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The Analysis of the Process in Spikelet Number Determination with Special Reference to Nitrogen Nutrition in Rice

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Abstract The relationship between spikelet number per unit area (spikelet density, SD) and spikelet number components (SNCs) was analyzed. The spikelet density was the product of five SNCs: panicle number per unit area (PN), the number of differentiated primary rachis-branches per panicle, the number of differentiated secondary rachis-branches per differentiated primary rachis-branch (SB), the number of differentiated spikelets per differentiated secondary rachis-branch, and spikelet degeneration percentage. The relationship between SNCs and shoot nitrogen (N) or dry weight (DW) was also researched. By using multiple regression analysis, the PN and the SB were the most and the next most contributory factors to the SD, respectively. The PN and the SB had the highest correlation with N amount at the early spikelet differentiation stage (ESD) and the increment of N concentration from panicle initiation (PI) to ESD, respectively. It is concluded that the SD can be expressed by three parameters by using multiple regression analysis, which the parameters were N amount at the ESD, the increment of N concentration from PI to the ESD, and the DW per differentiated spikelet at heading.

Key Words: Dry weight, Nitrogen, Rice, Spikelet number.

Introduction

Spikelet number per unit area (spikelet density, SD) is a strong determinant of rice yield. Spikelet density is closely associated with nitrogen (N) nutrition in rice plants (Wada, 1969; Hasegawa et al., 1994; Kobayasi and Horie, 1994). One of the aims of nitrogen application is the control of SD.

Wada (1969) related the SD to the amount of N in the aboveground parts at the late spikelet differentiation stage (LSD). It has been thought that SD is determined only by N amount (NA) accumulated in the plants up to LSD and that the determination of SD does not depend on the time of N absorption (Wada, 1969; Matsushima, 1973). However, there are regional variations in the relationship between SD and NA (Murayama, 1969), and it is revealed that the efficiency of spikelet production (SD per unit N absorbed) in cooler areas is higher than that in warmer areas of Japan. Wada (1980) related low spikelet production efficiency in warmer areas of Japan to N nutrition at the vegetative lag phase (VLP) and revealed that N application at the VLP increased spikelet production efficiency through increasing spikelet number per panicle. Kobayasi and Horie (1994) showed that the number of differentiated spikelets per unit area (DSN) is determined by two factors: the amount of shoot N at the early spikelet differentiation stage (ESD) and the increment of shoot N concentration (NC) between panicle initiation (PI) and ESD. These findings show that SD is determined not only by total accumulated N in the shoots up to LSD but also by the time of N absorption

and NC at a specific stage, and suggest that the N nutritional condition at the specific stages affects the corresponding morphological parts which constitute SD.

By tracing the morphological process in spikelet determination, SD can be divided into five morphological spikelet number components (SNCs): panicle number per unit area (PN), the number of differentiated primary rachis-branches per panicle (PB), the number of differentiated secondary rachis-branches per differentiated primary rachis-branch (SB), the number of differentiated spikelets per differentiated secondary rachis-branch (SP), and spikelet degeneration percentage (SDP). It is probable that these five SNCs not equally contribute to the determination of SD. Thus in this study, the degrees of individual SNCs in the contribution to the SD were analyzed by using regression analysis. Then the correlations between SNCs and DW or NA at the specific stages were analyzed to reveal the most effective factor to increase each SNC among DW and NA at the specific stages. In this study, many data sets of rice grown under variable N nutrition conditions were collected to analyze the correlation between SD and SNCs, and SNCs and DW or NA to reveal the mechanism of determining SD. The objectives are to determine which SNC is the most effective in determining SD, and to clarify which factor about N and DW most closely linked to individual SNCs.

Table 1. Location, year, transplanting date, and N application of the collected data in this study.

