Diversity of the Rachis-Branching System in a Panicle in Japonica Rice

Junko Yamagishi, Keisuke Nemoto* and Chunsheng Mu

(Graduate School of Agricultural and Life Sciences, The University of Tokyo, Nishitokyo, Tokyo 188-0002, Japan; *Asian Natural Environmental Science Center, The University of Tokyo, Bunkyo, Tokyo 113-8657, Japan)

Abstract: Recently, rice varieties having large panicles with many spikelets are expected to produce high yield. However, the ripening, growth pattern, priority to photoassimilate partitioning and final grain weight in each spikelet vary with the position of the spikelet in a panicle. Therefore, not only the panicle size but also rachis-branching system in a panicle is an important factor determining the yield. In this report, we performed principal component analysis to characterize the rachis-branching system in 65 japonica varieties. In the principal component analysis, the proportions of variability explained were 49.6 and 22.2% for the first two attribute components. The first principal component was assumed as the factor of size in number, and the second principal component was assumed as the factor of shape of panicle. The distribution of the scores for each variety in the scatter diagram showed a large diversity in panicle characteristics in japonica varieties. A small number of varieties had scores distributed in the first quadrant of the scatter diagram. These varieties would be high-yielding because the number of spikelets is high in the panicle having a relatively large number of primary rachis-branches compared with the secondary rachis-branches. Some clusters in the scatter diagram were related with their origins.

Key words: Indica rice, Japonica-indica hybrid rice, Japonica rice, Primary rachis-branch, Principal component analysis, Secondary rachis-branch, Spikelet.

In rice, the varieties with large panicles are expected to produce high-yielding, and some varieties in the indica group have larger panicles with more spikelets on the second rachis-branches than japonica varieties (Hashimoto et al., 1983; Maruyama et al., 1988; Yamamoto et al., 1991; Saitoh et al., 1993; Fukushima 1999). High-yielding japonica-indica hybrid varieties, like Milyang 23 (developed in Korea) and Akenohoshi (developed in Japan), also have large panicles (Hashimoto et al., 1983; Takeda et al., 1984; Maruyama et al., 1988; Yamamoto et al., 1991). Furthermore, new plant type (NPT) varieties were raised in a breeding program at the International Rice Research Institute (IRRI) to produce high-yielding tropical japonica varieties with large panicles (Peng et al., 1999). Such a recent trend to increase the sink capacity by increasing panicle size suggested the necessity of analysis of the rachis-branching system in the panicle in many varieties with broad genetic diversity. This is because the spikelets within a panicle show variation in ripening, growth pattern, priority to photoassimilate partitioning and final grain weight depending on the position, and because the ripening is better in the spikelet on a primary rachis-branch than that on a secondary rachis-branch, and also better in the spikelet in the upper part of panicle than in the lower part of panicle (Iwatsuki, 1931; Nagato, 1941; Nagato and Chaudhry, 1969; Chaudhry and Nagato, 1970; Sashahara et al., 1982; Hoshikawa et al., 1984; Nakamoto et al., 1988; Yamagishi et al., 1996; Yang et al., 2000). These studies indicated that a large panicle with a large number of spikelets is not directly related to high yield, and that the rachis-branching system in a panicle is an important factor for attaining high yield.

From this viewpoint, several studies have been done on the rachis-branching system in a panicle (Sasahara et al., 1982; Hashimoto et al., 1983; Komatsu et al., 1984; Kobayashi et al. 1997). Sasahara et al. (1982) mentioned that indica varieties having a large number of spikelets on the secondary rachis-branch in the upper part of panicle were desirable for increasing the yield. Kobayashi et al. (1997) concluded that the rachis-branching system in a panicle of Japanese japonica varieties did not show broad variation and was not desirable architecture for high yield with the results of Sasahara et al. (1982) and Hashimoto et al. (1983). However, the main purpose of these studies was the comparison among japonica, indica and japonica-indica hybrid varieties and the number of japonica varieties
Table 1. Rice varieties belonging to three groups and their origins.

