

Genetic variation of typhoon-induced spikelet sterility in introgression lines with genetic background of Indica group rice (*Oryza sativa* L.) variety IR 64

Asami Tomita , Nashir Uddin , Mitsuhiro Obara , Hiroki Saito & Yoshimichi Fukuta

To cite this article: Asami Tomita , Nashir Uddin , Mitsuhiro Obara , Hiroki Saito & Yoshimichi Fukuta (2020): Genetic variation of typhoon-induced spikelet sterility in introgression lines with genetic background of Indica group rice (*Oryza sativa* L.) variety IR 64, Plant Production Science, DOI: [10.1080/1343943X.2020.1816138](https://doi.org/10.1080/1343943X.2020.1816138)

To link to this article: <https://doi.org/10.1080/1343943X.2020.1816138>



© 2020 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group.



[View supplementary material](#)



Published online: 08 Sep 2020.



[Submit your article to this journal](#)



Article views: 187



[View related articles](#)



[View Crossmark data](#)

Genetic variation of typhoon-induced spikelet sterility in introgression lines with genetic background of Indica group rice (*Oryza sativa* L.) variety IR 64

Asami Tomita^{a,b}, Nashir Uddin^c, Mitsuhiro Obara^d, Hiroki Saito^a and Yoshimichi Fukuta^a

^aTropical Agriculture Research Front, Japan International Research Center for Agricultural Sciences, Ishigaki, Japan; ^bGraduate School of Environmental and Life Science, Okayama University, Okayama, Japan; ^cDepartment of Biochemistry and Microbiology, School of Health and Life Sciences, North South University, Dhaka, Bangladesh; ^dBiological Resources and Post-Harvest Division, Japan International Research Center for Agricultural Sciences, Tsukuba, Japan

ABSTRACT

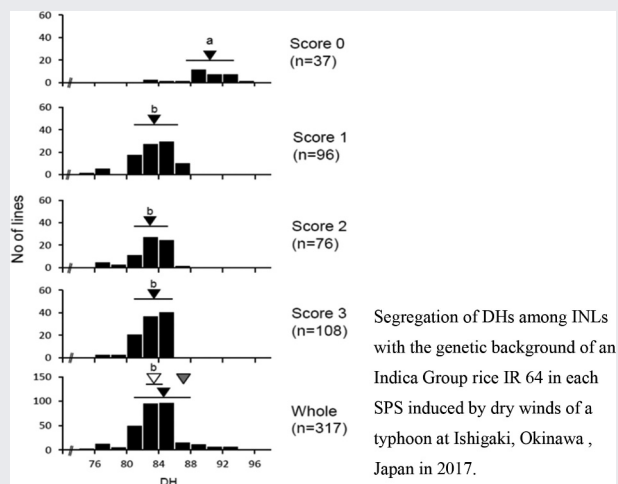
Wide variations of typhoon-induced spikelet sterility and days to heading (DH) were found among 317 introgression lines (INLs) originating from new-plant-type varieties with a genetic background of Indica Group rice variety IR 64. Sterility was induced by continuous dry winds from the typhoon. The most seriously affected were 194 INLs with DH ranging from 83 to 86 days. Positive correlations with the spikelet sterility score (SSS) were found for culm length (CL), panicle length (PL), and panicle weight (PW). Based on these traits and DH, the 194 INLs were classified into three groups: A1, A2, and B. The means of SSS and four traits (CL, PL, culm and leaf weight (CW), and panicle weight (PW)) were the lowest in group A1, and highest in group B. PN was significantly higher in group B than those in the others. Seven quantitative trait loci (QTL) for SSS were detected on chromosomes (chr.) 1, 2, 4, 7 (two), 8, and 11. Among them, the QTL of chr. 4 was located in the same regions as those of DH, CL, PL, CW, and panicle number (PN). Thus, the region on chr.4 might induce sterility in the INLs by modifying plant architecture, such as large panicles or high plant height with the minor effect of many tillers. The relationships among traits, and the QTLs will be useful information for genetic improvement of tolerance to typhoon damage in rice.

ARTICLE HISTORY

Received 2 April 2020
Revised 14 August 2020
Accepted 24 August 2020

KEYWORDS

Spikelet sterility; typhoon; QTL analysis; introgression line; rice (*Oryza sativa* L.); Indica Group




Spikelet sterility (or 'whitehead') induced by high temperatures and strong dry winds is a significant type of damage seen in rice (*Oryza sativa* L.) plants when typhoons or foehn winds pass during the cultivation period (Muramatsu & Kamota, 1979). It often occurs in the Hokuriku district of Japan (Muramatsu, 1976) and the eastern coastal area of Korea (Kang et al., 2003), where there are fields on the downwind side of mountains. Rice plants damaged in this way have decreased grain yield

components, including panicle number, number of fertile spikelets per panicle, ripening rate, and grain weight (Oida & Yuasa, 1999). To develop rice varieties tolerant to typhoon damage, clarification of the physiological and genetic mechanisms of spikelet sterility induced by typhoons is necessary.

Typhoon-induced spikelet sterility in rice is due to the loss of water potential when high temperatures, low humidity, and strong winds occur approx. Three– 5

CONTACT Yoshimichi Fukuta  zen@affrc.go.jp

 Supplemental data for this article can be accessed [here](#)

© 2020 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group.

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

days after panicles emerge from the flag leaf sheath (Muramatsu & Kamota, 1979; O'Toole et al., 1984). Ishihara et al. (1990) reported that increasing the vapor pressure deficit around rice leaves and difficulty in water transport through the panicle neck internodes might lead to the occurrence of spikelet sterility in the rice flowering period. The water potential of panicles decreases after heading due to the increasing resistance to water transport in the rice plant (Tsuda et al., 1992). Hirasawa (2000) clarified that panicle sterility is due to resistance to water transport of the panicle neck occurring from decreasing water potential and then bubbles forming inside the panicle neck. Panicle neck diameter, which is correlated with the cross-section area and number of vascular bundles, affects panicle size, such as the total number of spikelets per panicle (Liu et al., 2008). In addition, Tanimoto and Itoh (2000) reported that the degree of leaf rolling might affect the amount of transpiration per plant. Tanimoto and Itoh (2001) found that, compared with the leaf area, rice plant length and number of leaves were positively correlated with relative transpiration per plant in 13 rice varieties. Lim et al. (1988) and Lee et al. (1998) clarified that the degree of spikelet sterility induced by artificial dry wind was related to several agronomic traits such as culm length, panicle length, panicle number, no. of spikelets, flag leaf length and width, thickness of necknode, or 1000 grain weight. Therefore, investigating the relationship between typhoon-induced spikelet sterility and morphological traits or plant architectures will be a useful approach for clarifying the underlying mechanisms of damage induced by typhoons in rice.

A total of 334 introgression lines (INLs), harboring chromosome segments from nine new-plant-type (NPT) lines and a high-yielding Japanese cultivar, Hoshiaoba, were developed for genetic improvement of yield performance in an Indica Group cultivar, IR 64 (Fujita et al., 2010, 2009). Fujita et al. (2009), Fujita et al. (2010) clarified wide variations in these lines with respect to eight agronomic traits – days to heading (DH), culm length (CL), leaf width (LW), leaf length (LL), panicle length (PL), panicle number per plant (PN), 100-grain weight (GW), and total spikelet number per panicle (TS) – at the International Rice Research Institute in the Philippines, and detected 54 quantitative trait loci (QTLs) for them by association analysis. Uddin et al. (2016a) also clarified wide variations in 10 agronomic traits – DH, CL, PL, culm weight (CW), panicle weight (PW), harvest index [PW/total weight (TW)], PN, fertile spikelet number per panicle (FS), TS, and fertility rate (FS/TS) – in irrigated lowland and upland fields in Tsukuba, Japan, and detected 166 QTLs. Based on the information of these genetic variations, QTLs or genes for DH (Fujita et al.,

2011; Tagle et al., 2016), TS (Fujita et al., 2012, 2013; Koide et al., 2013; Sasaki et al., 2017), PN (Uddin et al., 2016b), CL, LL, LW, FS (Tagle et al., 2016), and GW (Ishimaru et al., 2017) have been identified using hybrid populations derived from crosses between IR 64 and the INLs. Recently, QTLs of root morphological traits have also been found: root length (Obara et al., 2014) and soil-surface roots (Tomita & Fukuta, 2019).