Year	Site	Transplanting date	Basal N (g/m^2)	Topdressing N (g/m^2)	Topdressing time
1989	Kyoto	May 15	0	0	-
			0	4	T
			0	8	T
			0	6	PI
			6	0	-
			6	4	T
			6	4	PI
			6	8	PI
			12	0	-
			24	0	-
		July 5	0	0	-
			6	4	ESD
1990	Kyoto	May 12	0	0	-
			0	8	PI
			0	8	PRB
			0	8	ESD
1992	Matsue	May 16	8	0	-
			3	7	T, BT
			2	8	PI, ESD
			2	6	T
1993	Matsue	May 19	12(LP)*	0	-
1994	Matsue	May 18	4	6	T, BT
			2	3	T, BT
			0	0	-
	Akana	May 16	4	6	T, BT
			2	3	T, BT
			0	0	-
1995	Matsue	May 10	12(LP)	0	-
			9(LP)	3	PI
		May 30	12(LP)	0	-
			9(LP)	3	PI
		June 29	12(LP)	0	-
			9(LP)	3	PI

Topdressing time: T, PI, PRB, ESD, and BT mean the tillering stage, the panicle initiation stage, the stage of primary rachis-branch differentiation, the early spikelet differentiation stage, and the booting stage, respectively.

*: Slow release N fertilizer (LP444E80) was used.

Materials and Methods

1. Data source

A lowland rice cultivar, Nipponbare was used. Table 1 shows the 33 data sets collected from 1989 to 1995 at three locations (Kyoto, Matsue, and Akana). The transplanting density was 22.2 hills/m^2. Dry weight (DW) and N concentration (NC) in the shoot were measured several times from PI to heading (HD). The NC was measured by using the Kjeldahl method. Panicles were sampled a few days before HD, and the numbers of differentiated and degenerated spikelets and primary and secondary rachis-branches were counted according to the method of Matsushima (1957). The developmental stages from PI to HD were detected with a binocular microscope in 2-3 day intervals. The SD and the DSN used in this study ranged from 18061/m^2 to 41569/m^2 and from 21202/m^2 to 56559/m^2, respectively.

2. The analysis methods

As has been mentioned in Introduction, the SD and the DSN can be divided as follows:

$SD = PN \times PB \times SB \times SP \times (1 - SDP)$.

$DSN = PN \times PB \times SB \times SP$.

SD = DSN - the number of degenerated spikelets.

Using linear interpolation, the DW and the NC at PI, ESD, LSD, and HD were calculated. The NA is the

products of the DW and the NC at the each developmental stage. The DSN is determined between PI and ESD, so that ,four SNCs (PN, PB, SB, and SP) and parameters at PI and ESD were used for DSN analysis. The DW and NA per differentiated spikelets at LSD, RD and H D for SDP analysis were used because spikelet degeneration occurs mainly after LSD and because it is hypothesized that the NA or the DW supplied for each differentiated spikelet determine the SDP. The correlations between SD, DSN, SNCs, DW and NA were tested for using simple and multiple linear regression analysis.

Results and Discussion

1. The relationship between spikelet number components (SNCs) and spikelet density (SD)

The SD had the highest and the next highest correlation with PN (r=0.818) and SB (r=0.497) among the SNCs, respectively (Table 2). The SD was little correlated with the PB, the SP, and the SDP. The similar results were obtained in the case of DSN. The DSN had the highest and the next highest correlation with PN (r=0.814), and SB (r=0.445), respectively.

Mutual correlations between the SNCs were analyzed with simple regression. The PN was not significantly correlated with other SNCs. The PB and the SB were relatively highly correlated with the SDP and the SP, respectively, indicating that rice having more differentiated primary rachis-branches degenerate more spikelets. This result was surprising because most of degenerated spikelets are on secondary rachis-branches.

To evaluate the contribution of SNCs to the SD or the DSN, multiple regression analysis was used (Table 3.). Comparing the standardized partial regression coefficients of SNCs, the PN is the most contributory factor to both the SD and the DSN. The SB is the next most contributory. The contribution of the PB to the DSN was relatively high, but that to the SD was little. This is because of a close correlation between the PB and the SDP.

Table 3 shows that the contribution of the SP to the SD was negligible. This result was also supported by the result of Manaka and Matsushima (1971) that the number of spikelets differentiating on 66.3% of the secondary rachis-branches was three and was not changed by the environments.

Table 2. Correlation coefficients among spikelet number and the components of spikelet number.

	SD	DSN	PN	PB	SB	SP
DSN	0.946**					
PN	0.818**	0.814**				
PB	0.087	0.276	-0.069			
SB	0.497**	0.445**	-0.007	-0.033		
SP	-0.299	-0.186	0.148	0.221	-0.878**	
SDP	0.044	0.343	0.140	0.560**	-0.011	0.237

**Significant at the 0.01 probability levels. SD: The number of final spikelets per unit area (spikelet density), DSN: The number of differentiated spikelets per unit area, PN: Panicle number per unit area, PB: The number of differentiated primary rachis-branches per panicle, SB: The number of differentiated secondary rachis-branches per differentiated primary rachis-branch, SP: The number of differentiated spikelets per differentiated secondary rachis-branch, SDP: Spikelet degeneration percentage.

