Introduction

Identifying and manipulating the genes controlling plant height is essential in soybean breeding to increase yield through the enlargement of the plant size while preventing lodging. The development of cultivars of short height is also beneficial for achieving high yields through fertilization management, because nitrogen fertilization stimulates excessive vegetative growth (Salvagiotti et al. 2008, Wallace et al. 1990). Quantitative trait loci (QTLs) for the lodging tolerance of soybean, which have been reported in numerous studies, are related to plant height (Lee et al. 1996, Mansur et al. 1993, Orf et al. 1999, Specht et al. 2001). Most of these studies reported QTLs for lodging in the proximal regions of E3 and Dt1. E3 controls time of flowering and maturity in soybean (Watanabe et al. 2009). Early maturing shortens plant heights and decreases lodging scores. In contrast, determinate growth habit, which is controlled by the Dt1 locus (Bernard 1972) shortens plant heights and may increase lodging tolerance. However, both characteristics decrease the number of nodes, which is one of the most important yield components of soybean (Egli 2013). Therefore, the identification of genes controlling only inter-node length will be beneficial to the development of soybean cultivars having shorter heights without having negative effects on yield potential and days to flowering.

Key Words: soybean, inter-node length, quantitative trait locus, near-isogenic line.

Manipulating the genetic control of plant height is essential in soybean breeding to increase yield through the enlargement of the plant size while preventing lodging. A Japanese soybean germplasm, Y2, has distinctively shorter inter-node lengths than those of recently developed Japanese cultivars and is expected to provide new variation to prevent lodging. A quantitative trait loci (QTL) analysis for plant height-related traits was conducted using F2 individuals derived from a cross between the elite Japanese cultivar Fukuyutaka and Y2. A major QTL for average inter-node length (AIL) and plant height was identified on chromosome 13 and named qSI13-1 (QTL for short inter-node on chromosome 13). The Y2 allele of qSI13-1 was partially dominant for plant height. qSI13-1 exhibited no effect on either days to flowering or number of main stem nodes. The AILs and plant heights of the near-isogenic lines containing the Y2 allele of qSI13-1 in the genetic background of Fukuyutaka were significantly less than those of Fukuyutaka. No significant differences between the near-isogenic lines and Fukuyutaka were observed for seed yield and flowering date, indicating that qSI13-1 will be useful in developing cultivars with short plant heights without having negative effects on yield potential and days to flowering.

Quantitative trait loci associated with short inter-node length in soybean

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Yamaguchi et al. (2014) analyzed a recombinant inbred line (RIL) population derived from a cross between the lodging-tolerant cultivar Toyoharuka and the ordinary lodging-cultivar Toyomusume to identify lodging-tolerance genes. These cultivars have similar maturity periods and the same growth habit, and a major QTL, qLS19-1, was reported on chromosome 19. qLS19-1 is expected to be useful for breeding because it rarely has negative effects on seed yield, quality or plant height. The identification of a soybean semi-dwarf gene will enhance the development of high lodging-tolerant cultivars by pyramiding with qLS19-1.

The Genebank project of the National Agriculture and Food Research Organization, coordinates the conservation of plants, microorganisms, animals and DNA materials in Japan (http://www.gene.affrc.go.jp/index_en.php). The seed-based propagation of preserved soybean germplasms is required to maintain seed viability, and we discovered a semi-dwarf Japanese soybean, Y2, during the seed propagation process.

In the present study, we investigated the inter-node length of Y2, which is clearly shorter than those of recently developed Japanese cultivars. The short inter-node length trait of Y2 should be useful in the development of cultivars having short plant heights. The objectives of this study were to identify the genetic factors that control inter-node length in Y2 and verify the gene’s effects on inter-node length and yield using near-isogenic lines (NILs).

Materials and Methods

Plant materials

A population of 94 F2 individuals was developed from a single F1 plant derived from a cross between the Japanese cultivar Fukuyutaka (NIAS Genebank: JP 29668) and the germplasm Y2, collected in Japan (NIAS Genebank: JP 29531). The detail location of Y2 collection site is unavailable. The Japanese cultivar Sachiyutaka was used for comparison of plant height and AIL. Flowering date of Sachiyutaka is approximately five days earlier than Fukuyutaka. Fukuyutaka and Sachiyutaka are leading cultivars in southwestern Japan. Sachiyutaka was included in analysis to investigate the relation between maturing date and inter-node length. The F2 individuals and their parents were grown in a field (Andosol soil) at the Kyushu Okinawa Agricultural Research Center (located at 32°52′N, 130°44′E) in 2011. The planting date was 17th July 2011. The inter-row and hill spacings were 70 cm and 14 cm, respectively.

Measurement of plant height, number of main stem nodes, inter-node length and flowering date

The plant heights, numbers of main stem nodes and inter-node lengths of Fukuyutaka, Y2 and the F2 individuals were measured after harvesting. Plant height was the distance from cotyledonary to terminal nodes. Average inter-node length (AIL) was calculated by dividing the plant height by number of main stem nodes. Seven F2 individuals were excluded from measurement because their main stems were damaged during growth. Flowering date is equal to the R1 stage defined by Fehr et al. (1971).

