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Article

Location Distribution Characteristics in Leaf Lateral Asymmetry of Hybrid Indica Rice

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Abstract: Rice leaves show lateral asymmetry. Differences in width, thickness, chlorophyll meter readings, nitrogen content, density, and yield on each asymmetrical have been reported. However, limited information is available on the distribution characteristics of the smooth side (SS) and rough side (RS) of rice leaves. The SS of rice leaves can be divided into two types according to its location in leaf: one is the smooth side appearing on the left (SSAL) of the leaf, while the smooth side of the other type appears on the right (SSAR). Through the investigation of four rice varieties, we identified that the proportion of SSAL or SSAR of flag leaves on main stems or tillers was close to 0.50 in the rice population. On the same tiller stem, SSAL and SSAR present alternately, and the SS always stretches ahead of the RS in the curled state. Among the tiller flag leaves of a single rice plant, the proportion of tiller flag leaves with SSAL or SSAR to the total number of tillers is a discrete random variable. Frequency distribution analysis of these proportions showed that the percent of frequency of some class limits was close to each other, and the ratios of percent of frequency of SSAL to SSAR were close to 1:1. To our knowledge, this is a novel finding in rice canopy morphology. According to this study, we can divide rice population into two groups in four hybrid rice varieties.

Keywords: Hybrid rice; leaf lateral asymmetry; rough side; smooth side

1 Introduction

As an important global food crop, rice feeds more than half of the world's population and is also a major model plant used in studies [1–3]. Rice leaves are the key organ used in photosynthesis and the main source of dry matter production and grain yield [4]. Consequently, there are numerous studies on rice leaves. Among these studies, we have noticed the rice leaf lateral asymmetry.

Rice leaves have a main central vein with two asymmetrical sides, one wider than the other [5]. One side is thicker than the other, with a 27.6 to 46.0% differences between the two sides [6]. Yuan et al. [7] showed that the wide side had about 24.5% greater leaf thickness and 17.0% greater leaf width than the narrow side.

Moreover, it was observed the leaf nitrogen concentration based on dry weight and leaf area, and chlorophyll meter reading (SPAD) of the narrow side were on average 9.9%, 7.8%, and 7.7% higher respectively than that of the wide side [7]. This showed that the narrow side maintained a higher nitrogen concentration than the wide side. Therefore, it was speculated that there was a difference in photosynthetic rate between the two sides of rice leaf. Among the top three leaves at heading stage, it was also found that the magnitude of leaf lateral asymmetry in the third leaf was the greatest followed by the second and the flag leaf [7]. Li et al. [8] reported that one side of rice leaves was relatively smooth compared to the other, and that the SPAD of the smooth side (SS) of flag leaves was higher than that of the rough side (RS) while the RS had a higher absolute value of the cycle growth rate of SPAD. It was also found that the contribution of the SS to yield was higher than that of the RS [9]. The difference in texture on both sides of the flag leaf was mainly due to the difference in the concave and the convex state of lateral vein and of the upper and lower epidermis tissue. Intuitively, the SS is narrower than the RS, which means that the SS is the narrow side while the RS is the wide side in rice leaves [9].

The SS of rice leaves can be divided into two types according to its location. The first type is the smooth side of appearing on the left (SSAL) of leaf and the second is the smooth side of appearing on the right (SSAR) of the leaf. Yuan et al. [7] noticed that the wide or narrow side was located on the right or left side alternatively depending on leaf position. Li et al. [8] indicated that the probability of SSAL or SSAR in the flag leaf of main stem was close to 0.50 in two rice varieties (Qyou6 and Zhunliangyou527). Besides the information in these studies, there is no more information on these traits in rice. We cannot determine whether the ratio of SSAR to SSAL in the flag leaves of a single rice plant is consistent with that in the main population. It is also unknown whether the ratio of SSAR to SSAL in the flag leaves of all tillers in the rice population is consistent with that of main stems in the rice population, except for the ratio of 1:1, and whether there are other ratios such as 1:3 or 3:1. The purpose of this study was to understand in depth the distribution characteristics of SSAL or SSAR in leaf lateral asymmetry of rice.

