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Differences in lamina joint anatomy cause cultivar differences in leaf inclination angle of rice

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ABSTRACT

Leaf erectness is an important agronomic trait for improving canopy photosynthesis in rice. It is well known that leaf inclination angle (LIA) decreases after expansion during ripening. However, the high-yielding *indica* cultivar ‘Takanari’ retains a greater LIA during ripening than the high-quality *japonica* cultivar ‘Koshihikari’. To clarify the cause of the cultivar difference in LIA, we investigated anatomical characteristics of the lamina joint of a flag leaf. We found a close linear correlation between LIA at the centre and at the base of the leaf blade in both cultivars during ripening. The length of the lamina joint increased significantly more on the adaxial side of a leaf (the margin of the collar) than on the abaxial side (the abaxial side of the central part of the collar) in ‘Koshihikari’ after leaf expansion, but there was no clear difference in ‘Takanari’. We found a close linear correlation between the ratio of lamina joint length on the adaxial to abaxial sides and LIA in ‘Koshihikari’ and ‘Takanari’ during ripening. In ‘Koshihikari’, the average length of cells on the adaxial side increased significantly after leaf expansion, with no significant increase in that on the abaxial side and no significant change in cell number on either side. In ‘Takanari’, cell length and cell number showed no significant changes on either side of the lamina joint. We conclude that the cultivar difference in LIA during ripening is caused mainly by cell elongation on the adaxial side of the lamina joint.

List of Abbreviations: *k*: light extinction coefficient; LIA: leaf inclination angle; QTL: quantitative trait locus

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Cell length; cell number; lamina joint; leaf inclination angle; rice

1. Introduction

Improving rice production to meet the needs of the growing global population is a major challenge in rice breeding (Kubo & Purevdorj, 2004). Plant architecture is crucial to the efficiency of photosynthesis, and its manipulation is a feasible approach to increasing canopy photosynthesis and crop production per unit land area (Hall, 1993; Kumura, 1995; Li, Paterson, Pinson, & Stansel, 1999). The light extinction coefficient (*k*), an important parameter of canopy architecture, represents the characteristic of light interception by the canopy (Monsi & Saeki, 2005). Varietal differences in *k* are found in rice, and there is a close linear relationship between the leaf inclination angle (LIA) and *k* in both *japonica* and *indica* rice cultivars (Soda, Ookawa, Motobayashi, & Hirasawa, 2010).

Erect leaves (large LIA) minimize shading by the upper leaves, allowing more light penetration into the canopy for higher photosynthesis, denser planting with a higher leaf area index, and thus higher grain yield in

rice (Kumura, 1995; Morinaka et al., 2006; Sakamoto et al., 2006; San-Oh, Yoshita, Ookawa, & Hirasawa, 2006; Sinclair & Sheehy, 1999). High-yielding rice cultivars such as ‘IR8’ and ‘Milyang 23’ have a high canopy photosynthetic rate and produce high biomass and grain yield with their erect leaves and small *k* value (Hall, 1993; Saitoh, Shimoda, & Ishihara, 1990). Erect leaves are crucial to improving photosynthesis and sustaining greater rice production.

After full elongation of the leaf blade and leaf sheath, the leaf blade bends away from the vertical culm with the development of the lamina joint (also called leaf collar: the white portion between the leaf blade and the leaf sheath) to set LIA (Hoshikawa, 1989). LIA changes with growth stage, becoming lower during ripening (Kumura, 1995; San-Oh, Mano, Ookawa, & Hirasawa, 2004; Soda et al., 2010) under the control of the lamina joint (Maeda, 1961; Maeda & Saka, 1968). Cell division, cell elongation, and vascular bundle formation in the lamina joint determine the LIA in rice (Ning, Zhang, Wang, Zhou, & Xiong, 2011;

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

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Zhang et al., 2015; Zhao, Xiang, & Xue, 2013). Anatomical studies of LIA have used mutants or transgenic plants to examine the roles of plant hormones in cell division and elongation in the lamina joint (Ning et al., 2011; Zhao, Hu, Guo, Qian, & Xue, 2010; Zhao et al., 2013). Genetic studies of leaf inclination in rice have made remarkable progress, and several associated quantitative trait loci (QTLs) and the roles of phytohormones in the regulation of LIA have been reported (Li et al., 1999; Sakamoto et al., 2006). Nevertheless, information on the reasons for the change of LIA with growth and the differences in LIA among rice cultivars at different growth stages is limited.