Therefore, these INLs are useful materials with which to investigate the relationship between variations in spikelet sterility induced by typhoons and morphological traits. In addition, rice varieties have genetic differences with respect to spikelet sterility induced by typhoons (Matsuo et al., 1951); however, no reports have performed genetic analysis for spikelet sterility. By using these INLs and their genotype data, it is possible to detect QTLs for spikelet sterility induced by typhoons.

Typhoon Lan passed the eastern area of the Yaeyama islands of Okinawa, Japan, from October 20 to 22, 2017, and it closely approached our agricultural research station at Ishigaki on October 21. After this typhoon, we observed spikelet sterility in rice plants in irrigated lowland fields of Ishigaki. In this study, we clarified the genetic variations in the spikelet sterility score (SSS) induced by the typhoon among the INLs, and we investigated the relationship between variations in the SSS and the agronomic traits. Moreover, QTLs for SSS and agronomic traits were detected by association analysis. Based on these results, we discuss the relationship between spikelet sterility induced by the typhoon and the agronomic traits and genetic factors involved in tolerance to the damage in rice genome chromosomes.

Materials and methods

Plant materials and cultivation

Fujita et al. (2009), Fujita et al. (2010) developed 334 INLs derived from a cross between an Indica Group cultivar IR 64 and 10 donor parents, including nine NPT lines and one Japonica Group variety, through backcross breeding. These INLs were divided into 10 sib-groups: 33 lines in YP1-INLs, 13 lines in YP3-INLs, 45 lines in YP4-INLs, 58 lines in YP5-INLs, 28 lines in YP6-INLs, 21 lines in YP7-INLs, 29 lines in YP8-INLs, 16 lines in YP9-INLs, 38 lines in YP10-INLs, and 36 lines in YP11-INLs, which were originated from each donor parent. In this study, we used 317 of these INLs and IR 64. These materials were cultivated in irrigated lowland fields of the Tropical Agriculture Research Front (TARF), Japan International Research Center for Agricultural Sciences (JIRCAS), Maezato, Kawarabaru, Ishigaki, Okinawa, Japan (24°22' N, 124°11'E) and were used for the investigation of

spikelet sterility induced by the typhoon and DH from 26 July 2017 to December 2017 in the second season of 2017, and for investigation of six agronomic traits (CL, PL, CW, PW, PW/TW, and PN) from 26 February 2018 to July in the first season of 2018.

Seeds were sterilized by treating overnight with 0.5% (w/v) agrochemicals ('Benrate T wettable powder 20', Thiuram 20.0%, and Benomyl 20.0%; Hokko Chemical Industries, Ltd., Tokyo, Japan). They were then sown in seedling trays ('Naedoko', 274 × 602 × 23 mm, 37 × 2 planting strips per tray; Minoru Industrial Co., Ltd., Okayama, Japan) filled with sterilized soil containing chemical fertilizer (N, 0.7 g/4 kg; P, 1.0 g/4 kg; K, 0.8 g/4 kg), and grown in a greenhouse for 4 weeks. Basal fertilizer at rates of 48 kg of N, 64 kg of P, and 32 kg of K per hectare was applied to the irrigated lowland fields before transplanting. In the lowland fields, 10 seedlings of each line were transplanted, one per hill 20 cm apart, in a single row, with 30 cm between lines.

Evaluation of degree of spikelet sterility induced by the typhoon

Typhoon Lan passed the eastern area of the Yaeyama islands of Okinawa, Japan, from October 20 to 22, 2017, and closely approached Ishigaki on October 21. Temperatures were around 25°C in the day and night times during those 3 days (Supplemental Fig. S1). Among those 3 days, the maximum instantaneous wind speed at Ishigaki was highest (21.7 m/s) at 16:00 on October 21. After that time, relative humidity changed dramatically: It ranged from 75% to 95% until 16:00 on October 21, decreased to 58.5% at 0 on October 21, and then stood at around 60% during the entire day on October 22. The investigation for degree of spikelet sterility was performed on October 24.

The degree of spikelet sterility among the 317 INLs was evaluated visually and categorized by assigning a spikelet sterility score (SSS) of 0–3 according to the ratio of sterile spikelet in exerted spikelet from the leaf sheath as follows: 0, 0% sterile spikelet; 1, <30%; 2, 30%–80%; and 3, >80%, of one plant in each INL (Figure 2). The intermediate several plants of the sterility among 20 plants in one INL was evaluated, and the selected score was used as the representative data of each INL. The SSS of IR 64 was investigated using the intermediate plant of 20 replications, and the average value was used as representative data.

Evaluation of agronomic traits

Seven agronomic traits – DH, CL, PL, CW, PW, harvest index (PW/TW), and PN – were investigated in each INL

and in IR 64. DH was the number of days from sowing day (26 July 2017) until the day on which 50% of individual plants in each INL showed panicle exertion. The other six morphological traits were not able to investigate by the heavy damage of Typhoon. These were investigated using six individuals per line, and mean values were used as representative data in the first season of 2018. At 30 days after heading, these individuals were harvested and dried in a ventilated room. For each plant, CL was measured from the soil-surface to the neck of the panicle, and PL from the panicle neck to the topmost spikelet in the longest tiller. CW was measured as the weight of culm and leaf, and PW was the weight of the panicle including spikelets and rachis branches. PW/TW was calculated as the ratio of the average panicle weight to the total plant weight. PN was the number of productive panicles per plant.

Association analysis of SSS and agronomic traits

The genotype data of more than 200 simple sequence repeat (SSR) markers (McCouch et al., 2002) distributed across rice genome chromosomes of the INLs (Fujita et al., 2010, 2009) were used for association analysis. The associations between introgressed chromosomal segments and SSS and seven agronomic traits (DH, CL, PL, CW, PW, PW/TW, and PN) were detected by single marker analysis (SMA) within each sib-group of the INLs which had been exposed to the typhoon immediately after panicle heading, using version 2.5 of Windows QTL Cartographer software (Wang et al., 2011). A probability level of ≤ 0.01 was used as the threshold value to detect significant differences between genotypes of IR 64 and the donors. When multiple markers on the same chromosome segments were associated with a given trait, the QTL was located at the marker that had the highest *F*-score. The proportion of observed phenotypic variation attributable to a particular chromosomal region was estimated from the coefficient of determination (R^2).

Results

Genetic variations in DH and SSS among INLs

A wide genetic variation in DH ranging from 75 days to 96 days was observed among the 317 INLs. The mean value was 84.3 days (Figure 1). DH of IR 64 was 83.5 days. SSS varied also widely among these INLs: scores ranged from 0 to 3 and the mean value was 1.8. SSS of IR 64 was 2.2. Among the 317 INLs, 37 INLs (11.7% in the whole) had a score of 0, 96 (30.3%) had a score of 1, 76 (24.0%) had a score of 2, and 108 (34.1%) had a score of 3.