2 Materials and Methods

2.1 Field Experiment Design and Crop Management

The field experiment was conducted at Jiuzhou Town, Huangping County, Guizhou Province (26°54’54”–27°5’49.2”N, 107°38’45.6”–107°51’39.6”E) in 2019. This station is within the north subtropical monsoon humid climate area in the southeastern part of Guizhou Province, with an altitude of 698 m and an average annual temperature of 15.7°C. The frost-free period is 268 d, and average annual rainfall is 1200 mm. In this study, a single factor experiment was designed at the three fields: F1, F2, and F3. Four rice varieties, Nei5you5399 (medium indica hybrid rice), Qyou6 (medium indica hybrid rice), Yixiangyou2115 (medium indica hybrid rice), and Zhongzheyou8 (late indica hybrid rice), were planted in every field. The plot was 36 m^2, and the fertilization was the same in each plot. Nitrogen fertilizer was split-applied a rate of 75 kg N ha^{-1} with 35% as basal fertilizer, 20% at early tiller stage (7 days after transplanting), 30% at spikelet promoting stage and 15% at spikelet sustaining stage. Phosphorus fertilizer was applied as basal fertilizer at a rate of 96 kg P_2O_5 ha^{-1}, and potassium fertilizer was split-applied at a rate of 180 kg K_2O ha^{-1} as 50% basal fertilizer and 50% panicle initiation fertilizer. Urea, superphosphate and potassium chloride were used as nitrogen, phosphorus and potassium fertilizers, respectively. Soil samples were taken from the 0–20 cm layer before transplanting rice. The soil chemical properties are listed in Tab. 1. Rice seedlings were transplanted at a hill spacing of 20 cm × 30 cm with one seeding per hill. The application of water and fertilizer during rice growth was closely monitored and insects were intensively controlled by chemicals.

Table 1: The soil chemical properties of three paddy fields

Field number	Total N (g kg^{-1})	Organic Matter (g kg^{-1})	Alkali-hydrol N (mg kg^{-1})	Olsen-P (mg kg^{-1})	Avail-K (mg kg^{-1})	pH
F1	1.54	14.70	107.43	13.90	112.94	6.38
F2	2.59	27.71	194.03	13.43	99.15	5.28
F3	1.63	17.87	126.93	2.81	71.03	5.22

2.2 Measurements and Methods

2.2.1 Investigation Contents and Sampling Method

Five aspects of leaf lateral asymmetry were investigated in this study: (i) The expansion sequence of SS and RS of flag leaves (in F1, the sample was 30); (ii) The location distribution of SS among the top four leaves of the main stem (in F2, the sample was 30); (iii) The probability of SSAL in the flag leaf of the main stem in the rice population (in F2, the sample was 400); (iv) The tiller ratio of having the SSAL of the flag leaf in single-hill rice plant (in F3, the sample was 200); and (v) the probability of SSAL of flag leaves in rice population (the sample is the same as (iv)). The investigations were mainly carried out at full heading stage (18–21 August). Random sampling was used for all samples.

2.2.2 Judgment of SS and RS of Rice Leaf

On the surface of the upper epidermis in rice leaves, the one side of the main vein with a more convex lateral vein is the RS while the other side is the SS. On the surface of the lower epidermis in rice leaf, the SS is smoother to the touch than the RS. The SS is visibly narrower than the RS in width. In this study, the SS and RS of the surface of lower epidermis in four rice varieties are illustrated in Fig. 1.

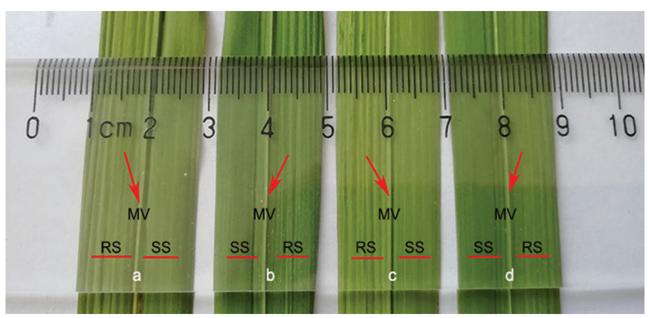

Figure 1: The SS and RS of both sides of the main vein on the surface of the lower epidermis in rice leaf. MV, main vein of rice leaf. SS, smooth side; RS, rough side. The a is Nei5you5399; b is Zhongzheyou8; c is Yixiangyou2115; d is Qyou6

2.2.3 Position Judgment of SSAL and SSAR of Leaf

When the tip of a leaf is upward and the upper epidermis of the leaf is facing the investigator, the leaf is recorded as SSAL when the SS appears on the left of the investigator and as SSAR when the SS appears on the right of the investigator.

