Relationship between Dry Weight at Heading and the Number of Spikelets on Individual Rice Tillers

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Abstract: The objectives of this study were to identify the growth parameters involved in determining the number of spikelets on an individual tiller (ST) and to elucidate how ST is determined in rice (Oryza sativa L.). We examined the correlation of ST with the dry weight (DWT), leaf area (LAT), and the amount of nitrogen (NT) at heading for individual tillers grown under different conditions that were expected to affect spikelet production. In 1999, the japonica rice cultivars “Minesashi” (short-duration), “Hinohikari” (intermediate-duration), and “Akebono” (long-duration) were transplanted in a paddy field on two different dates (EARLY and LATE). In 2000, Hinohikari was grown under three different treatments (gibberellic acid application, nitrogen topdressing, and thinning of hills at panicle initiation) and without treatment (control). Covariance and partial correlation analyses indicated that ST was positively and essentially correlated with DWT rather than with LAT and NT. The regression of ST on DWT was stable within each cultivar regardless of the treatment, year, tiller order, and number of differentiated spikelets. The slope of the regression was the steepest in the short-duration cultivar. These results suggest that the steep slope is desirable for high-yielding cultivars with large panicles. We conclude that ST is mostly determined by dry matter production of an individual tiller regardless of the number of differentiated spikelets. We present a diagram showing the relationship between dry matter production and the number of differentiated, surviving, and degenerated spikelets on an individual tiller.

Key words: Dry weight, Gibberellic acid, Number of spikelets, Rice, Spikelet degeneration, Spikelet differentiation.
have been made, although the environmental conditions could affect ST. In addition, the factors affecting these parameters are not clear. Although SP was shown to increase with nitrogen topdressing and thinning (Matsushima, 1957), these treatments do not seem to directly increase these parameters but rather to enhance a physiological process, e.g., photosynthesis or nitrogen uptake, which determines the dry weight and amount of nitrogen in an individual tiller.

Our objectives were to identify the growth parameters of an individual tiller that affect the process determining ST and to elucidate how ST is determined. The leaf area of each tiller at late differentiation of the panicle is positively correlated with the number of differentiated spikelets on each tiller (ST dif) (Sheehy et al., 2001), which suggests that leaf area is involved in determining ST. The parameters involved in the process that determines ST are expected to be stably related to ST despite variations in growth conditions. Therefore, we analyzed the relationships among ST, dry weight (DWT), amount of nitrogen (NT), and leaf area (LAT) at heading for each tiller of cultivars grown with two different transplanting dates, gibberellic acid application, nitrogen topdressing, and thinning, which were all expected to affect spikelet production. We also examined the effects of the treatments on the number of differentiated and surviving spikelets on the main tiller. We propose a diagram showing the relationship between dry matter production and the number of differentiated, surviving, and degenerated spikelets on an individual tiller.

Materials and Methods

1. Plant materials

In 1999, we conducted a field experiment in an irrigated paddy field at the National Agricultural Research Center for the Western Region in Fukuyama, Japan (34°30'N, 133°23'E), to analyze the relationships among ST, DWT, and LAT in three rice cultivars with two transplanting dates. The japonica rice cultivars “Mineasahi” (short-duration), “Hinohikari” (intermediate-duration), and “Akebono” (long-duration) were transplanted at a density of three seedlings per hill and 22.2 hills m⁻² on 30 April (EARLY) and 16 June (LATE). We applied 2.67 g N m⁻², 2.67 g P₂O₅ m⁻², and 2.67 g K₂O m⁻² as the base fertilizer, and we applied the same amount of fertilizer twice for the topdressing. The first topdressing was applied on 2 and 15 July for Mineasahi, 15 July for Hinohikari, and 20 July for Akebono in the EARLY group; and on 31 July for Mineasahi, 9 August for Hinohikari, and 13 August for Akebono in the LATE group. The experimental design was a split plot with three blocks, in which the transplanting dates determined the main plots, and the cultivars represented the subplots. The plot area was 25.9–28.1 m².