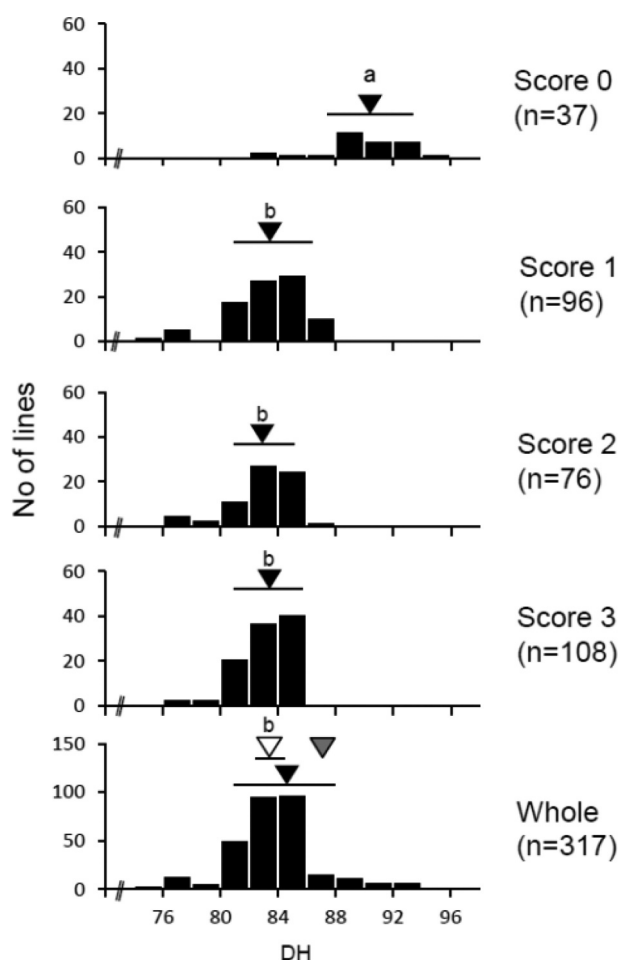


Figure 1. Segregation of DH among INLs in each score of SPS induced by a typhoon. A total of 317 INLs were used for the investigations of DH and spikelet sterility induced by Typhoon Lan. Typhoon Lan passed the eastern area of the Yaeyama islands of Okinawa, Japan, from October 20–22, 2017. Assignment of spikelet sterility score (SSS) was by visual evaluation conducted at the irrigated lowland fields of TARF, JIRCAS, Ishigaki, Okinawa, on October 24. The degree of sterile spikelets in exerted panicles in each INL was categorized into one of four scores: 0, no sterile spikelets; 1, less than 30%; 2, 30%–80%; 3, more than 80%. DH was the duration from the day of sowing, 26 July 2017, to panicle exertion in half of the plants in the INL. Black triangles and horizontal lines indicate mean and SD of DH, respectively, among the INLs. White triangle and horizontal line indicate those of IR 64. Gray triangle indicates October 21 (DH = 87 days after sowing), when the typhoon closely approached Ishigaki. Values denoted by the same letter are not significantly different from one another at $P = 0.05$ according to the Tukey-Kramer test.

Typhoon Lan approached Ishigaki closely on 21 October 2017, corresponding to a DH of 87 days after sowing. Of the 317 INLs, 270 INLs had headed before that day (DH = 75 to 86 days) and 194 (61.2%) had a DH in the four-day range of 83 to 86 days and were thus exposed to the

typhoon immediately after heading. Among those 194 INLs, five had a score of 0 (2.6%), 58 had a score of 1 (29.9%), 53 had a score of 2 (27.3%), and 78 had a score of 3 (40.2%) (Figure 4). The mean value, 2.1, was similar to that of IR 64 (Figure 4). In contrast, the other 47 INLs with the later DH of 87 to 96 days showed lower SSS of 0.4. These results indicate that the 194 INLs with DH from 83 days to 86 days and IR 64 were seriously exposed to the typhoon immediately after panicle heading, and the variation in SSS among the 194 INLs might be induced by other factors, not only by DH.

Relationship between SSS and agronomic traits in 194 INLs

Wide variations in six agronomic traits – CL, PL, CW, PW, PW/TW, and PN – were found among the 194 INLs (Figure 3). CL varied from 45.0 to 81.6 cm, PL from 19.0 to 27.5 cm, CW from 10.6 to 37.1 g, PW from 13.9 to 54.8 g, PW/TW from 39.6% to 64.9%, and PN from 7.8 to 22.5. The mean CL in these INLs was significantly higher than that of IR 64, and the mean values of CW, PW, and PN were significantly lower (Figure 3, Table 2). The mean values of PL and PW/TW were similar to those of IR 64. Thus, in terms of plant architecture, the 194 INLs mainly included taller plants and those with lower dry matter production compared with IR 64.

Among the 21 combinations of the six agronomic traits plus DH, 13 showed significant correlations (Supplementary Table 1). Correlation coefficients of 11 of those combinations (between DH and CL, DH and PL, CL and PL, CL and CW, CL and PW, PL and CW, PL and PW, CW and PW, CW and PN, PW and PW/TW, and PW and PN) were positive values from 0.26 to 0.71. Correlation coefficients were negative for the remaining two combinations: between CL and PW/TW (–0.20), and CW and PW/TW (–0.46). Moreover, these seven agronomic traits showed significant positive correlations between Ishigaki and Tsukuba (Supplementary Table 2). Thus, we confirmed that the variations of agronomic traits in the 194 INLs cultivated in Ishigaki and Tsukuba corresponded. Also the 194 INLs cultivated in Ishigaki tended to increase in DH, CL, PL, PW, CW, and PN, together. According to the rising PW/TW, the values of PW increased and values of CL and CW decreased.

Three traits – CL, PL, and PW – showed significant positive correlations with SSS among the 194 INLs investigated in Tsukuba and Ishigaki (Table 1). DH and PN showed positive and negative correlations, respectively, only in Tsukuba, and PW/TW were positive in Ishigaki.



Figure 2. Typhoon-induced sterile spikelet. Panicle shows the most serious damage, score 3.

The remaining one, CW, showed no correlation in both places. Therefore, among the INLs, those types with large panicles and high plant height experienced a higher degree of typhoon damage.

The 194 INLs were classified into three cluster groups – A1, A2, and B – by cluster analysis using the variation data of the six agronomic traits plus DH (Supplemental Fig. S2). Cluster group A1 included 31 INLs, group A2 included 119, and group B included 44 (Figure 3). Significant differences among the three cluster groups were found in traits CL, PL, CW, and PW (Table 2). The values of these traits were lowest in cluster group A1 and highest in group B, and the values in group A2 were intermediated between those in A1 and B. PW/TW of cluster group A2 was lower than those of groups A and B, and PN of group B was significantly higher than those of A1 and A2. There was no significant difference between cluster groups in terms of DH. The mean values of SSS in cluster groups A1, A2, and B were 1.7, 2.0, and 2.4, respectively, and that of group B was significantly higher than those of the other two groups (Figure 4). These results indicate that the SSS was elevated with the effects of increase in four traits – CL, PL, PW, and CW – and that the INLs with high PN also induced high SSS.

QTLs for SSS and agronomic traits

Association analyses for SSS and seven agronomic traits were performed within the 194 INLs of nine sib-groups: eight lines in YP1-INLs, 43 lines in YP4-INLs, 33 lines in YP5-INLs, 16 lines in YP6-INLs, nine lines in YP7-INLs, 20 lines in YP8-INLs, 12 lines in YP9-INLs, 18 lines in YP10-INLs, and 34 lines in YP11-INLs, except for one line in YP3-INLs. A total of seven QTLs for SSS were detected in five sib-groups: one QTL on chr. 1, one on chr. 2, one on chr. 4, two on chr. 7, one on chr. 8, and one on chr. 11 (Figure 5, Table 3). The F values of these QTLs ranged from 8.2 to 40.0, and R^2 values were from 0.23 to 0.83. One QTL, $qSSS7.1-YP9$, showed the highest F and R^2 values among them. Introgressed alleles of two QTLs ($qSSS4.1-YP11$ on chr. 4, and $qSSS7.1-YP9$ on chr. 7) increased the score, and those of the other five QTLs ($qSSS1.1-YP11$ on chr. 1, $qSSS2.1-YP9$ on chr. 2, $qSSS7.2-YP5$ on chr. 7, $qSSS8.1-YP10$ on chr. 8, and $qSSS11.1-YP6$ on chr. 11) decreased the score. Two QTLs – $qSSS7.1-YP9$ detected in sib-group YP9-INLs and $qSSS7.2-YP5$ in YP5-INLs – overlapped in the same region on chr. 7. In the two QTLs, $qSSS8.1-YP10$ and $qSSS11.1-YP6$, IR 64 types were increased and did not fit with 1:1 segregations. These results indicate that both alleles of IR 64 and donor varieties among the seven