2.2.4 Expansion Sequence Judgment of SS and RS in Flag Leaf

Tiller stems with half-unfurled flag leaves were selected to investigate the expansion sequence of SS and RS. The sample size for both SSAL and SSAR leaves was 30.

2.2.5 Judgment of Main Stems and Tillers in Per Hill Rice Plant

The tiller stem whose flag leaf tip was the highest point in the plant was determined to be the main stem in a single rice plant. The remaining tiller stems were considered tillers.

2.2.6 Calculations of Probability and Proportion

The proportion of SSAL of flag leaves on the main stem in rice = the number of main stems with SSAL of flag leaf/the total number of main stems investigated × 100%; the proportion of SSAL of flag leaves in a single rice plant = the number of tillers with SSAL of flag leaf/the total number of tillers in a single rice plant × 100%; the probability of SSAL of flag leaves in rice population = the number of tillers with SSAL of flag leaf/the total number of tillers in the rice population × 100%; the calculation methods of SSAR of leaves was the same as that of SSAL of leaves.

2.3 Statistical Analysis

Data were organized and analyzed by Microsoft Excel 2010 using mainly probability statistics, frequency distribution, and the chi-square test.

3 Results

3.1 Expansion Sequence of SS and RS in Flag Leaf

The data (Tab. 2) shows that the SS always stretches ahead of the RS in the curled state regardless of whether the SS is on the left or the right side of the leaf. It was obvious that the four rice varieties were consistent in expansion sequence of the flag leaf, which showed that this is an inherent characteristic of rice. This may further indicate that the growth and development of the SS occurs earlier than that of the RS.

Table 2: The expansion sequence of SS and RS of flag leaf in rice

Variety	Leaf trait	Sample size	SS first expanding		RS first expanding	
			Number	Proportion (%)	Number	Proportion (%)
Qyou6	SSAL	30	30	100	0	0
	SSAR	30	30	100	0	0
Yixiangyou2115	SSAL	30	30	100	0	0
	SSAR	30	30	100	0	0
Zhongzheyou8	SSAL	30	30	100	0	0
	SSAR	30	30	100	0	0
Nei5you5399	SSAL	30	30	100	0	0
	SSAR	30	30	100	0	0

SSAL, smooth side appearing on the left; SSAR, smooth side appearing on the right. SS, smooth side; RS, rough side. Data were taken from F1.

3.2 Position Distribution of SS among the Top Four Leaves of Main Stems

When the flag leaf on the main stem of a rice plant presents as SSAL, the second leaf from the top must be SSAR, followed by a SSAL in the third leaf from the top, and so on (Tab. 3). The same rule exists when the flag leaf in the main stem of a rice plant is SSAR. The four rice varieties all showed this rule. That being said, SSAL and SSAR of leaves are displayed alternately among upper and lower adjacent leaves. This is also true for the leaves on other tillers.

Table 3: The location distribution of SS in top four leaves of main stem of rice

Variety	L_1		L_2		L_3		L_4	
	SSAL	SSAR	SSAL	SSAR	SSAL	SSAR	SSAL	SSAR
Qyou6	+	–	–	+	+	–	–	+
	–	+	+	–	–	+	+	–
Yixiangyou2115	+	–	–	+	+	–	–	+
	–	+	+	–	–	+	+	–
Zhongzheyou8	+	–	–	+	+	–	–	+
	–	+	+	–	–	+	+	–
Nei5you5399	+	–	–	+	+	–	–	+
	–	+	+	–	–	+	+	–

The sample size was 30. SSAL, smooth side appearing on the left; SSAR, smooth side appearing on the right. SS, smooth side. L_1 is the flag leaf, L_2 is the second leaf, L_3 is the third leaf, L_4 is the fourth leaf. '+' indicates existence, '–' indicates nonexistence. Data were taken from F2.