In 2000, we conducted an experiment in the same paddy field to analyze the relationships among ST, DWT, LAT, and NT under treatment conditions expected to affect spikelet production. Hinohikari was transplanted on 13 June 2000 in the same way as in 1999. For the base fertilizer, we applied 4 g N m⁻², 4 g P₂O₅ m⁻², and 4 g K₂O m⁻²; for topdressing, we applied 2 g N m⁻², 2 g P₂O₅ m⁻², and 2 g K₂O m⁻² on 2 and 15 August, respectively. At panicle initiation (21 July, 32 d before heading), one of three different treatments was applied. For the gibberellic acid treatment (GA), a 50-ppm gibberellic acid (GA₃) solution was applied at a rate of 0.5 L m⁻². The concentration is equal to that in Yamagishi et al. (1994) and the application rate is slightly less than that in Yamagishi et al. (1994). For the nitrogen topdressing (N), 2 g N m⁻² and 2 g K₂O m⁻² were applied. For the thinning treatment (THIN), the hills were thinned to half the original density. We also established a control group that received no treatment (CONT). The experimental design was a completely randomized block design with four blocks. The plot area was 19.0–20.6 m².

2. Measurements

At heading, some of the main, primary and secondary tillers were harvested for measurement. The hills, including the basal parts of the tillers, were harvested, and carefully divided into three plants. The individual plants were divided into main, primary, and secondary tillers based on the regularity of the tiller arrangement (Hoshikawa, 1989). No tertiary tillers were found. The leaf area of each tiller was measured using a leaf area meter (AAM-7 or AAM-8; Hayashidenkoh, Tokyo, Japan). The tillers and leaves were dried at 80°C for 3 d and then weighed. The number of spikelets was counted for each harvested tiller. In 1999, the leaf area was measured on 32–35 tillers (16–19 main, 9–12 primary, and 4–5 secondary tillers) for each combination of cultivar and transplanting date, with three blocks; the dry weight was measured for 17–20 tillers (2–4 main, 9–12 primary, and 4–5 secondary tillers). In 2000, the leaf area was measured for 32–35 tillers, and the dry weight was measured for 36 tillers (9–12 main, 12–14 primary, and 10–12 secondary tillers) for each treatment, with four blocks. For the nitrogen determinations, four each of main, primary, and secondary tillers were ground, and the nitrogen content was determined using a N-C analyzer (Sumigraph NC-800; Sumika Chemical Analysis Service, Osaka, Japan).

To measure the number of differentiated spikelets on the main tiller, we harvested two panicles from two hills in 1999, and eight panicles from four hills in 2000 for each plot just before heading and stored them in
formalin : acetic acid : 50% ethanol, 1 : 18 : 1 (FAA). We counted the number of degenerated spikelets under a binocular microscope according to Kobayasi et al. (2001a) and the number of surviving spikelets by eye. The total number of differentiated spikelets was defined as the sum of degenerated and surviving spikelets.

For top dry weight measurements, eight hills in the THIN treatment group and 15 hills in the other treatment groups were harvested at heading for each plot in both years, dried at 80°C for 3 d, and weighed. At maturity, a 2.16-m² portion of each plot was harvested to measure S, P, and SP in both years. We analyzed two types of parameters, population means (DWP and SP) and individual tiller values (DWT, ST, LAT, and NT). DWP is the mean of the DWT values, and SP is the mean of the ST values, as below:

\[
\text{DWP} = \frac{\sum_i DWT_i}{P},
\]

\[
\text{SP} = \frac{\sum_i ST_i}{P},
\]

where, DWTᵢ is the DWT of tiller i, and STᵢ is the ST of tiller i.

3. Data analysis

Covariance and correlation analyses among DWT, LAT, NT, and ST were performed using the REG and GLM procedures in SAS (ver. 9.1; SAS Institute, Cary, NC, USA). Partial correlation analyses among DWT, LAT, and ST and among DWT, NT, and ST were performed using R software (ver. 1.7.1; R Foundation for Statistical Computing, Vienna, Austria). In 1999, analysis of variance (ANOVA) was performed on S, P, SP, and DWP with a completely randomized block design for each cultivar between transplanting dates, using the GLM procedure in SAS. In 2000, Tukey's test was conducted on S, P, SP, DWP, and the mean numbers of differentiated and surviving spikelets on the main tiller among treatments using the GLM procedure in SAS.

To analyze S and SP, we obtained the regression of ST on DWT, as follows:

\[
ST = aDWT + b,
\]

where a and b are constants. ST, was obtained by substituting DWT, into equation (3):

\[
STᵢ = aDWTᵢ + b.
\]