| Japonica varieties | Indica varieties | Japonica-Indica varieties |
|--------------------|------------------|--------------------------|
| No.                | Name             | Origin                   | No.            | Name            | Origin     | No.            | Name            | Origin |
| 1                  | Kotobuki Mochi   | Japan                    | 33             | Dawasam         | Bhutan      | 71             | Milyang 23     | Korea           |
| 2                  | Rikuto Kemochi   | Japan                    | 34             | Gemjiya Iyann   | Bhutan      | 72             | Suweon 258     | Korea           |
| 3                  | Kibi             | Japan                    | 35             | Jumali          | Nepal       | 73             | Suweon 264     | Korea           |
| 4                  | Mansaku          | Japan                    | 36             | NHTA5           | India       | 74             | Akenohoshi     | Japan           |
| 5                  | Kameno          | Japan                    | 37             | NHTA            | India       |                |                 |                  |
| 6                  | Nipponbare       | Japan                    | 38             | Rathal           | Sri Lanka   |                |                 |                  |
| 7                  | Aedal            | Korea                    | 39             | Rathal           | Sri Lanka   |                |                 |                  |
| 8                  | Beonjo           | Korea                    | 40             | Luk Takhal       | Afghanistan|                |                 |                  |
| 9                  | Deokjoseokjodo    | Korea                    | 41             | Gerdeh           | Iran        |                |                 |                  |
| 10                 | Heukyung         | Korea                    | 42             | Gharb            | Iran        |                |                 |                  |
| 11                 | Patbyeo          | Korea                    | 43             | MAINIMOLOTSY     | Madagascar |                |                 |                  |
| 12                 | Ta Hung Ku       | China                    | 44             | OS 4             | West Africa |                |                 |                  |
| 13                 | Hei Chiao Chui   | Li Hsiang Keng           | 45             | Morobekete       | Guinea      |                |                 |                  |
| 14                 | Y Chang Ju       | China                    | 46             | LAC23            | Liberia     |                |                 |                  |
| 15                 | Ta-Mao-Tao       | China                    | 47             | RT1031-69        | Zaire       |                |                 |                  |
| 16                 | Hu-Lo-Tao        | China                    | 48             | Fossa            | B.Fase      |                |                 |                  |
| 17                 | Haifagoya        | Taiwan                   | 49             | Yanceousse       | Ivory C.    |                |                 |                  |
| 18                 | Khao Dam         | Laos                     | 50             | IRAT 13          | Ivory C.    |                |                 |                  |
| 19                 | Hawn Om          | Thailand                 | 51             | Rexoro           | USA         |                |                 |                  |
| 20                 | Silat            | Malaysia                 | 52             | Carolina Gold    | USA         |                |                 |                  |
| 21                 | Tan Sibuku       | Malaysia                 | 53             | Igupe Cateto     | Haiti       |                |                 |                  |
| 22                 | Padi Kasalle     | Indonesia                | 54             | Cuba 65          | Cuba        |                |                 |                  |
| 23                 | Kaniangga        | Indonesia                | 55             | Lambayque 1      | Peru        |                |                 |                  |
| 24                 | Aries            | Indonesia                | 56             | IAC25            | Brazil      |                |                 |                  |
| 25                 | Gog Lempuk       | Indonesia                | 57             | Cana Roxa        | Brazil      |                |                 |                  |
| 26                 | Maray            | Indonesia                | 58             | Dourado Precoce  | Brazil      |                |                 |                  |
| 27                 | Azcena           | Indonesia                | 59             | Bico Branco      | Brazil      |                |                 |                  |
| 28                 | Malagut Pirutong | Philippine               | 60             | Pacholinha       | Brazil      |                |                 |                  |
| 29                 | Davao            | Philippine               | 61             | IR65598-112-2    | Philippine  |                |                 |                  |
| 30                 | Kinandang Patong | Philippine               | 62             | IR66740-AC1-3    | Philippine  |                |                 |                  |
| 31                 | Binulawang       | Philippine               | 63             | IR65600-27-1-2   | Philippine  |                |                 |                  |
| 32                 | Dangrey          | Bhutan                   | 64             | IR65600-42-5-2   | Philippine  |                |                 |                  |
| 33                 | Dular            | India                    | 65             | IR66738-118-1-2  | Philippine  |                |                 |                  |

Recently, the japonica group was recognized to
include temperate and tropical japonica varieties (Glassmann, J.C., 1987; Zhang et al., 1992; Mackill, D.J., 1995). Therefore, we performed principal component analysis to characterize the rachis-branching system in the panicles of japonica varieties using the core collection of IRRI, including broad genetic diversity, and NPT varieties. In addition, we discuss the relationship between the origin of varieties and the rachis-branching system in the panicle. This characterization of rachis-branching system in the panicle may be useful to select the varieties for the genetic analysis like quantitative trait loci in the panicle characteristics.