'Takanari', the highest yielding *indica* cultivar in Japan, has a higher net assimilation rate after heading and produces more dry matter and grain yield than other Japanese cultivars owing to its erect leaves, small *k* value, and high individual photosynthetic rate (Takai et al., 2006; Taylaran, Adachi, Ookawa, Usuda, & Hirasawa, 2011). 'Koshihikari', an elite *japonica* cultivar, produces high-quality rice and is widely grown in Japan, but its LIA and leaf photosynthetic rate are not as large and its grain yield is not as high as those of 'Takanari' (Taylaran et al., 2011). These two cultivars offer the opportunity to study varietal differences in LIA. We conducted this study to investigate the differences in the LIA of the flag leaf between 'Koshihikari' and 'Takanari' following full expansion and to examine the causes of the difference from full heading to the end of ripening through anatomical examinations of the lamina joint.

2. Materials and methods

2.1. Cultivation

'Koshihikari' and 'Takanari' were grown in a paddy field on the farm of the Tokyo University of Agriculture and Technology (35°41'N, 139°29'E; 48 m a.s.l.) in 2012 and 2013. Germinated seeds were sown in nursery boxes and grown in a greenhouse for 3 weeks. Seedlings at the fourth-leaf stage were transplanted at 22.2 hills m⁻² (30 cm × 15 cm) with one plant per hill. The experiment was laid out in a randomized complete block design with three replications. As a basal dressing, manure was applied at ~15 t ha⁻¹, and chemical fertilizer was applied at a rate of 30 kg N, 60 kg P₂O₅, and 60 kg K₂O ha⁻¹. One-third of the total N was applied as nitrogen sulphate, one-third as slow-release urea (LP-50; Chisso Asahi Fertilizer, Tokyo, Japan), and one-third as very-slow-release urea (LPS-100; Chisso Asahi Fertilizer). No top dressing was applied. The plants were grown under flooded conditions until a week before harvest. The

experiment was laid out in a complete randomized block design with three (in 2013) or four (2012) replications.

2.2. Measurement of LIA and light intensity

LIA of the flag leaf on a main stem was measured with an Apple iPod Touch (Yamashita, Tanabata, Yamamoto, Ookawa, & Hirasawa, 2012). Four leaves were measured in each replication. The light intensity was measured with a light meter (LI-205A, LI-COR, Lincoln, NE, USA). We measured the diurnal changes in the LIA on a clear day.

2.3. Observations of the collar tissue anatomy

After measuring the LIA, we collected the collar, including 3 cm of leaf blade and 3 cm of leaf sheath, and fixed and stored it in formalin acetic alcohol (FAA) solution (formalin 5%, acetic acid 5%, ethanol 45%, water 45%) for anatomical examination.

Collar length on the adaxial side of a leaf (margin of the collar) and abaxial side of a leaf (abaxial side of mid-collar) was measured with digital calliper (Shinwa Rules, Sanjo, Japan) after washing the FAA-fixed samples in water. To measure cell length and cell number, we cut longitudinal sections 10 μm thick with a hand microtome (Nippon Optical Works Co., Ltd, Tokyo, Japan) and dyed them with 1% safranin. We measured cell length and cell number of the parenchyma cell at the second layer from the surface, on both adaxial and abaxial sides under a light microscope (Olympus, Tokyo, Japan) with Image J v. 1.49 software. All measurements were taken for three to four collars in each replication.

3. Results

3.1. Relationship between LIA at centre and base of leaf blade

The flag leaf blade expands straight upward in both 'Koshihikari' and 'Takanari'. The relationship between LIA at the centre and at the base of the leaf blade was linear (1:1) at both full heading and 3 weeks after full heading (Figure 1). These results indicate that the LIA of the flag leaf is determined at the base of the leaf blade.

3.2. Diurnal changes in LIA

Diurnal changes in LIA of 'Koshihikari' at 2 weeks and 'Takanari' at 1 week after full heading were measured

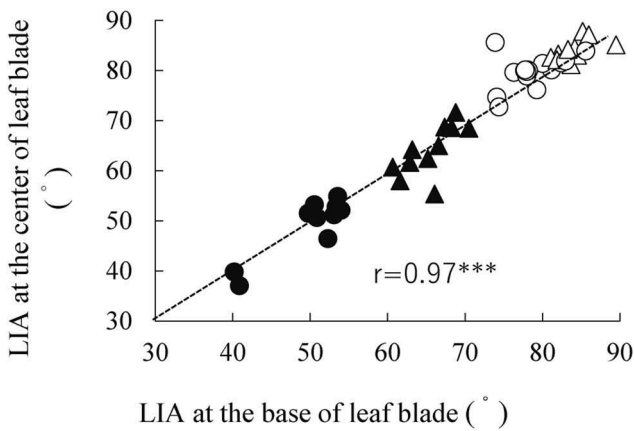


Figure 1. Relationship between LIA at the centre of the leaf blade and LIA at the base of the leaf blade at $\blacktriangle\Delta$ full heading and $\bullet\circ$ 3 weeks after full heading in $\blacktriangle\bullet$ 'Koshihikari' and $\Delta\circ$ 'Takanari'. The dashed line is 1:1.