S was obtained by summing equation (4) for all tillers per square meter:

\[
S = a\sum_i DWTᵢ + b\sum_i i,
\]

\[
= aDW + bP
\]

where DW is the top dry weight per square meter at heading. To examine whether equation (5) is valid under various conditions, we estimated S for Hinohikari and Akebono cultivars by substituting the DW and P values obtained from other experiments. These data were not used to determine the parameters of equation (3). The relationship between SP and

| Year | Cultivar | Treatment | Panicles (m⁻²) | Spikelets per panicle | Spikelets (10² m⁻²) | Dry weight per panicle (g) |
|------|----------|-----------|----------------|----------------------|---------------------|---------------------------|
| 1999 | Mineasahi| EARLY     | 420 ± 2NS      | 100 ± 3*             | 422 ± 12*           | 2.26 ± 0.07NS             |
|      |          | LATE      | 399 ± 10       | 86 ± 1               | 344 ± 7             | 1.74 ± 0.07              |
|      | Hinohikari| EARLY     | 416 ± 16NS     | 85 ± 1NS             | 354 ± 15NS          | 2.75 ± 0.21NS            |
|      |          | LATE      | 367 ± 3        | 85 ± 2               | 314 ± 8             | 2.33 ± 0.13              |
|      | Akebono  | EARLY     | 400 ± 21NS     | 85 ± 2NS             | 332 ± 17NS          | 2.98 ± 0.07NS            |
|      |          | LATE      | 391 ± 6        | 86 ± 3               | 335 ± 12            | 2.57 ± 0.06              |
| 2000 | Hinohikari| GA        | 371 ± 4b†      | 90 ± 2b              | 333 ± 12b           | 3.17 ± 0.05a             |
|      |          | N         | 420 ± 19a      | 86 ± 1c              | 362 ± 14a           | 2.74 ± 0.13b             |
|      |          | THIN      | 258 ± 12c      | 109 ± 1a             | 280 ± 12c           | 3.16 ± 0.20a             |
|      |          | CONT      | 402 ± 14ab     | 83 ± 2c              | 333 ± 13b           | 2.74 ± 0.09b             |

Data are means ± SE.

*Significant at P < 0.05 between transplanting dates in 1999 (ANOVA).

NS, not significant at P < 0.05.

†, Means followed by the same letter are not significantly different at P < 0.05 in 2000 (Tukey's test).

CONT is the no-treatment control.
DWP was obtained by dividing equation (5) by P:

\[
SP = \frac{aDWP + b}{P}
\]

(6)

Degenerated ST, ST_{deg}, is expressed as follows:

\[
ST_{deg} = ST_{dif} - ST_{dif} = ST_{dif} - aDWT - b
\]

(7)

Results

1. Effect of treatments on spikelet production

In 1999, the values of S and SP were significantly higher in the EARLY planting group than in the LATE planting group for the short-duration cultivar Mineasahi (Table 1). For the intermediate- and long-duration cultivars, Hinohikari and Akebono, there was no significant difference in S, P, or SP between the transplanting dates. For all cultivars, DWP was larger in the EARLY than in the LATE groups, although this difference was not significant.

In 2000, the value of P was significantly lower in the THIN group than in the control. P was lower in the GA group and higher in the N group in comparison with the control, but not significantly so. The SP value was higher in the GA and THIN groups than in the control (Table 1). The value of S was higher in the N group in comparison with the control, although SP was not. The DWP was higher in the GA and THIN groups than in the control, whereas the DWP in the N group was equal to the control value. Thus, the SP value was affected by the transplanting date in the Mineasahi cultivar and by gibberellic acid application and thinning. Nitrogen topdressing affected S but not SP.

2. Relationship between dry weight of an individual tiller at heading (DWT) and number of spikelets on the tiller (ST)

The DWT was positively correlated with ST for each treatment in 1999 and 2000 (Fig. 1, left). For the Mineasahi cultivar, the covariance analysis showed that a single regression of ST on DWT was applicable to both transplanting dates. For the Hinohikari cultivar, the covariance analysis for each year showed no difference in the slope of the regression among the treatments. The slope in 1999 was almost equal to that

Fig. 1. Dry weight of each tiller at heading (DWT) with the number of spikelets on each tiller (ST) in three rice cultivars. Regression was analyzed using analysis of covariance. Comparisons among transplanting dates in 1999 and the treatments for Hinohikari in 2000 (left) and among tiller orders in 1999 (right). *** indicates significance at P<0.001.
in 2000. The intercept was larger in the EARLY than in the LATE group, and the range of six intercepts was 14.65. For the Akebono cultivar, the slopes of the regressions were equal between the two transplanting dates. In contrast to the results for Hinohikari, the intercept was larger in the LATE than in the EARLY group, with a difference of 9.68 between the intercepts.

We found no difference in the relationship between DWT and ST among the main, primary, and secondary tillers within the cultivars in 1999 (Fig. 1, right).