Materials and Methods

1. Plant materials

The rice varieties used in this study are listed in Table 1. Among 65 japonica varieties, 57 varieties were obtained from core collection of IRRI originated from 25 regions in the world, five were NPT varieties from IRRI and additional three varieties were from U.S. (cv. Rexoro) and Japan (cv. Nipponbare and Kamenoo). In addition, five indica varieties and four japonica–indica hybrid varieties were included to compare with japonica varieties. The seedlings of these 74 varieties were transplanted in paddy fields on the University Farm, Graduate School of Agricultural and Life Sciences, the University of Tokyo, on 17 June 1996. Eight plants of every variety were grown with 30 cm row spacing and 15 cm hill spacing (one plant in one hill) in one plot, and three plots were prepared. In one plot, 25 rows were prepared with three varieties planted in one row and around the whole plot two hills and two rows of Nipponbare were planted. Therefore, the size of one plot was 4.05 m × 8.4 m (28 hills × 29 rows). The positions of 74 varieties in each plot were randomly arranged, and the neighboring varieties of each variety were different among plots. The quantity of chemical compound fertilizer at basal application was 500 kg ha⁻¹ (N : P₂O₅ : K₂O = 12 : 18 : 16%) with no topdressing. The panicles of main stems were collected at maturity, and one panicle with medium panicle length was chosen from each variety in each plot. The number of primary rachis-branches, secondary rachis-branches and spikelets were counted with three varieties from each variety from three plots.

2. Panicle traits and statistical analysis

Principal component analysis was conducted for 10 traits of panicles with 65 japonica varieties. Examined traits were as follows; panicle length (PL), total number of primary rachis-branches per panicle (TPR), total number of spikelets on primary rachis-branches per panicle (TSSR), mean number of spikelets on a primary rachis-branch per secondary rachis-branch (SSR), total number of secondary rachis-branches per primary rachis-branch (SRPR), total number of spikelets on secondary rachis-branches per panicle (TSPR), mean number of spikelets on a secondary rachis-branch (TSSR), mean number of spikelets on a primary rachis-branch (NSOR), relative node order to the tip of panicle (NOR), and number of spikelets per primary rachis-branch (NSOR).

Results and Discussion

The means and ranges of four traits of panicle, PL, TPR, SRPR, TS, in three rice groups are shown in Table 2. Every trait was widely distributed and the ranges were very broad in japonica varieties. The ranges in indica and japonica–indica hybrid varieties were not so broad, though the numbers of these varieties examined are quite limited.

The total number of spikelets per panicle (TS) showed very high correlation with the traits relating to the number of secondary rachis-branches, TSR, SRPR, TSSR and SSR, in 65 japonica varieties, though the correlation coefficient of TS with TPR was not low (Table 3). NOR did not highly correlate with the other traits.
Table 3. Correlations among 10 panicle traits in 65 japonica varieties.

| Trait  | PL   | TPR  | TSPR | SPR  | TSR  | SRPR | TSSR | SSR  | TS   |
|--------|------|------|------|------|------|------|------|------|------|
| TPR    | 0.133|      |      |      |      |      |      |      |      |
| TSPR   | 0.162| 0.936|      |      |      |      |      |      |      |
| SPR    | 0.149| 0.092| 0.430|      |      |      |      |      |      |
| SR     | 0.215| 0.528| 0.333| -0.395|      |      |      |      |      |
| SRPR   | 0.228| 0.130| -0.064| -0.511| 0.902|      |      |      |      |
| TSSR   | 0.253| 0.489| 0.311| -0.356| 0.985| 0.899|      |      |      |
| SSR    | 0.383| 0.121| 0.049| -0.168| 0.678| 0.729| 0.780|      |      |
| TS     | 0.265| 0.672| 0.522| -0.226| 0.963| 0.785| 0.972| 0.706|      |
| NOR    | -0.152| 0.285| 0.252| 0.009| 0.133| -0.012| 0.129| -0.006| 0.187|

The correlation coefficients larger than 0.316 are significant at the probability level of 0.01.

* See the abbreviations.

