



Full Length Article

A Simple Tillering Model for Irrigated Japonica Rice Based on Measured Relative SPAD for Lower Reaches of Yangtze River Delta, China

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Abstract

We suggested using Relative SPAD of the 3rd and 4th leaf (from the apex) of the main stem (RSPAD), which contains information of both LNC and LAI as the sole input variable to predict tillering rate, and can be measured without destructive sampling. We studied the relationship between Tillering Rate Relative to Tillerable Tiller (TRTT) and LAI and RSPAD from a wide range of plant densities and N inputs. And, based on the "synchronously emerging characteristics" of tillers and the quantitative relationship between TRTT and RSPAD, a simple and applicable model for predicting rice tillering dynamics during tiller-increasing period (before jointing stage) have been presented. Moreover, the model was also validated using wide range of plant densities and N inputs data in two filed experiments. Results showed that TRTT decreased with the increase of LAI. The relationship between TRTT and LAI was affected by N input level, but not by planting density. At a certain LAI, the higher N input level resulted in a greater TRTT. The N input level had a significant effect on critical LAI (LAIc), which was greater in high N input level than lower level. Tillering stopped at LAI of 2.5 to 4.0 depending on N input level. Nonetheless, planting density had little effect on LAIc. TRTT increased with the increase of RSPAD. Neither N input level nor planting density had significant effect on the relationship between TRTT and RSPAD. The coefficient of determination (r^2) and the root mean squared error (RMSE) between the predicted and observed tiller number were ranged from 0.939 to 0.964 and 24.56 to 30.72, respectively. These values of r^2 and RMSE indicates that the model can predict tillering dynamics during tiller-increasing period (before jointing stage) of japonica rice. Although genotype specific calibrations are needed, the fact that one variety may be used for many years in a specific area, and production conditions in a specific area show slight inter-annual changes, and production practices are rather standardized implies a general applicability of our model. © 2013 Friends Science Publishers

Keywords: Rice; Tillering; Model; SPAD; Japonica rice

Abbreviations: TRTT, tillering rate relative to tillerable tiller; RSPAD, relative SPAD of the 3rd and 4th leaf (from the apex) of the main stem

Introduction

Tillering plays an important role in determining rice grain yield as it is closely related to panicle number per unit area (Miller *et al.*, 1991; Counce *et al.*, 1992; Zhong *et al.*, 2002; Li *et al.*, 2003; Shahidullah *et al.*, 2009). Too few tillers result in small number of panicles; while, excessive tillers lead to high tiller abortion, small panicles, poor grain filling and consequently reduction in grain yield (Zhong *et al.*, 1999). To achieve optimum number of panicles, the temporal pattern of tillering is also important (Miller *et al.*, 1991) and therefore regulating tillering dynamics is one of the key factors considered in rice crop management. The field investigation based methods show certain degree of accuracy, but are laborious. To facilitate in-season regulation

of tillering, simple, fast and accurate methods should be developed to predict the tillering rate (Zhong *et al.*, 1999).

Tillering models have been developed using empirical and mechanistic approaches (Zhong *et al.*, 1999). Gao *et al.* (1992) and Huang *et al.* (1996) estimated tiller production before jointing stage based on a logistic tiller growth curve. According to this approach, the intrinsic tiller growth rate constant of the curve was a variable that is affected by soil nitrogen status, temperature, solar radiation and water availability. Similarly, Meng *et al.* (2003) used an exponential function to describe the relationship between leaf appearance and potential increase of tillers. LAI and leaf nitrogen concentration (LNC) were quantified to adjust the potential increase of tillers for the actual increase of