3. Relationship between leaf area on an individual tiller at heading (LAT) and number of spikelets on the tiller (ST)

The LAT was positively and significantly correlated with ST within the treatments (Fig. 2). For Mineasahi, the covariance analysis showed no difference in the slopes of the regressions of ST on LAT between the transplanting dates, although there was a large difference (28.87) in the intercepts. For Hinohikari, the covariance analysis for each year showed that one regression equation was applicable to both transplanting dates in 1999. In 2000, the slopes of the regression lines did not differ among the treatments, but the intercepts differed. The slope was lower in 1999 than in 2000. The range of intercepts was 29.40, which was larger than that of the regressions of ST on DWT. For Akebono, one regression equation could be applied to both transplanting dates.

The correlation coefficients for LAT and ST were lower than those for DWT and ST, in all cultivars (Table 2). The partial correlation coefficients between DWT and ST, holding LAT fixed, were always higher than those for LAT and ST, holding DWT fixed, for both 1999 and 2000. The intercept was larger in the EARLY than in the LATE group, and the range of six intercepts was 14.65. For the Akebono cultivar, the slopes of the regressions were equal between the two transplanting dates. In contrast to the results for Hinohikari, the intercept was larger in the LATE than in the EARLY group, with a difference of 9.68 between the intercepts.

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| Year | Cultivar | Factor 1 | Factor 2 | Correlation coefficient | Partial correlation coefficient | n |
|------|----------|----------|----------|-------------------------|--------------------------------|---|
| 1999 | Mineasahi | ST | DWT | 0.957*** | 0.880*** | 36 |
|      |          |        | LAT | 0.805*** | 0.227NS | 36 |
|      | Hinohikari | ST | DWT | 0.888*** | 0.704*** | 35 |
|      |          |        | LAT | 0.808*** | 0.419* | 35 |
|      | Akebono  | ST | DWT | 0.861*** | 0.775*** | 39 |
|      |          |        | LAT | 0.750*** | 0.568*** | 39 |
| 2000 | Hinohikari | ST | DWT | 0.881*** | 0.783*** | 136 |
|      |          |        | LAT | 0.694*** | −0.316*** | 136 |

*, ***, Significant at P < 0.05 and 0.001, respectively.
NS, not significant at P < 0.05.
years and all cultivars. These results indicate that ST was more essentially correlated with DWT than with LAT.

4. Relationship between amount of nitrogen on an individual tiller at heading (NT) and number of spikelets on the tiller (ST)

In the covariance analysis, one regression of ST on NT was fitted across treatments in 2000 (Fig. 3). The correlation coefficients between NT and ST were lower than those between DWT and ST, in the GA and N treatment groups (Fig. 1). In contrast, the correlation coefficient between NT and ST was higher than that between DWT and ST in the no-treatment control group, although the latter also had a high value. The nitrogen concentration of each tiller at heading and the ST were not correlated (data not shown, r = −0.545 NS to −0.242 NS, n = 12).

The partial correlation coefficient between DWT and ST, holding NT fixed, was higher than that between NT and ST, holding DWT fixed (Table 3). This indicates that ST was more essentially correlated with DWT than with NT.

5. Differentiated and surviving spikelets on the main tiller

For Mineasahi, ST_{diff} on the main tiller in the EARLY group was slightly higher than the estimate based on the regression in Fig. 1, and that in the LATE group was almost equal to the estimated value (Fig. 4). The surviving ST on the main tiller was similar to that suggested by the regressions for the two transplanting dates. For Hinohikari, the ST_{diff} value was highest in the GA group, followed by THIN group, and lowest in the control and N groups. The surviving ST was higher in the THIN group than in the GA group, although not significantly, and was lowest in the control and N groups. Although ST_{diff} was much higher in the EARLY and GA groups than the spikelet number estimated from the regressions, the surviving ST approached that of the regression for each treatment. For Akebono, there was little difference between the ST_{diff} and surviving ST for the two transplanting dates. The
surviving ST was distributed around the regression values. The observed \( ST_{\text{deg}} \) on the main tiller was correlated with the estimated \( ST_{\text{deg}} \) using equation (7) and the parameters in Table 4 for Hinohikari (Fig. 5). ST was regressed on DWT across the treatments within each cultivar for simplicity. The \( R^2 \) value was still significant (Table 4). The estimates were distributed around the observed values.

6. **Application of the regression to number of spikelets per square meter (S)**

The regression of ST on DWT was applied to S to show that the regression was widely applicable. The intercepts and slopes in Table 4 were substituted into equation (5). For the data from other experiments, the value of S estimated by equation (5) was distributed around the observed values (Fig. 6), whereas two observations were overestimated for each cultivar.