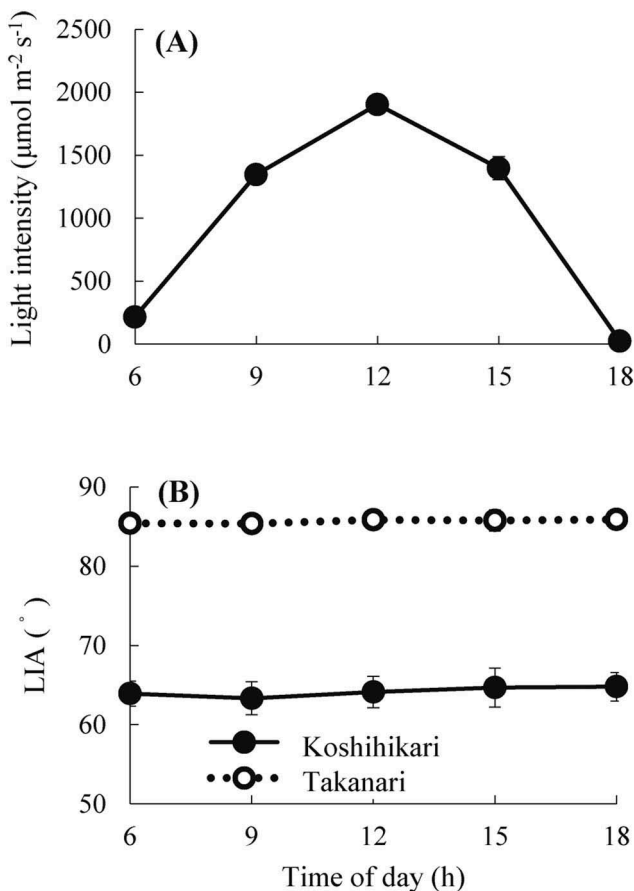


Figure 2. Diurnal changes in (A) light intensity and (B) LIA of 'Koshihikari' at 2 weeks and 'Takanari' at 1 week after full heading (measured on 28 August 2012). Vertical bars show SD ($n = 4$). Early morning dew was removed before measuring.

on 28 August 2012. The light intensity gradually increased from the early morning, reached the

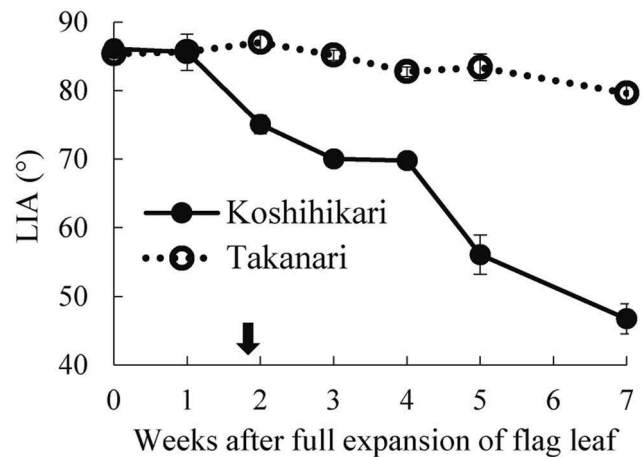


Figure 3. LIA of 'Koshihikari' and 'Takanari' with time after full expansion of the flag leaf in 2012. Vertical bars show SD ($n = 4$). Black arrow indicates full heading date.

maximum at 12:00, and declined steadily in the late afternoon (Figure 2(A)). The LIA remained constant throughout the day: 63.3° – 64.8° in 'Koshihikari' and 85.3° – 85.9° in 'Takanari' (Figure 2(B)).