tillers. Keulen and Seligman (1987) assumed tillering rate to be a function of carbohydrate supply and environmental factors affect tillering through altered carbohydrate availability. Penning de Vries *et al.* (1989) applied this assumption to rice and developed the TIL model to simulate tillering of rice crop, with crop growth rate (CGR) and development stage as input variables. Drenth *et al.* (1994) developed the SINK model from the TIL model, and the effect of LNC on tillering production was incorporated. But, as suggested by Zhong *et al.* (1999), the way in which nitrogen effect on tillering was accounted for SINK model is not effective. In both TIL and SINK model, parameters were given as constant, tabulated function of input variables (e.g. development stage or LNC) or derived from experimental data. On the other hand, based on the linear relationship between relative tillering rate and relative growth rate (RGR) (Schnier *et al.*, 1990; Dingkuhn *et al.*, 1991), Zhong *et al.* (1999) developed the RGR model to predict number of tillers using crop biomass as the sole input. Moreover, Miller *et al.* (1993), and Wu and Wilson (1998) predicted number of tillers of rice plants based on the "synchronously emerging characteristics" of tillers, leaf age and carbohydrate supply. Although all these models can predict number of tillers well with appropriate value of parameters (Zhong *et al.*, 1999), there are still some limitations. Firstly, these tillering models often need to be re-parameterized as the original parameters were derived from data sets covering a narrow range of plant density and nitrogen input. Secondly, some of the input variables (e.g. soil nitrogen status, LAI, CGR, RGR and LNC) used in predicting tillering rate were measured through destructive sampling and chemical analysis approaches that are accurate but laborious and time consuming, or simulated by other fast models (e.g. LAI model, growth model), but the accuracy of each depends not only on the tillering model itself, but also on the accuracy of the simulation of input variables as well. Therefore, a simple, fast and accurate model should be developed.

LAI and plant nitrogen status are two major factors that influence tiller production in rice crops. Quantifying the relationship between tillering rate, LAI and plant nitrogen status may help improve the predictability of the tillering models (Zhong *et al.*, 2002). Nevertheless, to get accurate value of LAI or LNC requires destructive sampling and chemical analysis, thus is laborious and time consuming. To avoid this, Wang *et al.* (2002) suggested to use an indirect index i.e. Relative SPAD (RSPAD), which can be measured without destructive sampling and has a stable quantitative relationship with LNC to measure the nitrogen nutrient status of rice plants. RSPAD is calculated as "(SPAD value of the 3rd leaf from the apex - SPAD value of the 4th leaf from the apex)/SPAD value of the 3rd leaf from the apex", it not only includes the information about N nutrient status, but also information on the vertical distribution of nitrogen among leaves of plants, which was considered in relation to the photosynthetic production of leaf canopy that was

mainly determined by LAI (Yin *et al.*, 2003). Therefore, RSPAD can be used as a composite index to predict tillering rate instead of LNC and LAI.

Therefore, in this study, we suggested using RSPAD as the sole input variable to predict tillering rate during tiller-increasing period. Based on this assumption, using data drawn from a wide range of plant densities and N inputs in two filed experiments conducted at lower reaches of Yangtze River delta, China, in 2009, we studied the relationship between tillering rate relative to tillerable tiller (TRTT), and LAI and RSPAD. Furthermore, based on the "synchronously emerging characteristics" of tillers and the quantitative relationship between TRTT and RSPAD, we presented a simple and applicable model for predicting rice tillering dynamics during tiller-increasing period before jointing stage. Moreover, the model has been validated using data drawn from a wide range of plant densities and N inputs in two filed experiments in 2010.

Materials and Methods

Field Experiments and Data Collection

Four field experiments were conducted between May to October in 2009 and 2010 at Jiangning Experimental Station, Nanjing Agriculture University, Nanjing city, Jiangsu province, China (32°2'N, 118°42'E, 80 m Alt). This experimental station is located at the lower reaches of Yangtze River delta, and dominated with rice-wheat crop rotation, where rice is cultivated for centuries. Weather conditions of experimental site during rice growing season (from May 20 to October 31) in both year were as follows: the total effective accumulated temperature (10°C as base temperature), total rainfall, total hours of sunshine were 2481.7 and 2455.2°C, 955.0 and 545.9 mm, 1007.0 and 1029.5 h in 2009 and 2010, respectively. Daily maximum and minimum temperature, relative humidity are shown in Fig. 1 and Fig. 2, respectively. The soil was Orthic Acrisols (FAO taxonomy) with pH 7.3, 16.7 g organic C kg⁻¹, 1.0 g total N kg⁻¹, and 11.6 cmol kg⁻¹ cation exchange capacity. Short-duration late japonica cultivar, Ningjing1 featured with the generation of 18 leaves from main stem (between emergence to maturity) and 6 internodes at maturity. All seeds were kept in water for 60 h and then sown into rectangular plastic containers (58 cm × 28 cm × 3 cm) with 120 g seeds per container. Special substrate was used for seedling (Chaimihe Biotechnology Ltd., China).