**Discussion**

1. **A parameter involved in determining the number of spikelets on an individual tiller (ST) and the regressions within each cultivar**

DWT, rather than LAT or NT, was found to be involved in the process that determines ST and to be stably and strongly correlated with ST under various treatments that affect spikelet production. Gibberellic acid application, thinning, and nitrogen topdressing, as well as transplanting date in Mineasahi, affected spikelet production (Table 1). The slopes of the regressions of ST on DWT and on NT were stable across treatments, whereas those of the regression of ST on LAT sometimes varied (Figs. 1–3). In the GA and N groups, the correlation coefficients between DWT and ST were higher than those between NT and ST (Figs. 1 and 3), and the partial correlation coefficients between DWT and ST were higher than those between LAT and ST (Table 2) and those between NT and ST (Table 3). These results indicate that ST was stably related to DWT and not to NT. The treatments except LATE in 1999 and CONT in 2000 for Hinohikari were conducted only for a year. Environmental conditions affect largely the characteristics such as DWT and ST. However, the result that the relationship between DWT and ST is stable has relevance because the relationship was stable under various treatments that affected spikelet

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**Table 4.** Intercepts and slopes of regression lines for the number of spikelets of an individual tiller (ST) on the dry weight (g) of the tiller at heading (DWT) for three rice cultivars across treatments.

| Cultivar   | Intercept | Slope  | \( R^2 \) | RMSE | n  |
|------------|-----------|--------|-----------|------|----|
| Mineasahi  | 12.79**   | 39.64*** | 0.916***  | 7.67 | 36 |
| Hinohikari | 14.88***  | 26.66*** | 0.781***  | 11.25| 179|
| Akebono    | 13.78NS   | 28.41*** | 0.742***  | 9.77 | 39 |

**, ***. Significant at \( P<0.01 \) and \( 0.001 \), respectively.
NS, not significant at \( P<0.05 \).
production.

It is widely accepted that nitrogen is involved in spikelet production. Hasegawa et al. (1994) and Kobayasi and Horie (1994) showed that the nitrogen concentration at the time of spikelet differentiation was important for spikelet production and that excessive dry matter production might result in inefficient spikelet production as a result of nitrogen dilution. However, these authors focused on S, rather than ST and SP, and S is a product of SP and P, which can also be affected by nitrogen. Furthermore, in our study, the nitrogen concentration of each tiller at heading was not correlated with ST. SP is positively correlated with DWP (Yao et al., 2000b) and the mean amount of nitrogen per panicle at heading (Wada, 1969; Yao et al., 2000b). The correlation coefficients between SP and DWP were higher than those between SP and amount of nitrogen per panicle (Yao et al., 2000b). In data of Yao et al. (2000b), we found that shading decreased SP compared to regression of SP on the amount of nitrogen per panicle, but did not affect the relationship between SP and DWP, which also suggests that dry matter production is more essential to spikelet production than the amount of nitrogen. The fact that SP is reduced by shading (Matsushima, 1957; Yao et al., 2000b) supports our conclusion because shading decreases dry weight, but not the amount of nitrogen, per hill (Kobayasi et al., 2001c). Dry matter production per panicle is related to SP (Kobata and Notsu, 1991; Yao et al., 2000a), but the relationship between DWT and ST has not been reported.

The relationship between DWT and ST was not affected by tiller order (Fig. 1, right). Thus, the reason that the main tiller produces the most spikelets, followed by primary and then secondary tillers (Pham et al., 2004) is simply that the DWT of the main tiller is highest, followed by primary and secondary tillers (Fig. 1). Similarly, Yamagishi et al. (1992, 1994) reported that tiller order does not affect the regression of ST on the diameter of the uppermost internode.

The surviving ST on the main tiller was similar to the value predicted by regression of ST on DWT, regardless of ST_{dif} (Fig. 4). Thus, the difference in the number of surviving spikelets on the main tiller between the THIN and GA groups was attributable to the greater dry weight of the main tiller with thinning (Fig. 4), although ST_{dif} was lower in the THIN group than in the GA group. This suggests that ST was determined irrespective of ST_{dif} although Kobayasi et al. (2001c) proposed that the promotion of spikelet differentiation would result in an increase in S and Yao et al. (2000b) considered that the number of surviving spikelets per panicle depends on the number of differentiated spikelets per panicle.