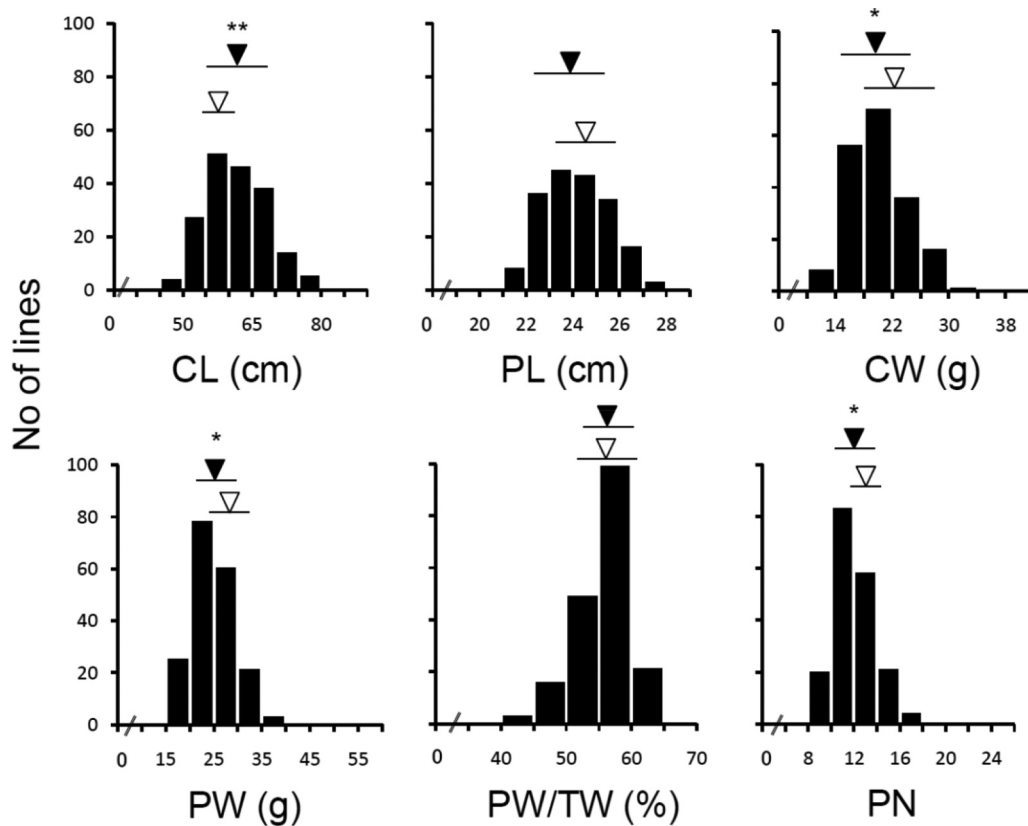


Figure 3. Segregation of traits related to yield components in INLs. Six agronomic traits – CL, PL, CW, PW, PW/TW, and PN – were investigated in 194 INLs grown in irrigated lowland fields of TARF, JIRCAS, Ishigaki, Okinawa. These INLs were those with DHs in the 4-day range from 83 to 86 days, when the typhoon inflicted the most serious damage after heading. Investigations were carried out in the first season of 2018. CL, Culm length; PL, Panicle length; CW, Culm weight; PW, Panicle weight per plant; PW/TW (total weight), Harvest index; PN, Panicle number per plant. White and black triangles and horizontal lines indicate mean values \pm SD of IR 64 and INLs, respectively. * and **: significantly different from IR 64 by *t*-test at $P = 0.05$ and 0.01 , respectively.

QTLs contributed to the variation of SSS occurring in the 194 INLs.

A total of 48 QTLs for seven agronomic traits were detected on all chromosomes except for chrs. 8 and 10: DH (six QTLs), CL (14), PL (eight), CW (four), PW (two), PW/TW (six), and PN (eight) (Figure 4, Table 3). The *F* values of these QTLs ranged from 7.7 to 37.6, and R^2 ranged from 0.16 to 0.71. Among them, abnormal segregations were found in the following 13 QTLs: *qDH11.2-YP6*, *qCL4.1-YP4*, *qCL4.1-YP6*, *qCL4.1-YP11*, *qCL6.1-YP10*, *qPL6.1-YP10*, *qPW6.1-YP10*, *qPW6.1-YP6*, *qPWTW3.1-YP9*, *qPN2.1-YP10*, *qPN4.2-YP5*, *qPN11.1-YP11*, and *qPN12.1-YP5* and these segregations of IR 64 and donor types did not fit the 1:1 ratio. In 11 regions on chrs. 2, 4 (two regions), 5, 6 (three), 7, 9, and 11 (two), several QTLs for different traits were detected together. Seven QTLs for SSS were detected on six regions (chrs. 1, 2, 4, 7 [two QTLs], 8, and 11), and among them three on chrs. 4, 7, and 11 were found with those for other traits originated from the same donor's alleles. In the region

for *qSSS4.1-YP11*, five QTLs originating from the same donor's alleles were found for five agronomic traits: DH, CL, PL, CW, and PN. The donor's alleles of *qSSS4.1-YP11* and the other QTLs increased the values of each trait except for PN. In the region of *qSSS7.2-YP5*, *qPWTW7.1-YP5* was located. The donor's alleles of *qSSS7.2-YP5* and *qPWTW7.1-YP5* decreased the values. The region of *qSSS11.1-YP6* overlapped with one QTL, *qDH11.2-YP6*. The IR 64 allele of *qSSS11.1-YP6* increased the value, and that of *qDH11.2-YP6* decreased. These results suggest that the plant architecture, such as large panicles or high plant height, made for a high SSS with introgressed alleles of the region for *qSSS4.1-YP11*.

Discussion

Ishigaki was subjected to continuous strong winds from Typhoon Lan over 3 days from October 20 to 22, 2017, accompanied by a sudden decrease in humidity after the

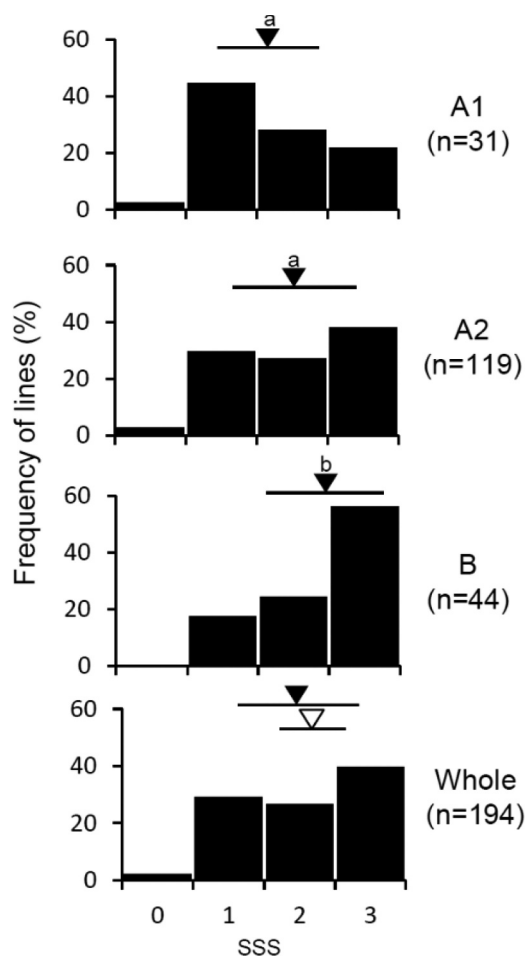


Figure 4. Segregation for SSS in INLs. A total of 194 INLs were classified into three cluster groups – A1, A2, and B – based on the data of segregation among seven agronomic traits: DH, CL, PL, CW, PW, PW/TW, and PN. The SSS segregation in each group was compared among the three cluster groups. The data of SSS and DH were collected at the irrigated lowland fields of TARF, JIRCAS, Ishigaki, Okinawa in the second season of 2017, and those of the other six agronomic traits were collected in the first season of 2018. SSS, Spikelet sterility score; DH, Days to heading; CL, Culm length; PL, Panicle length; CW, Culm weight; PW, Panicle weight per plant; PW/TW (total weight), Harvest index; PN, Panicle number per plant. White and black triangles and horizontal lines indicate mean values \pm SD of IR 64 and INLs, respectively. The mean values denoted by the same letter are not significantly different from one another at $P = 0.05$ according to the Tukey-Kramer test.

evening of October 21 (corresponding to DH of 87 days after sowing) (Supplemental Fig. S1). In that season, the 317 INLs showed a wide genetic segregation in DH and SSS (Figure 1). Among those INLs, IR 64 and 194 INLs whose DH ranged from 83 to 86 days were exposed to the effects of the typhoon immediately after heading, and SSS varied widely among them. INLs with later DH tended to show lower SSS and were able to avoid the damage. These results indicate that the wide variation in

SSS in the 317 INLs occurred mainly as a result of variation in DH. The rice flowering period (approx. 3–5 days after panicles emerge from the flag leaf sheath) is the time most sensitive to water stress-induced sterility (O’Toole et al., 1984). Transpiration amounts of panicles in rice plants are maximum at that time, and the amounts of transpiration decrease with aging (Ishihara et al., 1990; O’Toole et al., 1984). Hirasawa (2000) reported that panicle sterility induced by conditions of high temperature, low humidity, and high wind speed is due to a temporary increase in the panicle transpiration rate. In this study, the 194 INLs and IR 64 were seriously affected by the continuous strong dry winds immediately after panicle heading. Therefore, the variation in spikelet sterility induced in the INLs by the typhoon might have been due to a temporary increase in the panicle transpiration rate immediately after heading.