3.3 Probability of SSAL and SSAR of Flag Leaves of Main Stems in Rice Population

The investigations based on 400 flag leaves of main stems in rice (Tab. 4) showed that the ratio of SSAL to SSAR in four rice varieties was close to 1:1. The chi-square test showed that the difference was significant between the observation value only in Yixiangyou2115 and the theoretical value of 1:1. This may be related to the sample size. Therefore, it could be considered that the probability of SSAL or SSAR of flag leaves on the main stem is 0.5 in the rice population.

Table 4: The probability of SSAL and SSAR of flag leaves of main stems in rice population

Variety	Sample size	Frequency		Proportion (%)		χ_c^2
		SSAL	SSAR	SSAL	SSAR	
Qyou6	400	203	197	50.75	49.25	0.0625
Yixiangyou2115	400	225	175	56.25	43.75	6.0025*
Zhongzheyou8	400	198	202	49.50	50.50	0.0225
Nei5you5399	400	209	191	52.25	47.75	0.7225

SSAL, smooth side appearing on the left; SSAR, smooth side appearing on the right. Data were taken from F2. $P_{0.05} = 3.84$; $P_{0.01} = 6.63$.

3.4 Proportion of Tiller Having SSAL or SSAR Flag Leaves in a Single Rice Plant

The frequency distribution was similar between some class limits with regard to the proportion of tillers having SSAL or SSAR of flag leaves in a single rice plant (Tab. 5). Furthermore, the percent of frequency of some class limits was close to each other. Within the class limits of 18%–30%, 30%–42%, 42%–54%, 54%–68%, and 68%–80%, the ratio of percent of frequency of SSAL to SSAR was close to 1:1, and the average value of these ratios was 1.082. In addition, it was observed that there were all SSAL, all SSAR, or half SSAL of flag leaves among all tillers in single rice plant for three varieties, Qyou6, Yixiangyou2115, and Nei5you5399. Moreover, their percents of frequency were all about 7% in 200 rice plants. For all rice plants of Zhongzheyou8, however, only one had all SSAL of flag leaves, and none had all SSAR of flag leaves. Meanwhile, it was observed that 8.5% of 200 rice plants possessed half-SSAL flag leaves.

Table 5: Frequency distribution of the proportion of SSAL or SSAR of flag leaves on tillers in single rice plants

Class limit of proportion	Percent of frequency (%)										SSAL: SSAR
	Qyou6		Yixiangyou2115		Zhongzheyou8		Nei5you5399		Mean (%)		
	SSAL	SSAR	SSAL	SSAR	SSAL	SSAR	SSAL	SSAR	SSAL	SSAR	
–6%–6%	7.00	7.50	4.00	3.50	0.00	7.50	8.00	6.00	4.75	6.13	0.78
6%–18%	13.0	6.50	13.0	8.50	5.50	6.50	14.00	10.00	11.38	7.88	1.44
18%–30%	8.00	8.50	10.0	8.50	10.5	8.50	8.00	10.50	9.13	9.00	1.01
30%–42%	15.0	14.50	17.5	14.50	22.5	14.5	13.50	15.00	17.13	14.63	1.17
42%–54%	15.0	13.50	16.0	12.50	19.5	13.5	11.50	12.00	15.50	12.88	1.20
54%–68%	17.0	16.50	12.5	17.00	24.0	20.0	14.00	10.50	16.88	16.00	1.05
68%–80%	10.0	10.50	12.5	15.50	9.50	7.50	11.50	11.00	10.88	11.13	0.98
80%–92%	5.50	12.50	7.50	13.00	8.00	14.0	10.00	11.50	7.75	12.75	0.61
92%–104%	9.50	10.00	7.00	7.00	0.50	8.00	9.50	13.50	6.63	9.63	0.69

The sample size was 200. SSAL, smooth side appearing on the left; SSAR, smooth side appearing on the right. Data were taken from F3.