For all treatments, 18 days old seedlings (at 3rd to 4th leaf age) were transplanted on June 8 using a rice transplanter (model ZS-2(P28), Tongyang, China) in plots (size 5 m × 8 m) with 3-4 seedlings per hill. Field was kept flooded with 2-3 cm deep water layer before jointing stage to avoid water deficit during tillering stage. All four experiments were laid in randomized complete block design repeated in triplicate; details on experimental design were as

follows:

Exp. 1 and 2 were conducted in 2009. For Exp. 1, varying nutritional area for rice plants were given by different transplanting spacing (30 cm × 13 cm, 30 cm × 15 cm, 30 cm × 18 cm, 30 cm × 21 cm, 30 cm × 24 cm, 30 cm × 28 cm) treatments. Fertilizers including 81 kg N ha⁻¹ as urea, 21 kg P₂O₅ ha⁻¹ as single superphosphate, 78 kg K₂O ha⁻¹ as KCl were applied and incorporated in all plots 1 day before transplanting. Nitrogen topdressings were applied at 7 days after transplanting (DAT) (81 kg N ha⁻¹ as urea), panicle initiation (54 kg N ha⁻¹ as urea) and at the 2nd leaf from top stretching (54 kg N ha⁻¹ as urea). K topdressing was applied at panicle initiation (78 kg K₂O ha⁻¹ as KCl). The total N and K₂O rate were 270 and 156 kg ha⁻¹.

For Exp. 2, a randomized block design was used with six N input level treatments (0, 54, 108, 162, 216, 270 kg N ha⁻¹ as urea; 50% of which was applied 1 day before transplanting and remaining 50% at 7 DAT). Transplanting space was 30 cm × 13 cm. In addition to N treatments, 21 kg P₂O₅ ha⁻¹ as single superphosphate, 78 kg K₂O ha⁻¹ as KCl were applied in all plots 1 day before transplanting.

Exp. 3 and 4 were conducted in 2010. For Exp. 3, varying nutritional area for rice plants was given by different transplanting spacing (30 cm × 13 cm, 30 cm × 21 cm, 30 cm × 28 cm). Other conditions were the same as in Exp. 1.

For Exp. 4, three N input level treatments (0, 108, 216 kg N ha⁻¹ as urea 50% of which were applied 1 day before transplanting and remaining 50% at 7 DAT). Other conditions were the same as in Exp. 2.

All agronomic practices, including crop management and experimental methods were kept uniform across the years and experiments, except fertilizer application and transplanting spacing. Standard measures were adopted to keep field free of weeds, insects and disease.

In each experiment, rice plants from randomly selected 30 hills per plot were used to measure leaf age, tiller number, SPAD value (portable SPAD-502, MINOLTA, Japan) of the 3rd and 4th leaf from the top (specific site was 1/3 leaf length from leaf apex) at 3 d interval from 5 DAT to jointing stage. Meanwhile, 5 hills per experimental plot were sampled to measure leaf area of individual leaves through LI-3000 (LI-COR, Lincoln, NE, USA) and expressed as LAI. The Relative SPAD was calculated as follows:

$$RSPAD = \frac{(SPAD3 - SPAD4)}{SPAD3} \quad (1)$$

Where, SPAD3 and SPAD4 are the SPAD value of the 3rd and 4th leaf from the apex respectively.

