



A near-isogenic rice line carrying a QTL for larger leaf inclination angle yields heavier biomass and grain

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ABSTRACT

Manipulating plant architecture is a promising strategy for further improving rice production. The canopy extinction coefficient (k), the most important parameter of canopy architecture, represents the characteristics of light penetration into the canopy, and is determined mainly by the leaf inclination angle. With its erect leaves, the high-yielding *indica* cultivar ‘Takanari’ has a smaller k during ripening than the elite *japonica* cultivar ‘Koshihikari’. Using chromosome segment substitution lines derived from a cross between ‘Takanari’ and ‘Koshihikari’, we previously detected a quantitative trait locus (QTL) for leaf inclination angle on a chromosome 3. Here, we tested a near-isogenic line (NIL-3) carrying the ‘Takanari’ allele of a QTL for larger leaf inclination angle on chromosome 3, *qLIA3*, in the ‘Koshihikari’ genetic background for the effects of *qLIA3* on k , dry matter production, and grain yield. NIL-3 had leaves with a larger inclination angle from the full heading through ripening stages and a smaller k at the ripening stage than ‘Koshihikari’. There were no differences in plant height, panicle size, heading date, leaf area index, or individual leaf photosynthesis between NIL-3 and ‘Koshihikari’. Biomass at harvest was significantly greater in NIL-3 than in ‘Koshihikari’ owing to a higher net assimilation rate during ripening, resulting in a higher grain yield. *qLIA3* might incorporate a promising gene for improving rice production.

1. Introduction

Rice production has been improved tremendously over the past 50 years. This improvement is attributable to improved genetics and management (Evans, 1993; Kumura, 1995; Peng et al., 2009; Zhu et al., 2010). But during that period, overuse of nitrogen and other chemicals has imposed environmental problems and economic costs (Long et al., 2006; Peng et al., 2009; Zhang et al., 2015b). Recently, new genetic approaches have been used to develop new cultivars with high production potential (Yamamoto et al., 2009; Yamamoto et al., 2012). For further substantial improvements in rice yield, it is vital to increase canopy photosynthesis and dry matter production (Evans, 1993; Peng et al., 2000), which are determined mainly by plant architecture and individual leaf photosynthesis (Van Quyen et al., 2004; Long et al., 2006; Zhu et al., 2010). Much information and many genetic resources are available for canopy architecture of rice (Kumura, 1995; Yang and Hwa, 2008; Wu et al., 2013) compared with individual leaf photosynthesis (Ishii, 1995; Kanemura et al., 2007). Improving canopy

architecture might be more promising for further enhancing crop productivity in a near future, while it is estimated that improving individual leaf photosynthesis has higher potential for improving yield but that approach would take a long time for the achievement (Van Quyen et al., 2004; Zhu et al., 2010; Sage et al., 2017).

Plant architecture, in terms of light penetration into the canopy, can be characterized quantitatively by the canopy extinction coefficient, k (Monsi and Saeki, 2005). A lower k promotes canopy photosynthesis. Values of k have been improved modestly during the past 50 years through breeding (Takeda et al., 1984; Kumura, 1995; Taylaran et al., 2009; Soda et al., 2010). They can also be improved through cultivation management (Matsushima, 1995; San-oh et al., 2008). Although k is determined by many leaf morphological and physical characters, the most important is the degree of leaf inclination or erectness (De Costa and Dennett, 1992; Monsi and Saeki, 2005; Hay and Porter, 2006). Leaf inclination angle (LIA) showed a close correlation with k among several cultivars with different values of LIA (Soda et al., 2010). To date, several mutant or transgenic lines with altered LIA have been identified,

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and ways to alter LIA are under investigation (Wu et al., 2013). However, studies about the effects of LIA on dry matter production and grain yield in field conditions are limited (Sakamoto et al., 2006; Morinaka et al., 2006).

‘Takanari’, a high-yielding *indica* cultivar, is one of the most productive cultivars in Japan. One reason is its greater individual leaf photosynthetic rate after full heading through ripening (Taylaran et al., 2011). Another is its erect leaf posture, which gives it a smaller *k* at the early ripening stage than other Japanese cultivars (Xu et al., 1997; Taylaran et al., 2009). ‘Koshihikari’, an elite *japonica* cultivar, produces high-quality rice and is widely grown in Japan. But its LIA and leaf photosynthetic rate are not large and its grain yield is not as high as in ‘Takanari’ (Xu et al., 1997; Taylaran et al., 2009). In a previous study using chromosome segment substitution lines (CSSLs) derived from a cross between ‘Koshihikari’ and ‘Takanari’, we detected seven quantitative trait loci (QTLs) at which ‘Takanari’ alleles increase LIA in the ‘Koshihikari’ genetic background (Ootsuki et al., 2013). Here, we selected the QTL on chromosome 3 because of its relatively larger effect on LIA and developed a near-isogenic line (NIL-3) carrying a ‘Takanari’ allele of a QTL on chromosome 3 (*qLIA3*) which increases LIA in the ‘Koshihikari’ genetic background, and the effects of *qLIA3* on *k*, dry matter production, and grain yield in paddy field conditions were investigated.