3.3. Changes in LIA with time after full expansion of the flag leaf

In both 'Koshihikari' and 'Takanari', LIA of the flag leaf was 85° – 86° at full expansion and 1 week afterwards (Figure 3). After full heading, however, that of 'Koshihikari' began to decrease, reaching 46.7° at 7 weeks after full expansion, whereas that of 'Takanari' did not obviously decrease and was still almost 80° at 7 weeks after full expansion.

3.4. Changes in collar length of 'Koshihikari' and 'Takanari' with time after full expansion of flag leaf

The length of the leaf collar is greater on the adaxial side of a leaf (the margin of the collar) than the abaxial side (the abaxial part of the central part of the collar (mid-collar)) from the side view (Figure 4(A)). In the cross section of the collar, it curves to surround a stem and the thickness decreases remarkable from the mid-collar to the marginal part as shown in Figure 5. The obvious difference was observed in the collar size between 'Koshihikari' and 'Takanari'; the collar length was longer in 'Takanari' than in 'Koshihikari' (Figure 4(B,C)) and the thickness of the collar was larger in 'Takanari', especially at the mid-collar than in 'Koshihikari' (Figure 5(A,B)). No obvious difference was observed in tissue characteristics such as the distribution of sclerenchyma (Figure 5(A,B)). In 'Koshihikari', collar length on the adaxial side of leaf increased gradually from ~ 1.6 mm at full expansion of the flag leaf to ~ 1.9 mm at 7 weeks after, but that on the abaxial side of a leaf did not

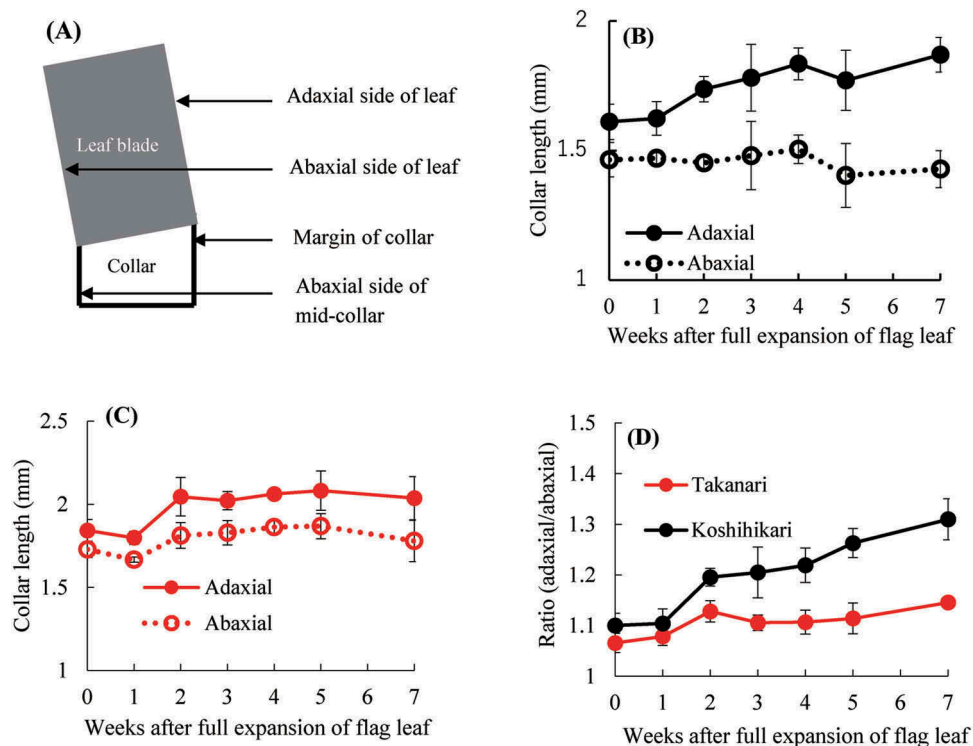


Figure 4. Schematic diagram of (A) leaf collar, changes in collar length of (B) 'Koshihikari' and (C) 'Takanari', and (D) ratio of collar lengths on adaxial to abaxial sides with time after full expansion of the flag leaf in 2012. Collar length at the margin of the collar and at the abaxial side of the mid-collar was measured for the collar length on adaxial and abaxial sides, respectively. Vertical bars show SD ($n = 4$).