The 194 INLs showed significant positive correlations between SSS and the three traits of CL, PL, and PW (Table 1). Based on the data of seven agronomic traits, these INLs were classified into three cluster groups: A1, A2, and B (Supplemental Fig. S2). The means of SSS and those of the four traits of CL, PL, CW, and PW were the lowest in group A1 and highest in group B (Table 2). PW/TW of group A2 and PN of group B were significantly higher than those of the other groups. SSS of group B was significantly higher than those of the others (Figure 4). These results indicate that the plant architecture of large panicles, or high plant height, seriously contributed to the higher degree of typhoon-induced spikelet sterility in the INLs, with the minor effect of many tillers.

Previous studies also reported that the spikelet sterility induced by artificial dry wind was positively correlated with PL, TS (Lee et al., 1998; Lim et al., 1988), CL, flag leaf length (Lim et al., 1988), 1000-grain weight, flag leaf width (Lee et al., 1998), and negative with PN (Lee et al., 1998; Lim et al., 1988). The typhoon-induced spikelet sterility appears to have been caused by the imbalance between water uptake and transpiration from panicles and the difficulty in water transport through panicle neck internodes. Ishihara et al. (1990) reported that several vessels of the panicles’ vascular bundles are not yet completely mature in the rice flowering period. Hirasawa (2000) clarified that water transport through the panicle neck is remarkably restricted by air bubbles increasing in the vessels, leading to panicle sterility. Liu et al. (2008) found that the panicle neck diameter, which is correlated with thickness and number of vascular bundles, affected panicle size, such as total spikelet number per panicle. Lim et al. (1988) and Lee et al. (1998) reported that the panicle neck diameter was positively correlated with the spikelet sterility induced by artificial dry wind. In addition, plant height and

Table 1. Correlations between SSS and agronomic traits in 194 INLs.

Trait	<i>r</i> value													
	DH		CL		PL		CW		PW		PW/TW		PN	
	Site investigated													
	Tsukuba	Ishigaki	Tsukuba	Ishigaki	Tsukuba	Ishigaki	Tsukuba	Ishigaki	Tsukuba	Ishigaki	Tsukuba	Ishigaki	Tsukuba	Ishigaki
SSS	0.28***	-0.03	0.33**	0.33***	0.36***	0.36***	-0.04	0.00	0.15*	0.20*	0.12	0.27***	-0.18	-0.09

A total of 194 INLs with DH from 83 days to 86 days in the second season of 2017 were used for the calculation of correlation coefficients between SSS and seven agronomic traits. The data of DH and SSS were investigated at TARF, JIRCAS, Ishigaki, and Okinawa in the second season of 2017, and those of the other six agronomic traits were investigated at the irrigated lowland fields of Tsukuba, 2012 (Uddin et al., 2016a) and of Ishigaki in the first season of 2018. SSS: Spikelet sterility score; DH: Days to heading; CL: Culm length; PL: Panicle length; CW: Culm weight; PW: Panicle weight per plant; PW/TW (total weight): Harvest index; PN: Panicle number per plant. *, **, and ***: significant correlation coefficient at $P = 0.05$, 0.01 , and 0.001 , respectively.

Table 2. Mean values of agronomic traits in each cluster group.

Cluster group	No. of INLs	DH (days)		CL (cm)		PL (cm)		CW (g)		PW (g)		PW/TW (%)		PN	
A1	31	84.4 ± 1.1	a	52.1 ± 3.3	a	22.8 ± 1.2	a	15.4 ± 2.1	a	21.2 ± 4.1	a	57.7 ± 4.6	a	11 ± 1.3	a
A2	119	84.5 ± 1.1	a	61.6 ± 4.5	b	24.2 ± 1.3	b	19.9 ± 3.4	b	23.9 ± 3.1	b	54.7 ± 4.2	b	11.6 ± 1.5	a
B	44	84.7 ± 1.1	a	67.6 ± 7.1	c	24.8 ± 1.3	c	23.9 ± 3.4	c	30.9 ± 5.2	c	56.3 ± 3	ab	13.8 ± 2.3	b
Whole INLs	194	84.5 ± 1.1	***	61.5 ± 6.9	**	24.1 ± 1.5		20.1 ± 4.2	*	25 ± 5	*	55.5 ± 4.2		12 ± 2	*
IR 64		83.5 ± 0.9		59.4 ± 2.9		24.5 ± 1.2		22.1 ± 4.1		27.1 ± 4.7		55.1 ± 5.5		12.9 ± 1.6	

A total of 194 INLs were classified into three cluster groups – A1, A2, and B – based on the data of seven agronomic traits – DH, CL, PL, CW, PW, PW/TW, and PN – and the relationships between these agronomic traits in each cluster group and SSS were investigated. The data of SSS and DH at the irrigated lowland fields of TARF, JIRCAS, Ishigaki, Okinawa in the second season of 2017, and those of the other six agronomic traits in the first season of 2018, were used as the representative data of each INL. SSS, Spikelet sterility score; DH, Days to heading; CL, Culm length; PL, Panicle length; CW, Culm weight; PW, Panicle weight per plant; PW/TW (total weight), Harvest index; PN, Panicle number per plant. Within the same column in each group, the values denoted by the same letter are not significantly different from one another at $P = 0.05$ according to the Tukey-Kramer test. *, **, and ***: significantly different from IR 64 by *t*-test at $P = 0.05$, 0.01 , and 0.001 , respectively.

number of leaves, which often corresponds with tiller number, were positively correlated with relative transpiration per plant in rice cultivars that differ in plant type, and the many leaf number types had high water transpiration due to the low degree of leaf width rolling (Tanimoto & Itoh, 2000, 2001). Therefore, INLs of the plant architecture of high plant height or large panicles with the minor effect of high tiller number might have suffered typhoon-induced spikelet sterility because resistance to water transport through the panicle neck or transpiration from leaves might have been increased in the flowering period in these plant types. Several INLs with different plant structures will be used for the investigation of their spikelet sterility as well as the transpiration rate under several artificial vapor pressure deficit conditions with wind, in order to demonstrate the relationships between SSS and these traits.

A total of seven QTLs for SSS were detected in the 194 INLs by association analysis (Figure 5, Table 3). Among them, five QTLs overlapped with those of agronomic traits on the three regions of chr. 4, chr. 7, and chr. 11. Introgressed alleles from YP11 on the QTL region of chr. 4 increased SSS, DH, CL, PL, and CW and decreased PN. Thus, big plant architecture, such as high plant height and high dry matter production with low panicle number, contributed to the high degree of spikelet sterility with the introgressed allele of the region for *qSSS4.1-YP11* on chr. 4. On the QTL region of chr. 4, the QTLs for PL, PN (Kobayashi et al., 2003a), leaf width (LW),

leaf length (LL), and leaf angle (Kobayashi et al., 2003b) were detected using a hybrid population derived from a cross between Japonica and Indica Group cultivars. Liu et al. (2008) detected QTLs for panicle neck diameter and panicle traits (PL, PN, TS, FS, primary branch number, and secondary branch number). Using the INLs allowed detection of QTLs for several agronomic traits: CL, PL, PW, PW/TW, PN, total spikelet number per panicle (TS), fertile spikelet number per panicle (FS), FS/TS, LW, and LL (Fujita et al., 2010, 2009, 2013; Tagle et al., 2016; Uddin et al., 2016a). Thus, this chromosomal region of chr. 4 affects morphological traits, including leaf size, spikelet number, and panicle number, in a cluster of QTLs (Fujita et al., 2013). Therefore, the QTL region of chr. 4 might induce spikelet sterility in the INLs by modifying plant architecture to that of a high plant height and large panicle type with introgressed alleles of chr. 4. In this study, the remaining QTLs did not correspond with those agronomic traits. Further study is necessary to investigate the physiological effects that these QTLs have on spikelet sterility.

Several loci of the QTLs detected for SSS and agronomic traits did not fit the theoretical segregating ratio (1:1) (Table 3). This might be due to the selection of the 194 INLs based on DH from 83 to 86 days among the 317 (Figure 1). Advance QTL analysis for the traits will be required using hybrid population derived from a cross between IR 64 and the INL selected, in order to confirm the chromosomal position and the effects.