Table 4. Principal component analysis performed on 10 traits of panicle for 65 japonica varieties.

| Trait  | Factor loading | PL   | TPR  | TSPR | SPR  | TSR  | SRPR | TSSR | SSR  | TS   |
|--------|----------------|------|------|------|------|------|------|------|------|------|
|        | Principal component | 1    | 2    | 3    |      |      |      |      |      |      |
| PL     | 0.323          | 0.049| 0.776|      |      |      |      |      |      |      |
| TPR    | 0.584          | 0.738| -0.132|      |      |      |      |      |      |      |
| TSPR   | 0.413          | 0.893| 0.042|      |      |      |      |      |      |      |
| SPR    | -0.314         | 0.646| 0.469|      |      |      |      |      |      |      |
| TSR    | 0.978          | -0.083| -0.099|      |      |      |      |      |      |      |
| SRPR   | 0.854          | -0.461| -0.014|      |      |      |      |      |      |      |
| TSSR   | 0.988          | -0.105| -0.033|      |      |      |      |      |      |      |
| SSR    | 0.763          | -0.283| 0.294|      |      |      |      |      |      |      |
| TS     | 0.987          | 0.125| -0.031|      |      |      |      |      |      |      |
| NOR    | 0.163          | 0.361| -0.585|      |      |      |      |      |      |      |

| Eigenvalue | 4.960 | 2.219  | 1.283 |
| Accumulated coefficient of determination | 0.496 | 0.718  | 0.846 |

* See the abbreviations.

In principal component analysis, which explains the variance-covariance structure through a few linear combinations of the original variables, the proportions of variability explained were 49.6, 22.2, and 12.8% for the three attribute components, respectively, and 71.8% for the first two components (Table 4). The first principal component for attributes was assumed as the factor of size in number, because most values of eigenvector were positive. The first principal component loaded primarily on TS, and the loading of the traits relating to the number of secondary rachis-branches, TSR, SRPR, TSSR and SSR was much larger than that of the traits relating to the number of primary rachis-branches. The second principal component primarily loaded on the traits relating to the number of primary rachis-branches, TPR, TSPR, SPR, and NOR, though it showed little association with TS and showed negative association with the traits relating to the number of secondary rachis-branches. Therefore, the second principal component was assumed to be the factor of shape, which is influenced by the relative balance between the numbers of primary and secondary rachis-branches. In addition, the second principal component showed a positive high correlation with NOR, indicating that the second principal component is the factor of panicle shape.
Fig. 1. Scatter diagram of scores in each variety of the first two principal components deduced from a principal component analysis of 10 traits of panicles with 65 japonica varieties. Principal component scores in 5 indica varieties and 4 japonica–indica hybrid varieties were calculated using the eigenvectors obtained by the principal component analysis with 65 japonica varieties. The number and signals in the figure identified varieties. ● : Japonica, □ : Indica, △ : Japonica–indica hybrid varieties. The numbers are shown in Table 1.

The first principal component

The second principal component

The scores of the five NPT varieties (from no. 61 to 65) were dispersed but distributed in characteristic positions almost on the edge of the flock, especially no. 61 showed a very high positive score of the first principal component.

Although the scores were scattered in Philippine varieties (from no. 27 to 31) and South American varieties (from no. 55 to 60), the Chinese varieties (from no. 12 to 16) had negative score of the first principal component and the Indonesian varieties (from no. 23 to 26) tended to have positive scores of the first principal component and negative scores of the second principal component. The Japanese varieties (from no. 1 to 6) had various scores of the first and second principal components and did not have a similar panicle shape as was reported by Kobayashi et al. (1997).

Indica (from no. 66 to 70) and japonica–indica hybrid varieties (from no. 71 to 73) except Akenohoshi (no. 74) were clustered in a limited area with negative scores of the second principal component and medium scores (near zero) of the first principal component, which means that they have relatively many second rachis-branches compared with the primary rachis-branches. Therefore, these indica and japonica–indica hybrid varieties in this experiment are not included in the high-yielding indica varieties proposed by Sasahara et al. (1982), which should have the scores in the first quadrant. All japonica varieties from Korea (from no. 7 to 11) and three varieties from Bhutan (no. 32, 33 and 34) were distributed in this group of indica and japonica–indica hybrid varieties excluding Akenohoshi.

Thus, the distribution of the scores in principal component analysis with 65 japonica varieties was very broad, showing the large diversity in panicle characteristics. However, the scores of relatively few varieties were distributed in the first quadrant of the scatter diagram, where the first and second principal components were positive. The varieties with scores in this area have a type of panicle desirable for high yield. Varieties in some
clusters of principal scores were related with their origins.

Acknowledgement

Authors wish to thank Mr. N. Washizu (University Farm, The University of Tokyo) for his technical assistance to manage the field.

References

Chaudhry, F.M. and Nagato, K. 1970. Role of vascular bundle in ripening of rice kernel in relation to the location on panicle. Proc. Crop Sci. Soc. Jpn. 39: 301-309.

Fukushima, A. 1999. Branching structure of panicle with reference to the number of spikelets in rice. Jpn. J. Crop Sci. 68: 71-76.