Table 3. Multiple regression analysis of spikelet density and the number of differentiated spikelets among spikelet number components.

Criterion variables		Predictor variables				
		PN	PB	SB	SP	SDP
SD	Partial regression coefficient	75.81	3319	12100	1233	-289.3
R^2=0.986**	Standardized partial regression coefficient	0.866	0.290	0.569	0.067	-0.249
DSN	Partial regression coefficient	99.96	5189	16530	2874	
R^2=0.989**	Standardized partial regression coefficient	0.824	0.327	0.560	0.112	

**Significant at the 0.01 probability levels.
PN, PB, SB, SP, and SDP: See Table 2.

2. The relationship between the spikelet number components and plant N status

It is probable that the stages when individual SNCs were determined correspond to each rice developmental stages. Namely, PN should be determined at tillering stage, PB in the period from PI and the stage of primary rachis-branch differentiation, SB at the stage of secondary rachis-branch differentiation, SP at the stage of spikelet differentiation, and SDP at the

Table 4. Correlation coefficients among spikelet number components and the agronomic traits.

	SD	DSN	IPB	ISB	PN	PB	SB	SP
NA at PI	0.445**	0.293	0.678**	0.275	0.476**	0.585**	-0.374*	0.546**
NA at ESD	0.646**	0.511**	0.726**	0.508**	0.548**	0.530**	-0.075	0.371*
NC at PI	0.299	0.194	0.514**	0.145	0.393*	0.342	-0.412*	0.556**
NC at ESD	0.547**	0.466**	0.612**	0.428*	0.510**	0.330	-0.075	0.365*
DW at PI	0.352*	0.284	0.454**	0.292	0.322	0.411*	-0.059	0.094
DW at ESD	0.353*	0.273	0.400*	0.304	0.263	0.390*	0.008	0.036
ΔNA(PI-ESD)	0.591**	0.554**	0.405*	0.573**	0.358*	0.165	0.400*	-0.083
ΔNC(PI-ESD)	0.453**	0.502**	0.172	0.522**	0.209	-0.029	0.631**	-0.365*
ΔDW(PI-ESD)	0.183	0.121	0.116	0.178	0.037	0.167	0.120	-0.079

*, **Significant at the 0.05 and 0.01 probability levels, respectively.
SD, DSN, PN, PB, SB, and SP: See Table 2.
IPB and ISB are the number of differentiated primary and secondary rachis-branches per unit area, respectively. NA, NC, and DW are nitrogen amount, nitrogen concentration, and dry weight, respectively.
ΔNA(PI-ESD) means the increment of NA between panicle initiation (PI) and the early spikelet differentiation stage (ESD).