Data from both experiments during 2009 were used for model development and the remaining two experiments conducted in 2010 were used for model validation. The method of model validation was as follows:

$$r^2 = \frac{\left(\sum_{i=1}^n (OBS_i - \overline{OBS})(SIM_i - \overline{SIM}) \right)^2}{\sum_{i=1}^n (OBS_i - \overline{OBS})^2 \sum_{i=1}^n (SIM_i - \overline{SIM})^2} \quad (2)$$

$$RMSE = \sqrt{\frac{\sum_{i=1}^n (OBS_i - SIM_i)^2}{n}} \quad (3)$$

Where, OBS_i is the observed value, \overline{OBS} is the mean values of the observed variables, SIM_i is the simulated value, \overline{SIM} is the mean values of the simulated variables, n is the number of samples.

Larger r^2 and smaller RMSE are indicators of greater model accuracy.

Model Description

The tillering model is based on the following two assumptions of rice growth processes:

(1). “synchronously emerging characteristics” means the emergence of a tiller from the subtending leaf sheath of the mother stem is strongly related with the number of leaves to have emerged on the mother stem, and that the number of leaves on a tiller increase synchronously with the number of leaves on the mother stem. This relationship was found not only between a main stem and the primary tillers but also between the primary and secondary tillers (Katayama, 1951). Generally, the first leaf of a new tiller at the subtending leaf sheath of the i^{th} leaf on the mother stem emerges synchronously with the $(i+3)^{\text{th}}$ leaf on the mother stem. For tiller with at least 3 leaves, there might be one or more new tillers emerging synchronously with the next leaf on this tiller, thus we call it tillerable tiller. TY_i is the tillerable tiller number at leaf age i .

(2). If a tiller bud stopped differentiating and developing due to environmental stress, it could not resume growing even the environment became suitable (Hanada, 1982; Jiang et al., 1994).

Generally, total number of tillers (including the main stem) of a single plant at any leaf age (i) during tiller increasing period can be described as equation (4).

$$TN_i = TN_{i-1} + \Delta TN_i \quad (4)$$

Where, TN_i and TN_{i-1} are the tiller number of a single plant at leaf age i and $i-1$ respectively; ΔTN_i is the number of new tillers synchronously emerging with the i^{th} leaf on the main stem.

When the leaf number on the main stem is not exceeding 3, there are not new tillers emerged, that is:

$$\begin{aligned} i=1, & TN_1 = 1, TY_1=0; \\ i=2, & TN_2 = 1, TY_2=0; \\ i=3, & TN_3 = 1, TY_3=1 \text{ (the main stem become tillerable).} \end{aligned}$$

When the leaf number on the main stem ≥ 3 , new tillers would emerging synchronously with the i^{th} leaf, the number

of which can be calculated as follows:

$$\Delta TN_i = TY_{i-1} \times TRTT_i \quad (5)$$

Where, $TRTT_i$ is TRTT at i^{th} leaf age, which is defined as the ratio of the actual number of new tillers at a specific leaf age (ΔTN_i) to the number of tillerable tillers at the previous leaf age (TY_{i-1}).

According to the “synchronously emerging characteristics” of tillers, we can infer that the number of tillerable tillers at leaf age $i-1$ (TY_{i-1}) was equal to the number of total tillers at leaf age $i-3$ (TN_{i-3}), that is because all the tillers at leaf age $i-3$ will have at least 3 leaves at leaf age $i-1$. Then equation (5) can be transformed as:

$$\Delta TN_i = TN_{i-3} \times TRTT_i \quad (6)$$

And $TRTT_i$ can be calculated as:

$$TRTT_i = \Delta TN_i / TN_{i-3} = (TN_i - TN_{i-1}) / TN_{i-3} \quad (7)$$

Where, TN_i , TN_{i-1} and TN_{i-3} were observed values for calculating TRTT during the model developing process.

Therefore, the total tillers (including main stems) number of a single plant can be calculated as equation (8):

$$TN_i = \begin{cases} 1 & (i \leq 3) \\ TN_{i-1} + TN_{i-3} \times TRTT_i & (i > 3) \end{cases} \quad (8)$$

And tiller number (including the main stems) per unit land area can be calculated as:

$$UTN_i = BTN \times TN_i \quad (9)$$

Where, UTN_i is the tillers number per unit land area at leaf age i , BTN is the basal plants number per unit land area.