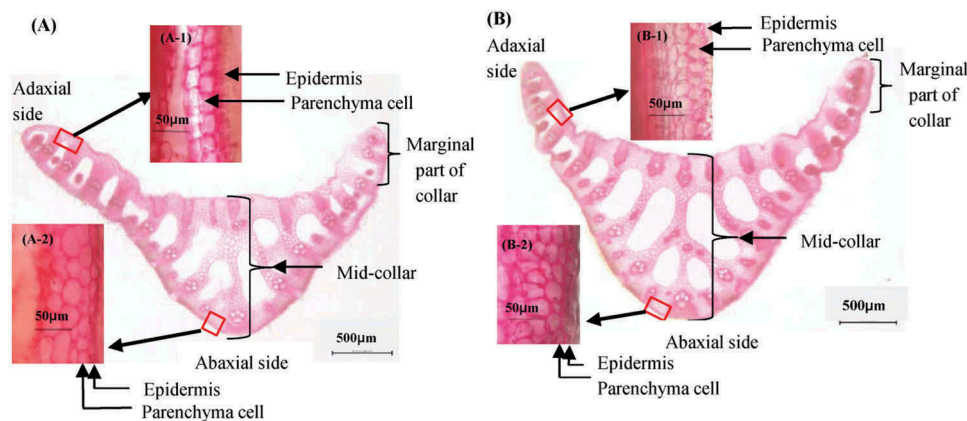


Figure 5. Cross sections of the leaf collar (A) 'Koshihikari' and (B) 'Takanari'. Inserted photos show longitudinal sections on (A-1, B-1) the adaxial side at the margin of the collar and (A-2, B-2) the abaxial side at the mid-collar.

change (Figure 4(B)). In 'Takanari', it increased obviously from 1 to 2 weeks after full expansion on both sides but did not change significantly after then (Figure 4(C)). The ratio of collar lengths on the adaxial to abaxial sides of a leaf increased from 1.10 at full expansion to 1.31 at 7 weeks after in 'Koshihikari' (Figure 4(D)), but from 1.07 to only 1.15 in 'Takanari'.

3.5. Relationship between LIA and ratio of collar lengths on adaxial to abaxial sides

There was a close negative linear correlation between LIA in the range of 56° – 88° and the ratio of collar length on the adaxial to the abaxial sides of a leaf in the range of 1.10–1.31 in 'Koshihikari' (Figure 6). With much smaller

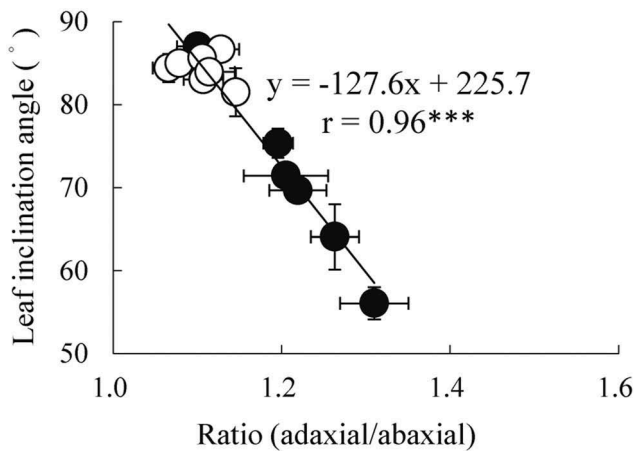


Figure 6. Relationship between LIA and ratio of collar lengths on adaxial to abaxial sides of ● 'Koshihikari' and ○ 'Takanari'. Bars represent SD ($n = 4$). ***Significant at 0.1% level.

ranges, values of 'Takanari' were plotted close to the 'Koshihikari' line. We can conclude that the changes in LIA of 'Koshihikari' were determined by the ratio of the

length of marginal part of the collar to the length of abaxial (outer) part of the mid-collar.

3.6. Cell length and cell number of collar tissues on adaxial and abaxial sides

To clarify the cause of the difference in the elongation of the collar between the marginal part and the abaxial (outer) part of the mid-collar, we prepared the longitudinal sections at the marginal part of the collar and at the mid-collar, and measurements of the number and size of the parenchyma cells (Zhou, Xiao, & Xue, 2017) at the second layer from the surface were taken at the adaxial (inner) side of the collar margin for the adaxial side of a leaf and at the abaxial (outer) side of the mid-collar for the abaxial side of a leaf as shown in Figure 5.