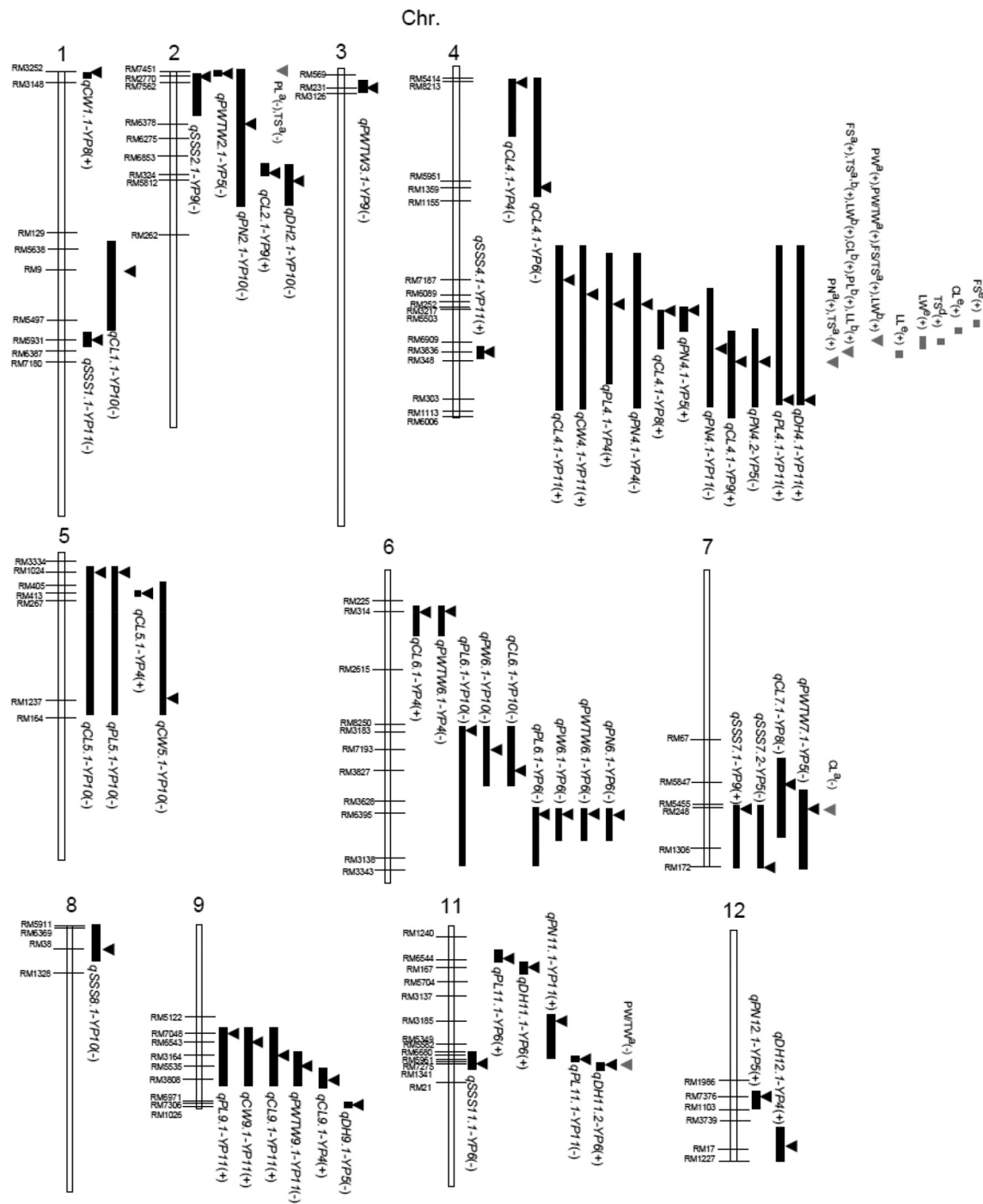


Figure 5. Chromosome locations of QTLs detected for SSS and other agronomic traits Among 317 INLs, 194 whose DH after sowing ranged from 83 days to 86 days, were used to detect QTLs for each trait by association analysis. These INLs were categorized into ten sib-groups which originated from crosses between ten different donor varieties and IR 64. The associations between genotypes of SSR markers (Fujita et al., 2010, 2009) and data of each trait were detected by single marker analysis (SMA) among INLs in each sib-group (Threshold: $P \leq 0.01$). Horizontal bars on each chromosome indicate the positions of SSR markers. Black bars on the right side of each chromosome indicate the chromosome region of association with traits detected, and arrowheads indicate the SSR marker with the highest F value. The SSR marker with the highest F value in the continuous region for association was taken to be the position of the QTL detected. Gray bars or triangles indicate regions of QTLs reported for agronomic traits in previous studies indicated here by superscript letters: a, Uddin et al. (2016a), b, Fujita et al. (2009), c, Fujita et al. (2010), d, Fujita et al. (2011), e, Fujita et al. (2013), and f, Tagle et al. (2016). (+) and (-) indicate, respectively, an increase and decrease in the SSS by introgressed allele. SSS, Spikelet sterility score; DH, Days to heading; CL, Culm length; PL, Panicle length; PW, Panicle weight per plant; PW/TW, Harvest index; PN, Panicle number per plant; FS, Number of fertile spikelets per panicle; TS, Total number of spikelets per panicle; FS/TS, Fertility rate; LW, Leaf width; LL, Leaf length.

Table 3. QTLs for SSS and agronomic traits by association analysis in each sib-group of 194 INLs.