According to equation (8) and (9), so long as we know the tillers number at the first three leaf age after transplanting (normally leaf age 4, 5, 6 for machine-transplanting rice) and TRTT at each leaf age, the tillers number at any leaf age before jointing stage could be estimated.

In the lower reaches of Yangtze River delta, China, rice seedlings are normally transplanted into field in middle or late June and attains the jointing stage in late July. During this period, daily minimum air temperature remained well above 15°C, which would not limit the tillering process. Therefore, the TRTT is mainly affected by genotype, water and nutrient supply, and LAI. To enhance emergence of productive tillers, water layer was ensured 2-3 cm above the soil to avoid water stress until number of total tillers reaches the objective panicle number. Therefore, only the effects of genotype, nitrogen supply and LAI on tillering process (TRTT) have been discussed.

Results and Discussion

Relationship between TRTT and LAI

In all treatments, TRTT decreased with the increase of LAI

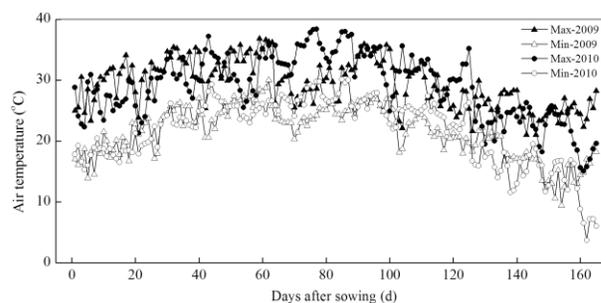


Fig. 1: Maximum and minimum air temperature at the experimental site during the whole rice growing season in 2009 and 2010

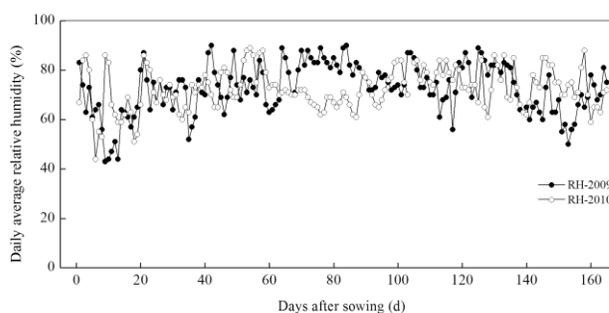


Fig. 2: Daily average relative humidity at the experimental site during the whole rice growing season in 2009 and 2010

(Fig. 3). This is in agreement with the results reported by Zhong *et al.* (2002) and Meng *et al.* (2003). Both of them found that the relative tillering rate decreased exponentially as LAI increased at a given nitrogen input level and planting density.

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 (Deregibus *et al.*, 1983; Casal, 1988). Shading inhibits tillering and enhances tiller mortality (Matsushima, 1970; Honda, 1997; Ong and Marshall, 1979; McMaster *et al.*, 1987; Yamamoto *et al.*, 1995; Caton *et al.*, 1997). Wang and Lei (1961) found that dead tillers were generally less than 60 cm tall and received very low light intensity.

At a given LAI, slight variation in TRTT was observed among different planting densities especially when LAI was lower than 0.8 or greater than 2.2 (Fig. 3A); At a given LAI from about 0.8-2.2, TRTT increased slightly with the increase of planting density (i.e. 30 cm × 13 cm > 30 cm × 15 cm > 30 cm × 18cm > 30 cm × 21cm > 30 cm × 24 cm > 30 cm × 28 cm) (Fig. 3A), which may result from the fact that plots with high planting density achieved a given LAI earlier than plots with lower planting density, and soil N status during early stage is often better than later stage. Thus, we can infer that planting density had little effect on the relationship between TRTT and LAI; similar findings