In both 'Koshihikari' and 'Takanari', the number of cells on the adaxial sides of a leaf was greater than that on the abaxial sides and no significant changes were observed in the cell number on both adaxial and abaxial sides

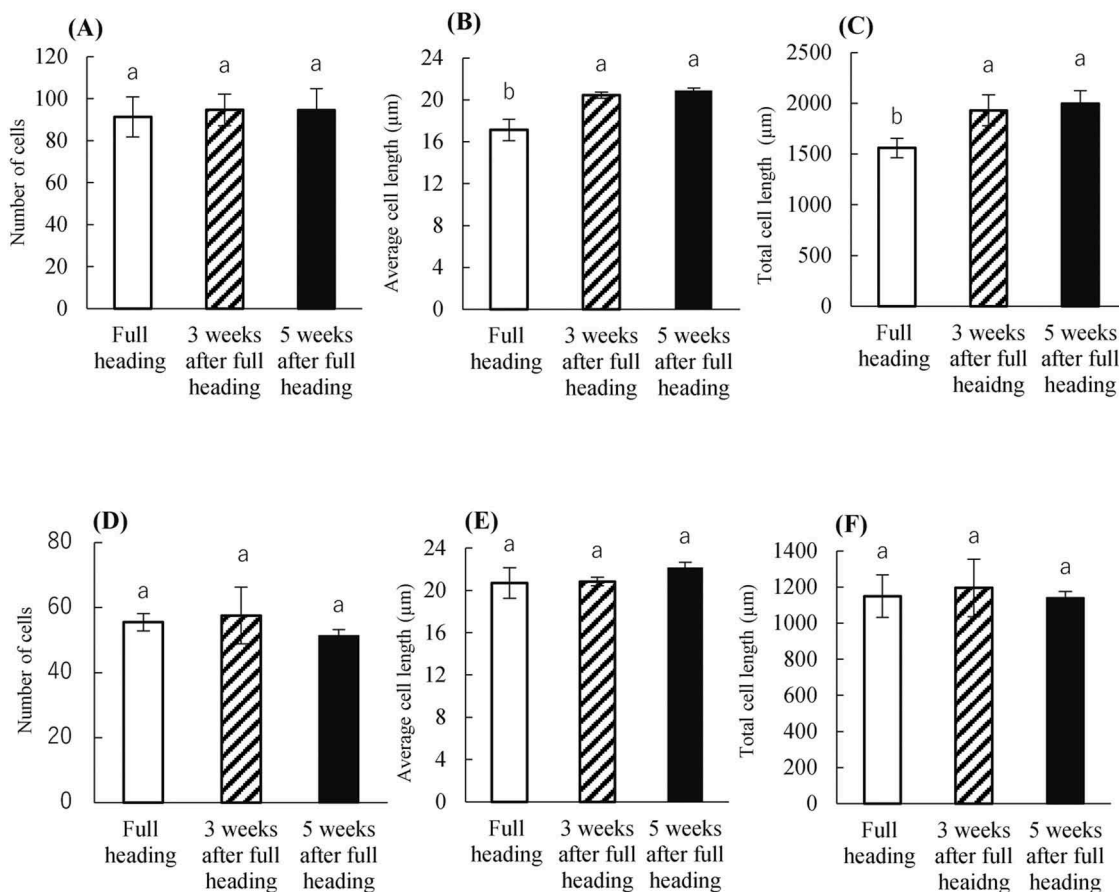


Figure 7. (A, D) Number of cells, (B, E) average cell length, and (C, F) total cell length on the (A–C) adaxial and (D–F) abaxial sides of the collar at full heading, 3 and 5 weeks after full heading of 'Koshihikari' in 2013. Parenchyma cells at the second layer from the surface at the marginal part of the collar and at the mid-collar were used for measurements on the adaxial and on abaxial sides, respectively. Vertical bars show SD ($n = 3$). Bars with the same letter are not significantly different at the 5% level by Tukey's test.