2. Process for determining the number of spikelets on an individual tiller (ST)

A process for determining ST is discussed separately with regard to spikelet differentiation and degeneration. Gibberellic acid and dry matter production from panicle initiation to spikelet differentiation are thought to affect ST_{dif} because ST_{dif} on the main tiller increased with gibberellic acid treatment and thinning (Fig. 4) and these treatments increased dry matter production of the main tiller after treatment application, i.e., panicle initiation. Similarly, the number of differentiated spikelets per panicle was positively correlated to dry weight increase per productive tiller between panicle formation stage to heading among cultivars (Ansari et al., 2003). Sheehy et al. (2001) showed that ST_{dif} was positively correlated with the leaf area of an individual tiller at late differentiation of the panicle and that the slope of the regression line for spaced plants was greater than that for crop plants. This implies an unstable relationship between leaf area and ST_{dif} across treatments, similar to the unstable relationship between LAT and ST in the present study. Therefore, leaf area must be indirectly related to ST_{dif} possibly through dry matter production, in the same way LAT was indirectly related to ST in our study. Even though ST_{dif} on the main tiller with nitrogen topdressing was not significantly higher than the control value in our study (Fig. 4), nitrogen topdressing during the vegetative period (Senanayake et al., 1996; Kobayasi et al., 2002; Ding and Maruyama, 2004) and reproductive period (Yao et al., 2000b) increased ST_{dif} on the main tiller and the number of differentiated spikelets per panicle was positively correlated with the amount of nitrogen per panicle at the end of spikelet differentiation (Wada, 1969).

The number of differentiated spikelets per panicle was positively correlated with the amount of nitrogen per productive tiller at panicle formation stage among japonica cultivars (Ansari et al., 2003). These findings suggest that the amount of nitrogen in each tiller affects ST_{dif}. Dry matter production or nitrogen might influence panicle primordia during the process of spikelet differentiation. The application of gibberellic acid enlarged the panicle primordia and increased the number of differentiated primary rachis branches and ST_{dif} on the main tiller for one of two cultivars in a previous study (Mu and Yamagishi, 2001). Therefore, gibberellic acid probably mediates the relationship between enlargement of panicle primordia and dry matter production or the amount of nitrogen. The size of the panicle primordium seems to primarily affect the number of differentiated primary rachis branches, given that the sizes of the panicle primordia correlates more closely with the number of differentiated primary rachis branches than with ST_{dif} (Kobayasi et al., 2001a, 2002; Mu and Yamagishi, 2001) and more closely with the number of primary rachis branches...
Fig. 7. Diagram, based on equation (4), showing the correlation of dry matter production with the numbers of differentiated (ST_{diff}), degenerated (ST_{deg}), and surviving spikelets (ST) on tiller \( i \). DWT_{max} is the dry weight of tiller \( i \) at heading (DWT_{i}) corresponding to ST_{diff}; in other words, DWT_{max} is the value of DWT, necessary to allow all differentiated spikelets to survive, and DWT_{n} is the dry weight of tiller \( i \) at the end of spikelet differentiation.

The value of ST_{deg} does not usually restrict ST_{i}. In addition, ST_{diff} did not affect ST on the main tiller (Fig. 4), as discussed previously. These results indicate that ST_{diff} does not usually restrict ST_{i}.

For DWT, values less than DWT_{max}, ST_{i} is positively regressed on DWT, regardless of ST_{diff}. We hypothesize that the number of surviving spikelets on tiller \( i \) is regulated such that when the dry weight of tiller \( i \) increases by \( \Delta DWT_{i} \), which occurs mainly through photosynthesis, the surviving spikelets increase by \( \Delta ST_{i} \), which is the product of \( a \) and \( \Delta DWT_{i} \). The proportion of dry matter gain used for spikelet growth seems to be kept constant. The integration of \( \Delta ST_{i} \) and \( \Delta DWT_{i} \), results in equation (4), suggesting that the photosynthesis by tiller \( i \) from emergence to heading determines ST_{i}. The regulatory mechanism of the surviving spikelets that results in equation (4) ensures that the number of surviving spikelets of tiller \( i \) match its source potential at heading.