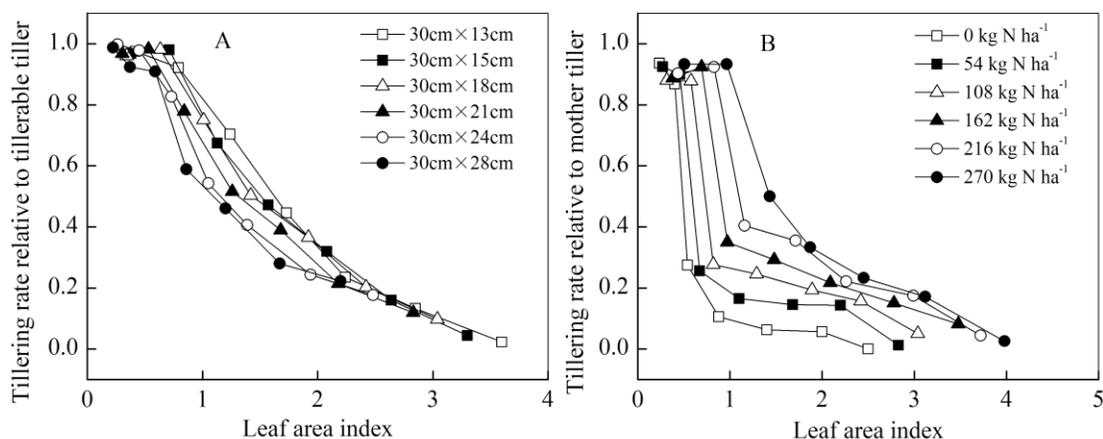


Fig. 3: Relationship between tillering rate relative to tillerable tiller and leaf area index among different transplanting density (A: Exp. 1) and different N input treatments (B: Exp. 2)

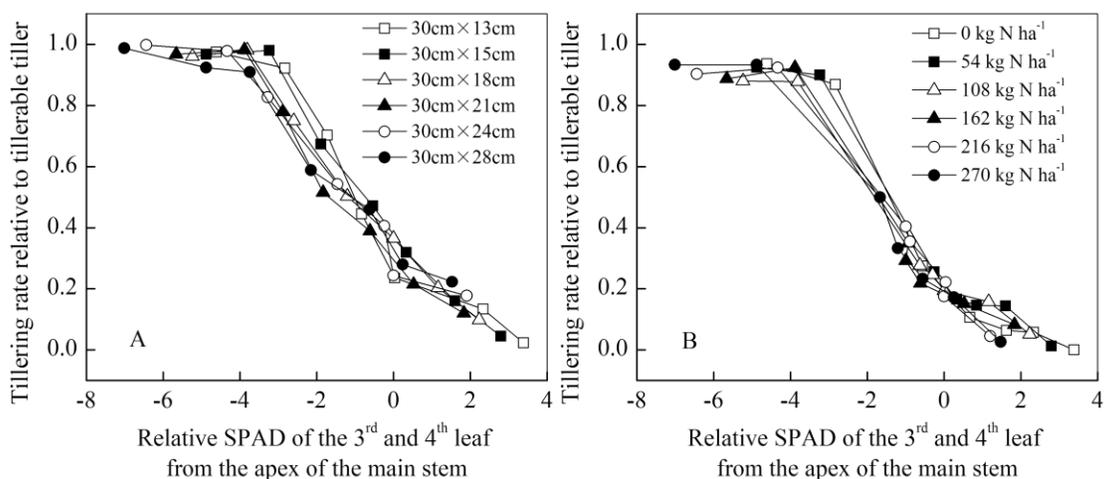


Fig. 4: Relationship between tillering rate relative to tillerable tiller and relative SPAD of the 3rd and 4th leaf from the top of the main stem among different transplanting density (A: Exp.1) and different N input treatments (B: Exp. 2)

were reported by Zhong *et al.* (2002). However, N input treatments had a significant effect on this relationship (Fig. 3B). At a certain LAI, the higher N input level resulted in a greater TRTT (270 kg N ha⁻¹ > 216 kg N ha⁻¹ > 162 kg N ha⁻¹ > 108 kg N ha⁻¹ > 54 kg N ha⁻¹ > 0 kg N ha⁻¹).