3.5 Distribution of SSAL and SSAR on Flag Leaves in Tillers

Interestingly, in the flag leaf of all tillers, although the proportion of SSAL was lower than that of SSAR, they were all close to 50% (Fig. 2). The four rice varieties all present this rule. In order to understand the specific relationship between this distribution and the tiller number in rice, we analyzed the distribution characteristics of SSAL and SSAR of leaves among different tiller numbers (Tab. 6). The tiller numbers of four rice varieties were distributed from 5 to 20 and were mainly concentrated from 9 to 12. As long as there were enough investigation samples, the proportion of SSAL and SSAR of flag leaves in the rice population was close to 50%, which meant that half of flag leaves had the SSAL, while the other half had the SSAR in tiller population.

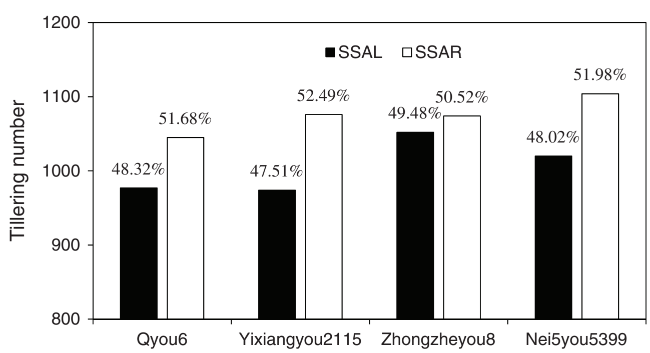

Figure 2: Distribution of SSAL and SSAR of flag leaf in all tillers of 200 hills of rice plants. SSAL, smooth side appearing on the left; SSAR, smooth side appearing on the right. Data were taken from F3. The sample is the same as Tab. 5

Table 6: Frequency distribution of different tiller numbers in single rice plants and the proportion of SSAL and SSAR of flag leaves

Tiller number	Qyou6			Yixiangyou2115			Zhongzheyou8			Nei5you5399		
	Frequency	SSAL (%)	SSAR (%)	Frequency	SSAL (%)	SSAR (%)	Frequency	SSAL (%)	SSAR (%)	Frequency	SSAL (%)	SSAR (%)
8	28	42.41	57.59	30	42.92	57.08	27	49.54	50.46	21	48.81	51.19
9	36	35.80	64.20	31	56.63	43.37	30	52.96	47.04	27	52.26	47.74
10	27	48.89	51.11	30	46.33	53.67	28	50.71	49.29	39	49.23	50.77
11	27	52.53	47.47	22	49.59	50.41	38	50.96	49.04	34	45.45	54.55
12	19	55.70	44.30	26	47.12	52.88	35	49.05	50.95	26	47.76	52.24
13	15	49.74	50.26	16	48.56	51.44	12	49.36	50.64	14	46.70	53.30

SSAL, smooth side appearing on the left; SSAR, smooth side appearing on the right. Data were taken from F3. The sample is the same as Tab. 5.

4 Discussion

In plant morphology and ecology, studies of fluctuating asymmetry have been carried out for decades [10]. Fluctuating plant asymmetry is mainly used to measure the impact of environmental pressure on plant growth and development, and to reflect the extent of external environmental pressure and the adaptability of organisms to the environment [11,12]. In these studies, leaf fluctuation asymmetry is mainly related to many factors such as region, altitude, competition and temperature [13,14]. For both sides of rice leaf (narrow and wide sides, smooth and rough sides, or left and right sides), differences in physiological and biochemical traits in leaf lateral asymmetry are affected by environmental conditions and other factors, such as nitrogen nutrition, determination period and measurement position [8,15]. Asymmetry is widespread in nature. In this study, the growth and development of both sides of rice leaves were not consistent, and the SS always stretches ahead of the RS in the curled state, which may be an important factor causing the leaf lateral asymmetry of rice.

Yuan et al. [7] analyzed the differences in width, thickness, nitrogen content and SPAD value between the smooth and rough sides, and Li et al. [9] presented the contribution of both sides to the yield. These studies are all based on the individual level to understand rice leaf lateral asymmetry. In our study, in addition to comparing the development speed and describing the distribution characteristics between the smooth and rough side of tillers at the individual level, we also investigated the location distribution characteristics of the smooth and rough side at the level of the entire rice population.