Glassmann, J.C. 1987. Isoenzymes and classification of Asian rice varieties. Theor. Appl. Genet. 74: 21-30.

Hashimoto, Y., Fujimaki, H., Matsuwa, K. and Harada, J. 1983. Panicle branching system of several promising rice cultivars with high yield potential. Bull. Hokuriku Natl. Agric. Exp. Stn. 25: 193-206.

Hoshikawa, K., Nakamura, T. and Otomo, K. 1984. Grain-filling ability within the ear of rice. Rep. Tohoku Br. Crop Sci. Jpn. 27: 51-53.

Iwatsuki, S. 1931. Some experiments on the ripening of rice. Proc. Crop Sci. Soc. Jpn. 3: 10-21. (Title was translated into English by authors.)

Kobayashi, K. and Imaki, T. 1997. Varietal differences of rice in differentiation and degeneration of secondary rachis-branches and spikelets in terms of their nodal distribution on a rachis. Jpn. J. Crop Sci. 66: 578-587.

Komatsu, Y., Kon, T., Matsuwo, K., Katayama, N. and Kataoka, T. 1984. Varietal characters of high-yielding foreign rice. Bull. Shikoku Agric. Exp. Stn. 43: 1-37.

Mackill, D.J. 1995. Plant genetic resources. Classifying Japonica rice cultivars with RAPD markers. Crop Sci. 35: 889-894.

Maruyama, S., Kabaki, N. and Tajima, K. 1988. Growth response to nitrogen in Japanese and Indica rice varieties. I. Varietal differences in the rate of increase in straw weight and number of spikelet due to nitrogen fertilization. Jpn. J. Crop Sci. 57: 470-475.

Nagato, K. 1941. An investigation in maturity of rice kernels in relation to the location on flower panicles of the plant. Proc. Crop Sci. Soc. Jpn. 13: 156-169.

Nagato, K. and Chaudhry, F.M. 1969. A comparative study of ripening process and kernel development in japonica and indica rice. Proc. Crop Sci. Soc. Jpn. 38: 425-433.

Nakamoto, T., Machida, H. and Matsuwasaki, A. 1988. Relationship between date of anthesis and grain weight on the panicle of rice. Jpn. J. Crop Sci. 57: 627-630.

Peng, S., Cassman, K.G., Virmani, S.S., Sheehy, J. and Khush, G. S. 1999. Yield potential trends of tropical rice since the release of IR8 and the challenge of increasing rice yield potential. Crop Sci. 39: 1552-1559.

Saito, K., Shimoda, H. and Ishihara, K. 1993. Characteristics of dry matter production process in high-yield rice varieties. VI. Comparisons between new and old rice varieties. Jpn. J. Crop Sci. 62: 509-517.

Sasahara, T., Abe, N. and Kambayashi, M. 1985. Inheritance of panicle types classified by the nodal distribution pattern of secondary spikelets in rice (Oryza sativa L.). Jpn. J. Breed. 35: 32-40.

Sasahara, T., Kodama, K. and Kambayashi, M. 1982. Studies on structure and function on the rice ear. IV. Classification of ear type by number of grain on the secondary rachis-branch. Jpn. J. Crop Sci. 51: 26-34.

Takeda, T., Oka, M. and Agata, W. 1984. Characteristics of dry matter and grain production of rice cultivars in the warmer part of Japan. IV. Comparison between grain production of Japanese and new Korean cultivars. Jpn. J. Crop Sci. 53: 28-34.

Yamagishi, T., Peng, S., Cassman, K.G. and Ishii, R. 1996. Studies on grain filling characteristics in “New Plant Type” rice lines developed in IRRI. Jpn. J. Crop Sci. 65 (Extra issue 2): 169-170.

Yamamoto, Y., Yoshida, T., Enomoto, T. and Yoshikawa, G. 1991. Characteristics for the efficiency of spikelet production and the ripening in high-yielding Japonica-Indica hybrid and semidwarf Indica rice varieties. Jpn. J. Crop Sci. 60: 363-372.

Yang, J., Peng, S., Visperas, R.M., Sanico, A.L., Zhu, Q. and Gu, S. 2000. Grain filling pattern and cytokinin content in the grains and roots of rice plants. Plant Growth Regulation 30: 261-270.

Zhang, Q.F., Maroof, M.A.S., Lu, T.Y. and Shen, B.Z. 1992. Genetic diversity and differentiation of indica and japonica rice detected by RFLP analysis. Theor. Appl. Genet. 83: 495-499.

*In Japanese with English abstract.

**In Japanese with English summary.

***In Japanese.