There was a significant effect of N application on the critical LAI at which tillering stopped (LAI_c), which ranged from 2.5 to 4.0 depending on N input level (Fig. 3B). The higher the N input level, the greater the LAI_c. Compared with N treatment, planting density had a relatively small influence on LAI_c which was about 3.6 in Exp. 1 (Fig. 3A). This is in agreement with the results reported by Zhong *et al.* (2002).

Relationship between TRTT and RSPAD

In all treatments (Exp. 1 and Exp. 2), TRTT remained nearly constant (~1) at a lower RSPAD (RSPAD ≤ -3), and decreased

with the increase of RSPAD when RSPAD > -3. At a given RSPAD, slight variation in TRTT was observed among different planting densities (Fig. 4A) and N input levels (Fig. 4B). This indicated that neither planting density nor N input level had significant effect on the relationship between TRTT and RSPAD. Fitting all the data in Fig. 4A and Fig. 4B, the relationship between TRTT and RSPAD was described quantitatively using Eq. 10 (Fig. 5). Eq. 10 fitted the data of all treatments (Exp. 1 and Exp. 2) well, with r^2 of 0.967 and RMSE of 0.06. The high r^2 and low RMSE suggests that the planting density, N input level and development stage did not have much effect on the relationship between TRTT and RSPAD. Therefore, RSPAD can be used as the sole input for predicting TRTT. To our knowledge, this is the first report on the concept of TRTT and on the quantitative relationship between TRTT and RSPAD in rice crop.

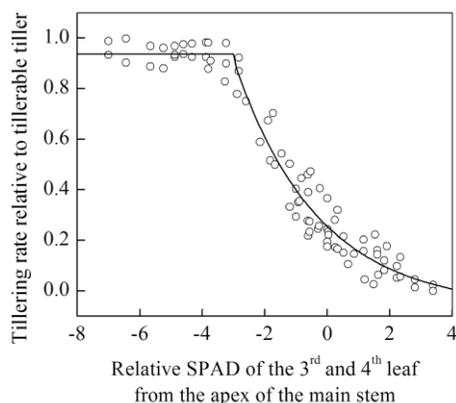
$$TRTT_i = \begin{cases} m & RSPAD \leq -3 \\ a \times b^{RSPAD_i - 1} + c & RSPAD > -3 \end{cases} \quad (10)$$

Table 1: r^2 and RMSE of the simulation for Exp. 3

Transplanting spaces	r^2	RMSE
30 cm × 13 cm	0.952	30.72
30 cm × 21 cm	0.958	30.72
30 cm × 28 cm	0.939	26.80

Table 2: r^2 and RMSE of the simulation for Exp. 4

N inputs	r^2	RMSE
0 kg N ha ⁻¹	0.964	24.56
108 kg N ha ⁻¹	0.962	25.70
216 kg N ha ⁻¹	0.957	25.41

**Fig. 5:** Relationship between tillering rate relative to tillerable tiller and relative SPAD of the 3rd and 4th leaf from the top of the main stem ($r^2=0.967$; RMSE=0.06)

Where, $RSPAD_{i-1}$ was RSPAD in leaf age $i-1$; m was the average value (0.936 in this study) of TRTT at lower RSPAD ($RSPAD \leq -3$) in both experiments (Exp. 1 and Exp. 2); a , b and c were cultivar parameters (0.319, 0.689 and -0.064 respectively in this study) fitted using experimental data.