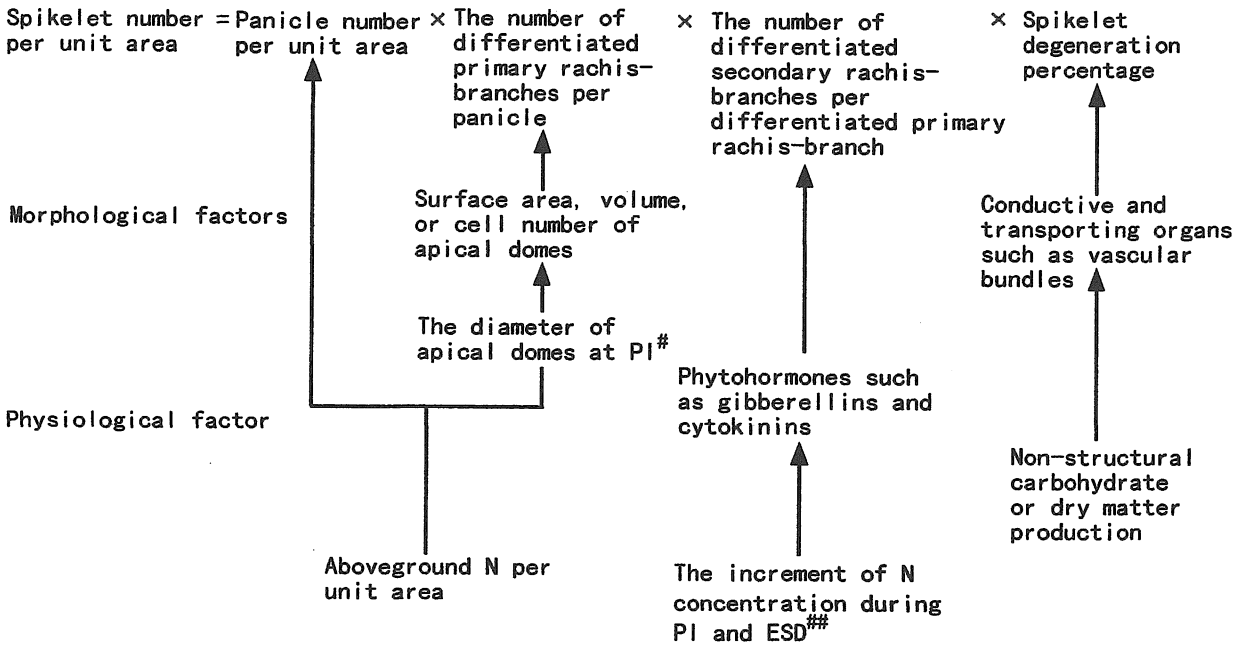

Fig. 1. Relationship between spikelet number components, nitrogen condition, and other characteristics for spikelet number.
#, ##: Panicle initiation and the early spikelet differentiation stage.

booting stage. Each SNC will be controlled by DW or NA at the stages of determining corresponding SNCs. Then, the relationships between NA, NC, or DW and SNCs were examined (Table 4).

The PN had the highest correlation with the NA at ESD. The correlation between the PN and the increment of NA between PI and ESD was relatively high, and this result was supported by the result of Wada (1981) that N application at the VLP increases tiller number and the percentage of productive tillers. The PN was a little correlated with DW at any stage. These results suggest that the period of determination of PN is long.

The PB had the highest correlation with the NA at PI. Both the PN and the PB were highly correlated with the NA at PI and ESD, indicating that the number of differentiated primary rachis-branches per unit area which is the product of the PN and the PB

Table 5. Correlation coefficients among spikelet degeneration percentage and the agronomic traits.

	SDP
NA per DSN at LSD	0.053
NA per DSN at HD	-0.134
DW per DSN at LSD	-0.130
DW per DSN at HD	-0.211
ΔNA(LSD-HD)/DSN	-0.343
ΔDW(LSD-HD)/DSN	-0.230

NA, DSN, DW: See Table 2 and 4.

SDP: Spikelet degeneration percentage. LSD and HD are the late spikelet differentiation stage and heading, respectively. Δ NA(LSD-HD)/DSN means the increment of nitrogen amount from LSD to HD per differentiated spikelet.

was highly correlated with the NA at PI and ESD.

The SB had the highest correlation with the increment of NC between PI and ESD, and this result agreed with the conclusion of Kobayasi and Horie (1994).

The SDP is thought to be controlled by the NA or dry matter (Wada, 1969) supplied to individual differentiated spikelets. The SDP was relatively highly correlated with the DW per differentiated spikelet (Table 5). In particular, the correlation between the SDP and the DW per differentiated spikelet at HD was relatively high ($r=-0.497$), indicating that there is some relationship between spikelet degeneration and dry matter or carbohydrate supplied to individual spikelets.

3. Conclusion

The analysis of this study showed that the NA at ESD (x1), the increment of NC between PI and ESD (x2), and DW per differentiated spikelet at HD (x3) were sufficient to evaluate the SD in building multiple regression equation. The x1, x2, and x3 corresponded to the number of differentiated primary rachis-branches per unit area (the product of PN and PB), SB, and SDP, respectively. The multiple regression equation to evaluate the SD was as follows:

$SD = 824.0x1 + 6114x2 - 489.9x3 + 38078 \quad R^2 = 0.567.$

The standardized partial regression coefficients of x1, x2, and x3 were 0.394, 0.305, and -0.369, respectively. This analysis showed that all the three variables nearly equally contributed to the SD. From previous and this studies, the schematic diagram about the process in determination of the SD (Fig. 1) was developed.

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