn 2 is probably the final result of the effect of LAI on both light intensity and light quality at the base of the canopy.

The results of this study suggest that tiller number can be predicted using Eqn 2 with LAI as the only input variable for a given N input treatment. However, the values of the three parameters in Eqn 2 are largely affected by plant N status and cultivar. The next step is to develop a tiller model with LAI and tissue N content as the input variable. It is expected that such a model will have the ability to predict tiller number across a wide range of N input levels for a given cultivar.

We thank A. L. Sanico and R. C. Laza for their assistance in managing the field experiments and data collection.

REFERENCES

Blum, A., Ramaiah, S., Kanemasu, E. T. & Paulsen, G. M. (1990). Wheat recovery from drought stress at the tillering stage of development. *Field Crops Research* **24**, 67–85.

Brown, D. & Rothery, P. (1993). *Models in Biology: Mathematics, Statistics and Computing*. Chichester: John Wiley & Sons.

Casal, J. J. (1988). Light quality effects on the appearance of tillers of different order in wheat (*Triticum aestivum*). *Annals of Applied Biology* **112**, 167–173.

Caton, B. P., Forin, T. C. & Hill, J. E. (1997). Mechanisms of competition for light between rice (*Oryza sativa*) and redstem (*Ammannia* spp.). *Weed Science* **45**, 269–275.

Davis, M. H. & Simmons, S. R. (1994). Tillering response of barley to shifts in light quality caused by neighboring plants. *Crop Science* **34**, 1604–1610.

Deregibus, V. A., Sanchez, R. A. & Casal, J. J. (1983). Effects of light quality on tiller production in *Lolium* spp. *Plant Physiology* **72**, 900–902.

Dingkuhn, M., Schnier, H. F., De Datta, S. K., Dorffling, K. & Javellana, C. (1991). Relationships between ripening-phase productivity and crop duration, canopy photosynthesis and senescence in transplanted and direct-seeded lowland rice. *Field Crops Research* **26**, 327–345.

Gao, L., Jin, Z., Huang, Y., Chen, H. & Li, B. (1992). *Rice Cultivational Simulation-optimization-decision Making Systems* (*RCSODS*). Beijing: China Agricultural Science and Technology Press.

Graf, B., Rakotobe, O., Zahner, P., Delucchi, V. & Gutierrez, A. P. (1990). A simulation model for the dynamics of rice growth and development. I. The carbon balance. *Agricultural Systems* **32**, 341–365.

Honda, T. (1977). A study of tillering in paddy rice with special reference to dry matter production. *Bulletin of Agricultural Research Institute*, *Tohoku University*, *Japan* **28**, 171–312.

Jiang, P. Y. (1994). Several biological principles for high-yielding rice. *Chinese Rice Bulletin* **2**, 43–45.

Lei, H. S. & Wang, T. D. (1961). Effects of planting density and nitrogen fertilizer on the total shoot number of rice communities. *Acta Biologiae Experimentalis Sinica* **7**, 227–239.

Matsushima, S. (1970). *Crop Science in Rice—Theory of Yield Determination and its Application*. Tokyo: Fuji Publishing Co. Ltd.

McMaster, G. S., Morgan, J. A. & Willis, W. O. (1987). Effects of shading on winter wheat yield, spike characteristics, and carbohydrate allocation. *Crop Science* **27**, 967–973.

Miller, B. C., Foin, T. C. & Hill, J. E. (1993). CARICE: A rice model for scheduling and evaluating management actions. *Agronomy Journal* **85**, 938–947.

Morgan, D. C. & Smith, H. (1981). Control of development in *Chenopodium album* L. by shade light: the effect of light quantity (total fluence rate) and light quality (red:far red-ratio). *New Phytologist* **88**, 239–248.

Ong, C. K. & Marshall, C. (1979). The growth and survival of severely shaded tillers in *Lolium perenne* L. *Annals of Botany* **43**, 147–155.

Peng, S., Khush, G. S. & 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. Los Baños, Philippines: International Rice Research Institute.

SAS Institute Inc. (1987) *SAS/STAT™ Guide for Personal Computers*, Version 6 Edition. Cary, NC: SAS Institute Inc.

Simon, J. C. & Lemaire, G. (1987). Tillering and leaf area index in grasses in the vegetative phase. *Grass and Forage Science* **42**, 373–380.

Su, Z. F., Zhang, J. & Wang, H. B. (1996). On the relationship between developmental trends of tiller and formation of yield in rice population. In *New Theory and Practice for High Yield and High Profit Rice Production*, *Proceedings of the Fifth National Conference on Theories and Practice of Rice Production*, pp. 25–31. Beijing: China Agricultural Science and Technology Press.

Suzuki, M. & Nakamura, K. (1978). Effect of climatic factors on rice yield and yield components in the warmer regions of Japan. *Japanese Journal of Crop Science* **47**, 529–535.

Tanaka, A., Kawano, K. & Yamaguchi, J. (1966). Photosynthesis, respiration, and plant type of the tropical

https://doi.org/10.1017/S0021859601001903 Published online by Cambridge University Press

rice plant. *Technical Bulletin* 7, 5–18. Los Baños, Philippines: International Rice Research Institute.

Wang, T. D. & Lei, H. S. (1961). Rules for changes in shoot number of rice and wheat communities grown in field at high planting density. *Acta Biologiae Experimentalis Sinica* **7**, 207–224.

Yamamoto, Y., Kurokawa, H., Nitta, Y. & Yoshida, T. (1995). Varietal differences of tillering response to shading and nitrogen levels in rice plant: Comparison between high tillering semi dwarf indica and low tillering japonica. *Japanese Journal of Crop Science* **64**, 227–234.

Yoshida, S. & Hayakawa, Y. (1970). Effects of mineral nutrition on tillering of rice. *Soil Science and Plant Nutrition* **16**, 186–191.

Zhong, X., Peng, S., Sheehy, J. E., Liu, H. & Visperas, R. M. (1999). Parameterization, validation and comparison of three tillering models for irrigated rice in the tropics. *Plant Production Science* **2**, 258–266.

https://doi.org/10.1017/S0021859601001903 Published online by Cambridge University Press