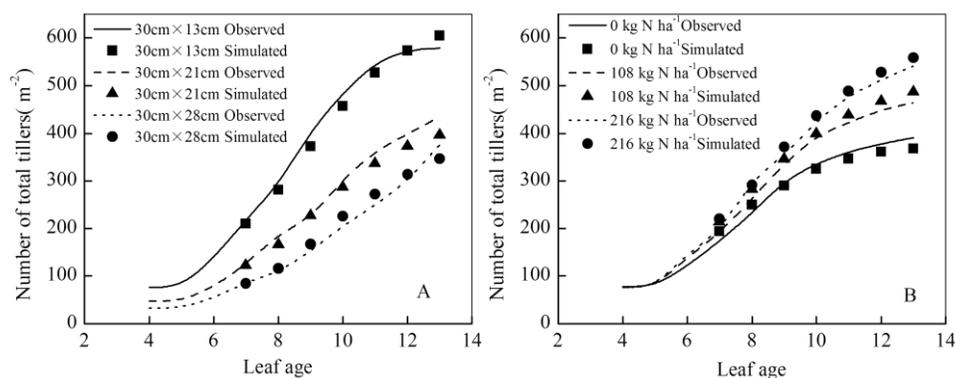
Model Validation

The tillering model presented in this paper was validated using experimental data from Exp. 3 and Exp. 4. Predicted

and observed values of number of total tillers at 7th to 13th leaf stages of each treatment were compared (Fig. 6). The r^2 and RMSE of each simulation ranged from 0.939 to 0.964 and 24.56 to 30.72, respectively (Table 1 and 2). Most of the predicted values of the number of total tillers were close to the observed values in all planting densities (Fig. 6A) and N input levels (Fig. 6B). This indicated that the model predicted the tillering dynamics during tiller-increasing period (before jointing stage) well despite the great variation in planting density and N input. The predictive ability of our model is good and comparable with other models e.g. TIL, SINK and RGR model (r^2 ranged from 0.93 to 0.95) as tested by Zhong *et al.* (1999) and the tillering model reported by Meng *et al.* (2003).

Moreover, as the input variable (RSPAD) of our model is measured using non-destructive method, the simplicity and ease of use are enhanced. In contrast, input variables of CGR in TIL and SINK model, RGR in RGR model, and LAI and LNC in the tillering model developed by Meng *et al.* (2003) were measured through destructive sampling and chemical analysis approaches that are accurate but laborious and time consuming, or simulated by other models (e.g. leaf area model, growth model) that are fast, but the accuracy depends not only on the tillering model itself, but on the accuracy of the simulation of input variables as well. Therefore, our tillering model is more simple and faster than most of the previous tillering model, without the reduction of accuracy.

Nevertheless, there are still some limitations. Firstly, our tillering model is actually a tiller-increasing model. To extend its ability to predict tiller-decreasing dynamics, it needs more efforts. Secondly, although data drawn from a wide range of planting density and N input levels was used for model development and validation, only one japonica rice variety was used. For other japonica varieties, cultivar parameters (i.e. m , a , b and c) in Eq. 10 may need to re-fit, because different varieties may show varying degree of sensitivities to RSPAD. In spite of this, the fact that one variety may be used for many years in a specific area, and production conditions in a specific area show slight inter-annual changes and production practices are rather

**Fig. 6:** Comparison between simulated value and observed value of number of total tillers before jointing stage (A: Exp. 3; B: Exp. 4)

standardized implies a general applicability of our model. Thirdly, the tillering model has been tested only at a specific location at the lower reaches of Yangtze River delta of China. It needs further studies to test its applicability to rice production practices in use to other areas, especially the other primary japonica rice planting area i.e. the northeast area of China.

Conclusions

TRTT decreased with the increase of LAI. The relationship between TRTT and LAI was affected by N input level, but not by planting density. At a certain LAI, the higher N input level resulted in greater TRTT. The N input level had a significant effect on LAIc, which was greater in high N input level than lower level. Tillering stopped at LAI of 2.5 to 4.0 depending on N input level. Planting density had little effect on LAIc. TRTT increased with the increase of RSPAD. Neither N input level nor planting density had significant effect on the relationship between TRTT and RSPAD.

Based on the stable quantitative relationship between TRTT and RSPAD, and the "synchronously emerging characteristics" of tillers, we presented a tiller-increasing model and validated it using data drawn from a wide range of plant densities and N inputs in two field experiments. The results indicate that the model can predict tillering dynamics during tiller-increasing period before jointing stage of japonica rice well at the lower reaches of Yangtze River delta of China. However, it needs more efforts to extend its ability to predict tiller-decreasing dynamics, and to test its applicability to rice production practices in use to other areas.

Acknowledgments

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