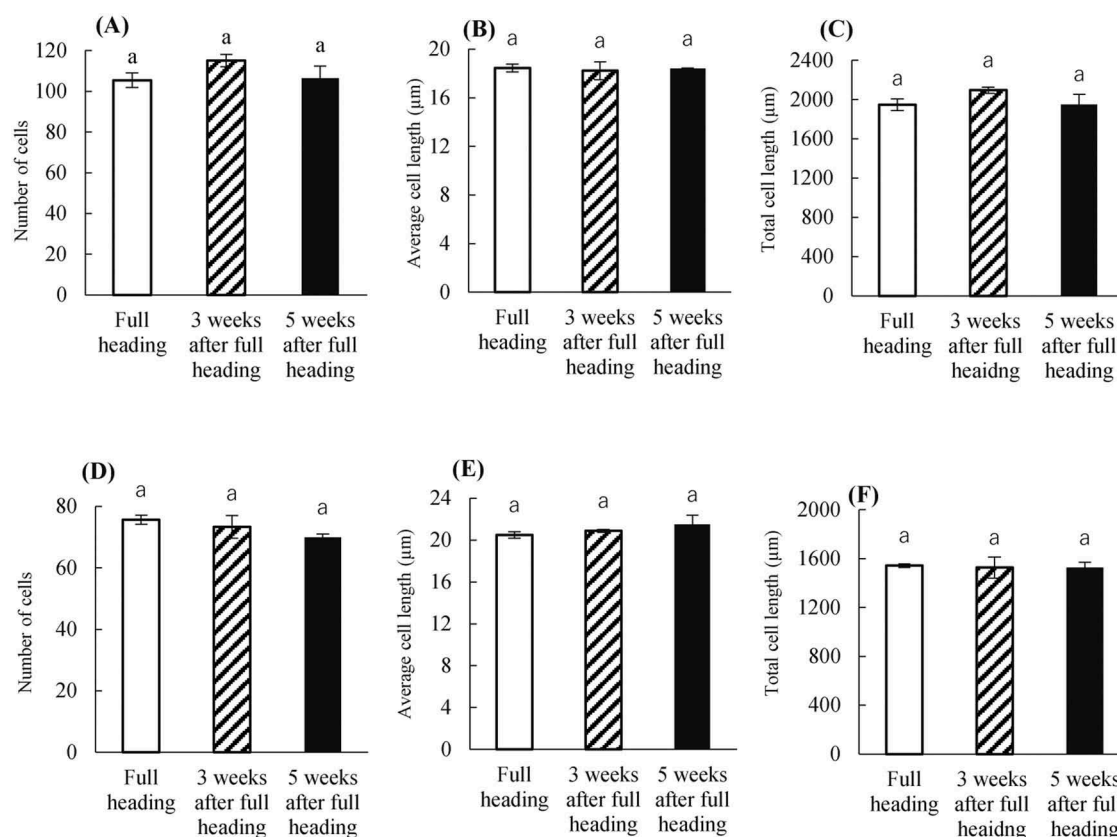


Figure 8. (A, D) Number of cells, (B, E) average cell length, and (C, F) total cell length on (A–C) adaxial and (D–F) abaxial sides of the collar at full heading, 3 and 5 weeks after full heading of ‘Takanari’ in 2013. Parenchyma cells at the second layer from the surface were taken on the adaxial side at the marginal part of the collar and on the abaxial side at the mid-collar. Vertical bars show SD ($n = 3$). Bars with the same letters are not significantly different at the 5% level by Tukey’s test.

throughout the ripening stage (Figures 7(A,D) and 8(A,D)). By contrast, the average cell length on the adaxial side, but not the abaxial side, increased significantly at 3 and 5 weeks after full heading in ‘Koshihikari’ (Figure 7(B,E)). As a result, the length of the lamina joint tissue on the adaxial side, but not the abaxial side, increased significantly from full heading to 5 weeks after full heading (Figure 7(C,F)). Even at the margin of the collar, the cell length at the abaxial (outer) side did not change with ripening (Figure S1). It was already large at the full expansion of a leaf. In ‘Takanari’, on the other hand, there were no changes in any cell length (Figure 8) on either side of the lamina joint.

4. Discussion

Increasing LIA is a promising way to maximize light interception by the canopy for photosynthesis and thus to improve rice production. The low k value during ripening due to erect leaves results in higher dry matter production and grain yield of ‘Takanari’ than that of ‘Koshihikari’ and other *japonica* cultivars (Taylaran et al., 2009; Xu, Ookawa, & Ishihara, 1997). Flag leaf is the uppermost and youngest

among leaves in the canopy and its inclination angle and photosynthesis affect the light penetration into the canopy and canopy photosynthesis, respectively. In cereals, flag leaves contribute to grain yield more than 50% in rice and wheat, and about 39% in barley (E1 Wazziki et al., 2015). A larger LIA of the flag leaf during ripening is crucial for higher crop growth rates and grain yields in rice (Kumura, 1995; Taylaran et al., 2009). The LIA of the flag leaf was determined by the angle at the base of the leaf (Figure 1), which was determined by the shape of the lamina joint (the ratio of the lengths of the adaxial to abaxial sides; Figure 6).