Trait	QTL	Chr.	Position (Mbp)	Nearest marker name	F	R ²	Additive effect	Positive allele	Segregation ratio		χ^2	P-value	
									IR 64	Donor type			
SSS	qSSS1.1-YP11	1	29.28	RM5931	9.6	0.26	-0.39	IR 64	23	13	2.8	0.01	
	qSSS2.1-YP9	2	0.81	RM7451	10	0.56	-0.56	IR 64	8	4	1.3	0.25	
	qSSS4.1-YP11	4	31.81	RM3836	8.2	0.23	0.34	YP11	17	19	0.1	0.74	
	qSSS7.1-YP9	7	29.34	RM248	40	0.83	0.62	YP9	5	7	0.3	0.56	
	qSSS7.2-YP5	7	29.56	RM172	18.9	0.58	-0.86	IR 64	16	10	1.4	0.24	
	qSSS8.1-YP10	8	2.12	RM038	14.9	0.43	-0.71	IR 64	14	4	5.6	0.02*	
	qSSS11.1-YP6	11	20.14	RM1341	8.3	0.67	-0.75	IR 64	14	3	7.1	0.01*	
	qDH2.1-YP10	2	15.9	RM5812	7.9	0.33	-0.38	IR 64	13	5	3.6	0.06	
DH	qDH4.1-YP11	4	28.76	RM303	18.9	0.28	0.62	YP11	16	20	0.4	0.51	
	qDH9.1-YP5	9	22.21	RM7306	10.9	0.31	-0.55	IR 64	16	10	1.4	0.24	
	qDH11.1-YP6	11	4.08	RM167	18.1	0.56	0.99	YP6	12	5	2.9	0.09	
	qDH11.2-YP6	11	20.14	RM1341	17.3	0.55	1.15	YP6	14	3	7.1	0.01*	
	qDH12.1-YP4	12	26.99	RM17	9.3	0.18	0.47	YP4	27	16	2.8	0.09	
	qCL1.1-YP10	1	23.33	RM009	8.5	0.35	-3.04	IR 64	13	5	3.6	0.06	
CL	qCL2.1-YP9	2	11.39	RM324	15.3	0.6	4.91	YP9	9	3	3.0	0.08	
	qCL4.1-YP4	4	4.45	RM8213	8.3	0.17	-5.40	IR 64	41	2	35.4	0.00*	
	qCL4.1-YP6	4	20.03	RM1359	17.7	0.62	-11.99	IR 64	17	0	17.0	0.00*	
	qCL4.1-YP11	4	27.65	RM7187	37.6	0.53	4.28	YP11	12	24	4.0	0.05*	
	qCL4.1-YP8	4	30.36	RM5503	24.6	0.58	3.55	YP8	12	8	0.8	0.37	
	qCL4.1-YP9	4	31.81	RM3836	24.8	0.71	4.66	YP9	7	5	0.3	0.56	
	qCL5.1-YP10	5	1.23	RM1024	17.4	0.52	-3.72	IR 64	13	5	3.6	0.06	
	qCL5.1-YP4	5	2.21	RM413	7.7	0.16	2.24	YP4	18	25	1.1	0.29	
	qCL6.1-YP4	6	4.85	RM314	18.9	0.32	3.18	YP4	17	26	1.9	0.17	
	qCL6.1-YP10	6	22.3	RM3827	21.7	0.54	-4.72	IR 64	15	3	8.0	0.01*	
	qCL7.1-YP8	7	23.65	RM5847	18.9	0.58	-3.92	IR 64	10	10	0.0	1.00	
	qCL9.1-YP11	9	18.92	RM3164	17.3	0.34	3.16	YP11	16	20	0.4	0.51	
	qCL9.1-YP4	9	20.55	RM3808	9.1	0.18	2.45	YP4	23	20	0.2	0.65	
	PL	qPL4.1-YP4	4	25.36	RM252	18.6	0.31	0.63	YP4	22	21	0.02	0.88
qPL4.1-YP11		4	28.76	RM303	13.7	0.24	0.68	YP11	16	20	0.4	0.51	
qPL5.1-YP10		5	1.23	RM1024	22.4	0.58	-1.22	IR 64	13	5	3.6	0.06	
qPL6.1-YP10		6	12.45	RM3183	25	0.61	-1.25	IR 64	13	4	4.8	0.03*	
qPL6.1-YP6		6	26	RM6395	10.1	0.42	-0.44	IR 64	8	9	0.1	0.81	
qPL9.1-YP11		9	16.94	RM7048	28.9	0.46	0.85	YP11	17	19	0.1	0.74	
qPL11.1-YP6		11	3.86	RM6544	7.7	0.36	0.41	YP6	11	6	1.5	0.225	
qPL11.1-YP11		11	19.08	RM6680	7.7	0.18	-0.55	IR 64	22	14	1.8	0.182	
CW		qCW1.1-YP8	1	0.3	RM3252	8.8	0.33	1.71	YP8	7	13	1.8	0.18
		qCW4.1-YP11	4	29.59	RM6089	14.7	0.3	1.1	YP11	15	21	1	0.32
	qCW5.1-YP10	5	18.02	RM1237	16.7	0.51	-1.61	IR 64	11	7	0.89	0.35	
	qCW9.1-YP11	9	17.75	RM6543	12.4	0.25	1.01	YP11	17	19	0.11	0.74	
PW	qPW6.1-YP10	6	19.91	RM7193	12.3	0.44	-2.45	IR 64	14	4	5.56	0.02*	
	qPW6.1-YP6	6	26	RM6395	15.1	0.52	-3.70	IR 64	8	9	0.06	0.81	
PW/TW	qPWTW2.1-YP5	2	0.81	RM2770	11.7	0.32	-3.23	IR 64	10	16	1.38	0.24	
	qPWTW3.1-YP9	3	2.45	RM231	9.4	0.48	-4.36	IR 64	11	1	8.33	0.004*	
	qPWTW6.1-YP4	6	4.85	RM314	13.9	0.25	-1.18	IR 64	17	26	1.88	0.17	
	qPWTW6.1-YP6	6	26	RM6395	8.2	0.38	-1.42	IR 64	8	9	0.1	0.81	
	qPWTW7.1-YP5	7	29.34	RM248	10.5	0.3	-3.08	IR 64	16	10	1.4	0.24	
	qPWTW9.1-YP11	9	19.23	RM5535	13.1	0.28	-2.15	IR 64	15	21	1.0	0.32	
PN	qPN2.1-YP10	2	5.48	RM6378	12.3	0.44	-0.85	IR 64	14	4	5.6	0.02*	
	qPN4.1-YP4	4	25.36	RM252	10.5	0.2	-1.04	IR 64	22	21	0.02	0.88	
	qPN4.1-YP5	4	30.36	RM5503	13.4	0.35	1.35	YP5	20	6	7.5	0.01*	
	qPN4.1-YP11	4	32.06	RM6909	14.6	0.3	-0.94	IR 64	17	19	0.1	0.74	
	qPN4.2-YP5	4	31.81	RM3836	14.4	0.37	-1.19	IR 64	20	6	7.5	0.01*	
	qPN6.1-YP6	6	26	RM6395	9.2	0.4	-1.46	IR 64	8	9	0.1	0.81	
	qPN11.1-YP11	11	9.23	RM3185	9.9	0.22	0.97	YP11	28	8	11.1	0.001*	
qPN12.1-YP5	12	23.51	RM7376	13.6	0.35	1.17	YP5	7	19	5.5	0.02*		

A total of 194 INLs with DH from 83 to 86 days were used to detect QTLs for SSS and agronomic traits.

Using genotype data of SSR markers (Fujita et al., 2010, 2009) and the values of these traits in these INLs, associations between them were detected by single marker analysis (SMA) (Threshold: $P < 0.01$).

SSS, Spikelet sterility score; CL, Culm length; PL, Panicle length; CW, Culm weight; PW, Panicle weight per plant; PW/TW (total weight), Harvest index; PN, Panicle number per plant. SMA in each sib-group was performed using Windows QTL cartographer v.2.5 (Wang et al., 2011).

Nearest Marker name indicates the QTL-linked marker with the highest F score.

A positive value for the additive effect indicates an increase in the trait's value with the introgressed allele, while a negative value indicates an increase in the trait's value with the allele of IR 64.

χ^2 and P values at each loci was calculated to confirm the segregating distortion in the INLs.

*, significant distortion from the 1:1 ratio at $P = 0.05$.

In this study, wide variations in SSS and DH were found among 317 INLs with a genetic background of

an Indica Group rice cultivar, IR 64. Among them, 194 INLs with DH ranging from 83 days to 86 days were

exposed immediately after heading to continuous strong dry winds induced by a typhoon, and their SSS varied widely. INLs with the architecture of high plant height or large panicles had a high SSS, with the introgressed alleles of the QTL on chr. 4, with the minor effect of high tiller number. This information on the relationships between SSS and agronomic traits and the QTLs will be useful for genetic improvement of tolerance to typhoon-induced spikelet sterility in Indica Group rice varieties.

Acknowledgments

This study was performed under the Japan International Research Center for Agricultural Sciences (JIRCAS) Research Projects “Development of breeding materials and basic breeding technologies for highly productive crops adaptable to adverse environments” (2016 onward). We sincerely thank Dr. T Sato (Tohoku University), Dr. K Suenaga (JIRCAS), and Dr. D Fujita (Saga University) for their comments and encouragement, and Dr. DJ Kang (Hiroshima University) for his help in the literature collection.

Disclosure statement

No potential conflict of interest was reported by the authors.