The model in Fig. 7 shows that ST_{deg} is expressed as follows:

\[
ST_{\text{deg}} = a(DWT_{\text{max}} - DWT_{i}).
\] (8)

Equation (8) indicates that ST_{deg} is proportional to the difference between the dry weight necessary to allow all differentiated spikelets to survive and DWT_{i}. The slope of the regression line, \( a \), indicates a decrease in ST_{deg} as well as an increase in ST, per unit increase in dry weight. The number of degenerated spikelets is positively correlated with the number of differentiated spikelets (Wada, 1969; Kobayasi and Horie, 1994; Yao et al., 2000a). The percentage of degenerated spikelets is negatively correlated to DWP (Yao et al., 2000b) and dry weight per differentiated spikelet (Yao et al., 2000a, b) and is a function of crop growth rate (Yoshida et al., 2006). These results suggest that the number of degenerated spikelets is affected by the number of differentiated spikelets and dry matter production. Both factors are included in equation (8). The estimates of ST_{deg} according to equation (7) that were equivalent to equation (8) were distributed around the observed values (Fig. 5). Therefore, we concluded that spikelet degeneration might be regulated on the basis of equation (8).

Spikelet degeneration does not seem to result from a shortage of dry matter required for spikelet growth, but instead seems to result from the regulation based on equation (8), as discussed previously, and consequently on equation (4). The panicle dry weight at heading ranged from 82 to 138 g m\(^{-2}\) in the present study (data not shown). In a previous study, the amount of carbohydrate stored in culms and leaves at heading ranged from 172 to 442 g m\(^{-2}\) (Weng et al., 1982). This suggests that the supply of dry matter is sufficient for higher spikelet survival, even though spikelet degeneration has been attributed to a shortage of resources for differentiated spikelets (Senanayake et al., 1996; Kobayasi, 2000).

The value of ST is positively correlated with the sectional area of the lowermost elongating internode (Matsushima, 1957), the leaf elongation rate (Yamamoto et al., 1994), and, as discussed previously, the size of the panicle primordium (Yamagishi et al., 1992). ST is also positively correlated with the diameter.
of the uppermost internode, reportedly through the size of the panicle primordium (Yamagishi et al., 1992). SP was reduced by root removal, defoliation, and shading and was increased by nitrogen topdressing and thinning (Matsushima, 1957). These treatments seem to primarily suppress or promote photosynthesis and consequently to decrease or increase DWT. Dry matter production by the tiller might affect the cross-sectional area of the lowermost internode and the leaf elongation rate. Thus, the correlation between ST and these parameters seem to occur through DWT.

The substances that mediate the relationship between dry matter production and spikelet production on a tiller remain to be elucidated. The involvement of photosynthesis suggests that carbohydrate might be a mediator. However, the content of carbohydrate (Mohapatra and Sahu, 1991; Kobayasi et al., 2001c; Ding and Maruyama, 2004), phosphate, and amino acids (Mohapatra and Sahu, 1991) were unrelated to spikelet production. Nevertheless, appropriate measurements conducted at the proper time may yet reveal the role of a carbohydrate. Ding and Maruyama (2004) reported that the protein content of young panicles determines the number of spikelets on the main tiller; but the protein content alone seems insufficient to directly mediate between dry matter production and spikelet production, and thus other substances must also be involved.

3. Effect of treatments on the mean number of spikelets per panicle (SP)

The regression of ST on DWT is also useful for analyzing the effects of treatments on SP. Equation 6 derived from the regression indicates that SP is regressed on DWP in the same way as ST is regressed on DWT.

The transplanting date affected SP in Mineasahi, such that SP was larger in plants transplanted at an early date than at a later date (Table 1). This may have occurred because DWP was greater in the EARLY group (Table 1), albeit not significantly, because the regression was not affected by transplanting date in Mineasahi (Fig. 1).

We found that the application of gibberellic acid increased SP through an increase in DWP resulting from a decrease in P. The application of gibberellic acid decreased P, although not significantly, and increased both DWP and SP (Table 1), whereas it did not affect the slope of the regression line of ST on DWT and increased the intercept slightly (Fig. 1). These results indicate that the positive effects of gibberellic acid on SP were attributable mainly to an increase in DWP through a decrease in P. The finding that S was equal in the GA and control groups (Table 1) supports this interpretation. Shigezumi and Tsunoda (1993) and Sekimoto et al. (1995) also reported that the application of gibberellic acid decreased P, increased SP, and consequently maintained or slightly decreased S. We re-analyzed the data of Yamagishi et al. (1994) and found a significant positive correlation between an increase in the dry weight of the main tiller and an increase in the number of spikelets on the main tiller with gibberellic acid application (r=0.710*, n=9, excluding two cultivars with little endogenous gibberellic acid). Many studies have reported that the application of gibberellic acid increased SP (Kawai and Takeoka, 1989; Shigezumi and Tsunoda, 1993; Yamagishi et al., 1994; Sekimoto et al., 1995); however, an increase in SP has not been attributed to an increase in DWP as a result of a decrease in P.