We already know that the probability of SSAL and SSAR in a single rice leaf is 50%. It is easy to imagine that the proportion of SSAR and SSAL in the flag leaves of a single hill rice plant is also 50%, however, the results of the investigation showed more diversity. Interestingly, the ratio of SSAR to SSAL of flag leaves in all tillers is close to 1:1, and is not 1:3 or 3:1. It is worth noting that four hybrid indica rice varieties were investigated in this study. Further investigation is needed to determine whether the results would be the same in ordinary indica and japonica rice.

Gene regulation of rice leaves in leaf length, leaf width, leaf thickness, leaf angle, and photosynthetic performance has been extensively reported [16–19]. However, only a few studies have shown that the *leaf lateral symmetry 1* (*LSY1*) gene is related to the traits such as the width on both sides of rice leaves [20,21]. These leaf traits are quantitative traits and controlled by multiple genes. As far as our research results were concerned, we have not seen the analysis of relevant literature at the gene level. However, it is clear that the positional phenotype of leaf lateral asymmetry in rice should be a qualitative trait. However, the rice population is closely related to rice tillers. Therefore, understanding the gene regulation of positional traits in leaf lateral asymmetry of rice may be more complicated than the explanation suggested by our results.

As a Gramineae plant, the tiller is an important agronomic trait of rice, which determines the panicle and yield. At present, research on the regulation of rice tillers has been quite detailed and in-depth [22–26]. In this study, there is no obvious trend for the distribution characteristics of leaf lateral asymmetry in a single rice plant. However, within the class limits of 18%–30%, 30%–42%, 42%–54%, 54%–68%, and 68%–80%, the ratios of percent of frequency of SSAL to SSAR were close to 1:1, and the average value of these ratios was 1.082. Moreover, it was observed that there were all SSAL, all SSAR, or half SSAL of flag leaves among all tillers in single rice plants for three varieties, Qyou6, Yixiangyou2115 and Nei5you5399. For example, out of a sample size of 200 plants, for 15 rice plants with an average tiller number of 8 (value was 8.47), the proportion of tillers having all SSAL flag leaves was 100%. Whether this is related to the sample size or due to other factors needs further study. At present, research on rice, especially genomics, has been in-depth [27–30]. It may only be a matter of time before genomics research explains this.

In application, paying attention to leaf lateral asymmetry of rice can more accurately detect the impact of environmental factors on rice growth. Considering rice leaf lateral asymmetry may also aid in the application of nitrogen nutrition diagnosis and yield prediction [8,15]. In superhigh-yielding practice, super rice can improve leaf area duration, light-harvesting capacity, light utilization, and photosynthetic efficiency for high crop productivity, thereby increasing phenotypic productivity by agronomic “reoptimization” of canopy topology in leaf vertical dispersion and orientation [31]. The function of distribution characteristics of rice leaf lateral asymmetry in this “reoptimization” require more research and exploration. In our study, the SS of half of the flag leaves of main stem of rice population was on the left and the that of other half was on the right, which means that we can divide the rice population into two groups in four rice varieties. Further analysis may reveal the difference between these two groups and provide valuable information on a neglected and fascinating aspect of leaf lateral asymmetry in rice plants.

5 Conclusion

Overall, the SS of rice leaves always stretches ahead of the RS in the curled state, and the SSAL and SSAR appear alternately on the same tiller stem in rice. There was no obvious trend for the proportion of SSAL or SSAR in the tillers of single rice plants. In the rice population, the proportion of SSAL and SSAR in flag leaves of main stem was close to 50%, and it also was close to 50% for the proportion of SSAL or SSAR in the flag leaves of all tiller stems. To our knowledge, this is a novel finding about location distribution characteristics of leaf lateral asymmetry in rice canopy morphology. According to this study, this means that we can divide the rice population into two groups in four hybrid rice varieties.

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Conflicts of Interest: The authors declare that they have no conflicts of interest to report regarding the present study.

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