2. Materials and methods

2.1. Materials

Among the BC₄F₃ plants, which were derived from a cross between ‘Koshihikari’ and ‘Takanari’ in the development of the CSSLs carrying a ‘Takanari’ chromosome segment in the ‘Koshihikari’ genetic background (Takai et al., 2014), the plants carrying the target segment of ‘Takanari’ on chromosome 3 were selected and self-pollinated. And the NIL-3 which carries 2.99Mb of a ‘Takanari’ chromosome segment was developed (Fig. 1).

Table 1

Dates of sowing, transplanting, average full heading, and harvest and replications in each year.

Year	Sowing date	Transplanting date	Full heading date	Harvest date	No. of replications
2013	May08	Jun01	Aug14	Sep29	3
2014	May08	May29	Aug13	Oct03	3
2015	May07	May28	Aug13	Sep21	4
2016	May06	May25	Aug04	Sep21	4

2.2. Cultivation of rice plants

Plants 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 alluvial clay loam for four years (2013–2016). The dates of sowing, transplanting, full heading, and harvest and replications are shown in Table 1. Every year, germinated seeds were sown in nursery boxes in early May and grown in a greenhouse for 3 weeks. Seedlings at the 4th-leaf stage were transplanted at 22.2 hills m⁻² (30 cm × 15 cm) with 3 plants per hill. All plants grown in the previous year were chopped up and incorporated into the soil and chemical fertilizer was applied at the rate of 2.0–3.0, 2.6 and 5.0 g m⁻² for N, P and K, respectively, before puddling as a basal dressing (Table S1). For N, one-third was applied as nitrogen sulfate, one-third as slow-release urea (LP-50; Chisso Asahi Fertilizer, Tokyo), and one-third as very-slow-release urea (LP-100; Chisso Asahi Fertilizer). At 10 days before heading in 2014 and 2015, 1.5 g m⁻² of N and 1.25 g m⁻² of K were top dressed. The experiment was laid out in a complete randomized block design. Plot size was 8–12 m². Plants were grown under flooded conditions until a week before harvest.

2.3. Measurement of leaf inclination angle (LIA)

LIA was measured by software with an Apple iPod Touch (Yamashita et al., 2012). We measured the angle from the horizontal of the base of a leaf blade on the main stem (Fig. S1), which is linearly

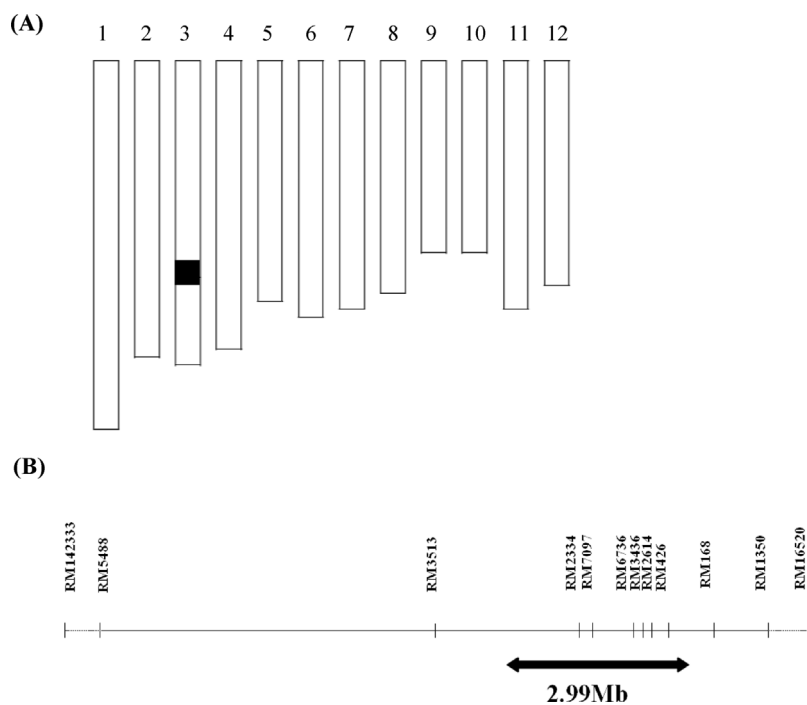


Fig. 1. (A) Graphical genotype of NIL-3. Black bar: region homozygous for ‘Takanari’ allele in ‘Koshihikari’ genetic background. (B) Genetic linkage map of chromosome 3 in NIL-3. Black arrow represents a region homozygous for ‘Takanari’ allele in ‘Koshihikari’ genetic background.

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