In legumes, the leaflet inclination angle changes throughout the day in response to turgor pressure in the pulvinus (Lambers, Chapin III, & Pons, 2008). Leaf water potential in rice decreases at midday and in the afternoon under intense transpiration even though the plants are growing in water (Hirasawa & Ishihara, 1978; Koizumi, Ookawa, Satoh, & Hirasawa, 2007). It was suggested that a reduction in the water potential of the lamina joint might decrease LIA (Cao & Chen, 1995). Yet even under conditions of intense transpiration under strong sunlight, the LIA stayed constant throughout the day (Figure 2),

indicating that the LIA might not be affected by the reduction of leaf water potential in a flooded paddy field. We conclude that LIA can be measured at any time of day in rice grown under flooded conditions, unlike in leguminous crops (Lambers et al., 2008; Saitoh, Inamura, & Ishihara, 1994) and *Arabidopsis* (Mullen, Weinig, & Hangarter, 2006). This trait would be favourable for quantitative trait locus (QTL) analysis, which requires measurements of many plants.

It is well known that LIA decreases after full heading until the end of ripening to an extent that depends on cultivar (Kumura, 1995; San et al., 2018; San-Oh et al., 2004; Soda et al., 2010). Likewise, we observed different decrease rates of LIA between 'Koshihikari' and 'Takanari' after full expansion of the flag leaf (Figure 3). The difference in the ratio of the lengths of the adaxial to abaxial sides of the lamina joint explains the difference in LIA between the cultivars (Figures 4(D) and 6).

It was reported that plant hormones affected LIA by causing cell elongation on the adaxial side of the lamina joint (Maeda, 1961; Maeda & Saka, 1968; Wada, Marumo, Ikekawa, Morisaki, & Mori, 1981). Recent studies of LIA showed that inhibition of the division of adaxial cells, suppression of the longitudinal elongation of adaxial parenchyma cells, and increased division of abaxial sclerenchyma cells of the lamina joint all lead to erect leaves (Cao & Chen, 1995; Sun et al., 2015; Zhang et al., 2009), while greater expansion of adaxial cells relative to dorsal cells in the lamina joint, asymmetric growth between adaxial and abaxial sides, and increased expansion or proliferation of adaxial parenchyma cells lead to inclined leaves (Zhang et al., 2015; Zhao et al., 2010; Zhou et al., 2017). In our results, the ratio of the collar lengths on the adaxial to abaxial sides of a leaf, which determines LIA, was determined mainly by cell elongation on the adaxial side (Figure 7), not by the cell elongation on the abaxial side (Figure S1), of the collar margin, and also not by the difference in the cell division (Figure 7). We can conclude that the difference in LIA between the cultivars could be explained by the difference in cell elongation between the adaxial and abaxial sides of the lamina joint (Figures 7 and 8 and Figure S1). This is the first report which clarified the cause of the varietal difference in LIA using commercial rice varieties, to our knowledge. The thickness of the collar was remarkably different between cultivars (Figure 5). Effects of such anatomical characteristics of the collar as well as the cell elongation at other parts of the collar on LIA remain to be investigated. It is also needed to investigate the causes of other varietal difference in LIA.

Application of brassinolide to the lamina joint of a fully expanded leaf inclines the leaf blade markedly (Wada et al., 1981) by promoting cell division and elongation

(Cao & Chen, 1995; Tong et al., 2014; Yamamuro et al., 2000). Brassinosteroid (BR) signalling regulates leaf erectness by controlling a specific U-type cyclin and inhibiting the proliferation of sclerenchyma cells on the abaxial side of the lamina joint (Sun et al., 2015); suppressing *OsBZR1*, the downstream BR signalling component BRZ1, leads to erect leaves (Bai et al., 2007). In addition, BR biosynthesis is involved in the regulation of LIA: loss-of-function mutants of BR biosynthesis genes have erect leaves, and BR deficiency leads to erect leaf orientation (Feng et al., 2016; Hong et al., 2005, 2002, 2003; Sakamoto et al., 2006). In addition to BR, signalling by or the synthesis of phytohormones such as auxin and gibberellins, as well as non-hormone-related genes, regulates LIA (Cao & Chen, 1995; Tong et al., 2014; Zhao et al., 2013). LIA is increased by a negative regulator of gibberellin signalling (Shimada et al., 2006) and is also affected by auxin-related processes (Attia et al., 2009; Li, Kang, Chen, & Qu, 2007; Song, You, & Xiong, 2009; Yoshikawa et al., 2014; Zhang et al., 2015). Identifying QTLs and genes associated with LIA is our next target to clarify the mechanisms underlying differences in LIA between 'Koshihikari' and 'Takanari'.

Disclosure statement

No potential conflict of interest was reported by the authors.

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