Nitrogen topdressing at panicle initiation increased P and S but did not increase SP in our study (Table 1), although it was previously reported to increase SP (Matsushima and Manaka, 1959; Senanayake et al., 1996; Yao et al., 2000b; Kobayasi et al., 2001b). We assume that because DWP did not increase as a result of an increase in P (Table 1), SP did not increase in our study. These results suggest that nitrogen topdressing increase SP indirectly through an increase in DWP.

Thinning decreased P and increased SP (Table 1), confirming the results of Matsushima (1957). The increase in SP was mainly attributable to an increase in DWP.

To discuss the applicability of the regression of ST on DWT, we assumed the regression to be identical within each cultivar across treatments. Differences in the intercepts among treatments are discussed later. Equation (6) indicates that when dry weight at heading is constant, SP decreases with P. This equation can explain the phenomenon that increasing plant density increases P but decreases SP (Yoshida, 1981; Akita and Tanaka, 1992; Peng et al., 1994; Kobayasi et al., 2001b).

4. Application of the regression to the number of spikelets per square meter (S)

The regressions of ST on DWT were basically applicable to S under the different conditions. The S values estimated by equation (5) were roughly coincident with the observed values (Fig. 6). Thus, the relationship between DWT and ST on each tiller is basically valid at the whole population level under the different conditions.

Equation (5) indicates that when DW is constant and b is small, S hardly increases with P. In Hinohikari, an additional 100 panicles m⁻² would increase S by only 1488 m⁻² (Table 4). This is coincident with the results of Peng et al. (1994) and Kobayasi et al. (2001b) that an increase in plant density increased P but had little effect on S.
5. **Intercepts of regression**

Differences in the intercepts could result from differences between the effects on ST of the dry matter produced during the vegetative and reproductive periods. Kobata and Notsu (1991) developed a linear model to estimate SP using mean dry matter production per tiller during the vegetative period and per panicle during the reproductive period. The coefficient of the former was about three times that of the latter, suggesting that the effects of dry matter production on SP may depend on the growth period.

Nitrogen could also be secondarily related to the intercepts because the partial correlation coefficient between NT and ST was significant (Table 3). Kobata and Notsu (1991) also indicated that nitrogen could improve the estimation of SP.

6. **Regressions among cultivars**

The slopes of the regression lines of ST on DWT were steeper in the short-duration cultivar Mineasahi than in the intermediate- and long-duration cultivars Hinohikari and Akebono (Fig. 1). This suggests that Mineasahi increases the number of spikelets to a greater degree than the other cultivars with increases in the dry weight of a tiller and thus has an advantage in spikelet production. In fact, the number of spikelets was greatest for Mineasahi in the EARLY group in 1999 (Table 1). The slopes appear to be genetically controlled because they were hardly affected by the treatments and years (Fig. 1). Similarly, Yao et al. (2000a) expressed SP as the product of DWP and the mean number of spikelets per unit dry weight and found varietal differences in the number of spikelets per unit dry weight, as well as DWP. However, equation (6) indicates that the number of spikelets per unit dry weight decreases with an increase in DWP. Therefore, the slope in equation (3) is more appropriate for Mineasahi in the EARLY group in 1999 (Table 1). The slopes appear to be genetically controlled because they were hardly affected by the treatments and years (Fig. 1).

In addition, whether the slopes in short-duration cultivars are generally steeper also remains to be elucidated. We re-analyzed the data of Yao et al. (2000a) and found a negative correlation between the number of spikelets per unit dry weight and the heading dates \((r = -0.542, P < 0.07, n = 12)\), suggesting that the slopes of short-duration cultivars can be generally steeper. Varietal differences were not found in the intercept of the regression (Fig. 1).

**Conclusion**

For each cultivar, the regression of ST on DWT was stable regardless of the treatments, year, tiller order, and \(ST_{dif}\). To increase S by crop management, it is necessary to increase dry weight at heading rather than to increase P. The slope \((a)\) of the regression lines differed among the cultivars. “Large panicles” have contributed to the development of high-yielding cultivars such as the new plant type cultivars at the International Rice Research Institute and super hybrid rice in China (Peng et al., 2004). Our study suggests that there are two kinds of cultivars with large panicles, one with a large \(a\) and one with a large DWP. Cultivars with a large \(a\) can produce many spikelets per dry weight, whereas cultivars with a large DWP require a heavy dry weight to produce many spikelets. Therefore, cultivars with a large \(a\) value are more desirable than cultivars with a large DWP for the production of many spikelets per square meter and high yield.

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