References

- Fujita, D., Santos, R. E., Ebron, L. A., Fukuta, Y., & Kobayashi, N. (2011). Characterization of quantitative trait locus for days to heading in near-isogenic lines with genetic background of Indica-type rice variety IR64 (*Oryza sativa*). *Plant Breeding*, 130(5), 526–532. <https://doi.org/10.1111/j.1439-0523.2011.01864.x>
- Fujita, D., Santos, R. E., Ebron, L. A., Telebanco-Yanoria, M. J., Kato, H., Kobayashi, S., ... Kobayashi, N. (2010). Development and characterization of introgression lines of an Indica-type rice variety, IR64, for unique agronomic traits. *JIRCAS Working Report*, 66, 1–95. https://www.jircas.go.jp/ja/publication/jircas_working_report/66
- Fujita, D., Santos, R. E., Ebron, L. A., Telebanco-Yanoria, M. J., Kato, H., Kobayashi, S., Kobayashi, S., Uga, Y., Araki, E., Takai, T., Tsunematsu, H., Imbe, T., Khush, G. S., Brar, D. S., Fukuta, Y., & Kobayashi, N. (2009). Development of introgression lines of an Indica-type rice variety, IR64, for unique agronomic traits and detection of the responsible chromosomal regions. *Field Crops Research*, 114(2), 244–254. <https://doi.org/10.1016/j.fcr.2009.08.004>
- Fujita, D., Tagle, A. G., Ebron, L. A., Fukuta, Y., & Kobayashi, N. (2012). Characterization of near-isogenic lines carrying QTL for high spikelet number with the genetic background of an Indica rice variety IR64 (*Oryza sativa* L.). *Breeding Science*, 62(1), 18–26. <https://doi.org/10.1270/jsbbs.62.18>
- Fujita, D., Trijatmiko, K. R., Tagle, A. G., Sapasap, M. V., Koide, Y., Sasaki, K., Tsakirpaloglou, N., Gannaban, R. B., Nishimura, T., Yanagihara, S., Fukuta, Y., Koshihara, T., Slamet-Loedin, I. H., Ishimaru, T., & Kobayashi, N. (2013). *NAL1* allele from a rice landrace greatly increases yield in modern *Indica* cultivars. *PNAS*, 110(51), 20431–20436. <https://doi.org/10.1073/pnas.1310790110>
- Hirasawa, T. (2000). Panicle dehydration causing a white head of paddy rice under the conditions of high temperature, low humidity and high wind velocity. *The Hokuriku Crop Science*, 35, 81–82. https://doi.org/10.19016/hokurikucs.35.0_81
- Ishihara, K., Kiyota, E., & Imaizumi, N. (1990). Transpiration and photosynthesis characteristics of the panicle in comparison with the flag leaf in the rice plant. *Japanese Journal of Crop Science*, 59(2), 321–326. <https://doi.org/10.1626/jcs.59.321>
- Ishimaru, T., Qin, J., Sasaki, K., Fujita, D., Gannaban, R. B., Lumanglas, P. D., ... Kobayashi, N. (2017). Physiological and morphological characterization of a high-yielding rice introgression line, YTH183, with genetic background of Indica group cultivar, IR 64. *Field Crops Research*, 213, 89–99. <https://doi.org/10.1016/j.fcr.2017.07.006>
- Kang, D. J., Yeo, U. S., Oh, B. G., Kang, J. H., Yang, S. J., Ishii, R., & Lee, I. J. (2003). Physiological studies on the foehn tolerance of rice (*Oryza sativa* L.). *Japanese Journal of Crop Science*, 72(3), 328–332. <https://doi.org/10.1626/jcs.72.328>
- Kobayashi, S., Fukuta, Y., Morita, S., Sato, T., Osaki, M., & Khush, G. S. (2003b). Quantitative trait loci affecting flag leaf development in rice (*Oryza sativa* L.). *Breeding Science*, 53(3), 255–262. <https://doi.org/10.1270/jsbbs.53.255>
- Kobayashi, S., Fukuta, Y., Sato, T., Osaki, M., & Khush, G. S. (2003a). Molecular marker dissection of rice (*Oryza sativa* L.) plant architecture under temperate and tropical climates. *Theoretical and Applied Genetics*, 107(8), 1350–1356. <https://doi.org/10.1007/s00122-003-1388-8>
- Koide, Y., Fujita, D., Tagle, A. G., Sasaki, K., Ishimaru, T., Fukuta, Y., & Kobayashi, N. (2013). QTL for spikelet number from a high-yielding rice variety, Hoshiaoba, detected in an introgression line with the genetic background of an indica rice variety, IR64. *Euphytica*, 192(1), 97–106. <https://doi.org/10.1007/s10681-013-0882-6>
- Lee, J. S., Lee, K. Y., Shin, D. K., Kim, S. C., & Suh, H. S. (1998). Varietal difference of tolerance for dry wind damage in rice plant. *RDA Journal of Crop Science*, 40(2), 19–24.
- Lim, S. J., Kim, C. Y., Moon, E. H., & Kim, J. H. (1988). Testing method of foehn tolerance and selection of tolerant varieties in rice. *Research Report of RDA*, 30(2), 7–13.
- Liu, G. L., Mei, H. W., Yu, X. Q., Zou, G. H., Liu, H. Y., Hu, S. P., Li, M. S., Wu, J. H., Chen, L., & Luo, L. J. (2008). QTL analysis of panicle neck diameter, a trait highly correlated with panicle size, under well-watered and drought conditions in rice (*Oryza sativa* L.). *Plant Science*, 174(1), 71–77. <https://doi.org/10.1016/j.plantsci.2007.09.011>
- Matsuo, T., Tsuboi, Y., & Tsunoda, S. (1951). Occurrence of withered and completely sterile ears in rice plants by attack of typhoon, with special reference to varietal resistance (1). *Journal of Agricultural Meteorology*, 6(3–4), 107–110. <https://doi.org/10.2480/agrmet.6.107>
- McCouch, S. R., Teytelman, L., Xu, Y., Lobos, K. B., Clare, K., Walton, M., & Stein, L. (2002). Development and mapping of 2240 new SSR markers for rice (*Oryza sativa* L.). *DNA Research*, 9(6), 199–207. <https://doi.org/10.1093/dnares/9.6.199>
- Muramatsu, K. (1976). The occurrence and damage to paddy field rice by foehn in the Hokuriku district, Japan. *Bulletin of Hokuriku National Agriculture Experimental Station*, 19, 25–44. <https://agriknowledge.affrc.go.jp/RN/2010823987>

- Muramatsu, K., & Kamota, F. (1979). On the foehn damage of rice plant I. Spouting water drops from a panicle. *Journal of Agricultural Meteorology*, 35(3), 173–176. <https://doi.org/10.2480/agrmet.35.173>
- O'Toole, J. C., Hsiao, T. C., & Namuco, O. S. (1984). Panicle water relations during water stress. *Plant Science Letters*, 33(2), 137–143. [https://doi.org/10.1016/0304-4211\(84\)90003-8](https://doi.org/10.1016/0304-4211(84)90003-8)
- Obara, M., Ishimaru, T., Abiko, T., Fujita, D., Kobayashi, N., Yanagihara, S., & Fukuta, Y. (2014). Identification and characterization of quantitative trait loci for root elongation by using introgression lines with genetic background of Indica-type rice variety IR 64. *Plant Biotechnology Reports*, 8(3), 267–277. <https://doi.org/10.1007/s11816-014-0320-9>
- Oida, T., & Yuasa, K. (1999). Whitehead of rice plant caused by typhoon No. 9 in 1997. *The Hokuriku Crop Science*, 34, 73–75. https://doi.org/10.19016/hokurikucs.34.0_73
- Sasaki, K., Fujita, D., Koide, Y., Lumanglas, P. D., Gannaban, R. B., Tagle, A. G., Obara, M., Fukuta, Y., Kobayashi, N., & Ishimaru, T. (2017). Fine mapping of a quantitative trait locus for spikelet number per panicle in a new plant type rice and evaluation of a near-isogenic line for grain productivity. *Journal of Experimental Botany*, 68(11), 2693–2702. <https://doi.org/10.1093/jxb/erx128>
- Tagle, A. G., Fujita, D., Ebron, L. A., Telebanco-Yanoria, M. J., Sasaki, K., Ishimaru, T., Fukuta, Y., & Kobayashi, N. (2016). Characterization of QTL for unique agronomic traits of new-plant-type rice varieties using introgression lines of IR64. *The Crop Journal*, 4(1), 12–20. <https://doi.org/10.1016/j.cj.2015.10.001>
- Tanimoto, T., & Itoh, R. (2000). Effect of leaf rolling on transpiration and water use efficiency in rice. *Japanese Journal of Crop Science*, 69(3), 406–412. <https://doi.org/10.1626/jcs.69.406>
- Tanimoto, T., & Itoh, R. (2001). Effects of plant type on transpiration in rice plant. *The Hokuriku Crop Science*, 36, 45–47. https://doi.org/10.19016/hokurikucs.36.0_45
- Tomita, A., & Fukuta, Y. (2019). QTL analysis for soil-surface roots originating from a New Plant Type rice (*Oryza sativa* L.). *Plant Breeding*, 138(2), 154–162. <https://doi.org/10.1111/pbr.12680>
- Tsuda, M., Takami, S., & Yokoe, D. (1992). Developmental change in panicle water potential in rice. *Japanese Journal of Crop Science*, 61(2), 213–217. <https://doi.org/10.1626/jcs.61.213>
- Uddin, M. N., Obara, M., Yanagihara, S., Ishimaru, T., Kobayashi, N., & Fukuta, Y. (2016a). Genetic characterization of introgression lines with the genetic background of the Indica-type rice (*Oryza sativa* L.) cultivar IR 64 under irrigated lowland and upland conditions. *Field Crops Research*, 191, 168–175. <https://doi.org/10.1016/j.fcr.2016.03.007>
- Uddin, M. N., Tomita, A., Obara, M., Yanagihara, S., & Fukuta, Y. (2016b). Identification of a low tiller gene from a new plant type cultivar in rice (*Oryza sativa* L.). *Breeding Science*, 66(5), 790–796. <https://doi.org/10.1270/jsbbs.16143>
- Wang, S., Bastin, C. J., & Zeng, Z. B. 2011. *Windows QTL Cartographer 2.5*. Department of Statistics, North Carolina State University. <http://stagen.ncsu.edu/qtlcart/WQTLCart.htm>
- Ward, J. H. (1963). Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association*, 58(301), 236–244. <https://doi.org/10.1080/01621459.1963.10500845>