Molecular marker analysis and linkage mapping

We constructed a linkage map based on the segregation data using simple sequence repeat (SSR) markers and 94 F2 individuals. Total genomic DNA was extracted from young fresh leaves (0.3 g) at the vegetative growth stage according to the procedure of Khosla et al. (1999). Polymorphisms between Fukuyutaka and Y2 were screened using 304 SSR markers from the SSR panel developed by Sayama et al. (2011). The genotypes of the F2 individuals were analyzed following the procedure of Sayama et al. (2011). To increase the marker density and decrease the gap distances in the linkage map, 56 additional SSR markers were chosen from the high-density integrated linkage map developed by Hwang et al. (2009). The PCR reaction was carried out using GoTaq Green Master Mix (Promega, Madison, WI, USA) following the manufacturer’s protocol, with minor modifications, on the GeneAmp PCR System 9700 (Applied Biosystems, Foster City, CA, USA). The PCR products were electrohoresed using the LabChip GX system (Caliper LifeSciences, Hopkinton, MA, USA).

Genetic mapping and QTL analysis

In total, 177 SSR marker genotypes of the F2 individuals were used to construct the linkage map. We used version 3.0b of MAPMAKER/EXP (Lander et al. 1987) to group and order the SSR marker loci. The linkage map distances were estimated using the Kosambi mapping function (Kosambi 1943). The minimum logarithm of odds (LOD) score and the maximum distance for linkage map construction were adjusted to 3.00 and 37.2 cM, respectively. The composite interval mapping method (Zeng 1993, 1994) implemented by version 2.5 of the Windows QTL Cartographer software (Wang et al. 2010) was used to estimate the QTL locations and effects. The “F2” cross-type and 1 cM walk-speed parameters were used. The default settings were used for other parameters. The LOD score criterion for QTL significance was estimated by means of a permutation test (Churchill and Doerge 1994) with 1,000 permutations. The thresholds of the LOD scores equivalent to 5% genome-wide Type I error rates were 3.95 for plant height, 4.04 for number of main stem nodes, 4.03 for AIL and 3.97 for days to flowering.

Evaluation of the QTL effect on AIL and plant height using F3 lines

The effect of the Y2 allele of a QTL for AIL, qSI13-1, was evaluated by comparing the AILs among F3 lines. F2 individuals that possess homozygous alleles of Fukuyutaka and Y2 at qSI13-1 were selected to produce F3 lines based on the genotypes of two SSR markers, Sat_375 and Satt657. The F3 lines derived from each F2 individual were planted...
in 4.5 m row in 17th July 2012 to confirm the effect of the Y2 allele of qSI13-1. Twenty plants were harvested for each lines and plant height, number of main stem nodes and AIL were measured. Marginal plants were excluded from the investigation. The inter-row and hill spacings were 70 cm and 14 cm, respectively.

**Evaluation of the effect of the QTL for AIL in backcrossed lines**

The Y2 allele of a QTL for AIL, qSI13-1, was introduced into Fukuyutaka by marker-assisted recurrent backcrosses to develop NILs. F1 seeds were obtained from a cross between Fukuyutaka and Y2, and backcrossed with Fukuyutaka to develop BC3 NILs. In each generation, the plants harboring qSI13-1 were selected based on the genotypes of two SSR markers, Sat_375 and Satt657. The BC3F3 NILs were planted in 2.5 m row. Ten individuals of the BC3F3 NILs were evaluated to verify the effects of the QTL on plant height, number of main stem nodes, AIL, flowering date and seed yield. Marginal plants were excluded from the investigation. The planting date was 14th July 2017. The inter-row and hill spacings were 70 cm and 14 cm, respectively.

**Results**

**QTL analysis of plant height, AIL, number of nodes, and flowering date**

The days to flowering of Y2 was longer than that of Fukuyutaka, while the plant heights of Y2 were shorter than those of Fukuyutaka (Table 1). Although the plant height of Y2 was larger than early flowering cultivar, Sachiyutaka, the AIL of Y2 was significantly shorter than that of Sachiyutaka. The inter-node lengths of Y2 were shorter than those of Fukuyutaka regardless of node positions, and significant differences between Y2 and Fukuyutaka were detected in first to 13th inter-nodes (Fig. 1). The frequency distributions of plant height, number of main stem nodes, AIL and days to flowering of the F2 individuals derived from the cross between Fukuyutaka and Y2 were continuous (Fig. 2), suggesting that these traits are quantitatively controlled by multiple loci. Estimated broad-sense heritability of plant height, number of main stem nodes and AIL were 0.90, 0.65 and 0.50, respectively. Therefore, we constructed a linkage map to carry out QTL analyses for these traits.

**Table 1.** Plant height, number of main stem nodes, average inter-node length, and days to flowering among Y2, Fukuyutaka, and Sachiyutaka

| Cultivars   | Plant height (cm) | Number of main stem nodes | Average inter-node length (cm) | Days to flowering |
|-------------|-------------------|---------------------------|-------------------------------|------------------|
| Y2          | 38.8 ± 2.0b       | 17.0 ± 0.9c               | 2.3 ± 0.2a                    | 48               |
| Fukuyutaka  | 50.1 ± 3.3c       | 13.7 ± 1.1b               | 3.7 ± 0.3c                    | 40               |
| Sachiyutaka | 34.7 ± 2.6a       | 12.0 ± 0.8a               | 2.9 ± 0.2b                    | 35               |

Values with the same alphabet are not significantly different by Tukey’s multiple comparison test at the 5% significance level. Ten plants were investigated for each cultivar.

A genetic linkage map of the F2 population was constructed using the segregation data for 177 SSR loci in 94 F2 individuals, and it revealed 25 linkage groups, covering 2,186.5 cM. The linkage groups and the arrangement of loci corresponded well with the order reported by Hwang et al. (2009). Composite interval mapping revealed a QTL for plant height and AIL on chromosome 13 (Table 2). We have provisionally designated this QTL as qSI13-1 (QTL for short inter-node on chromosome 13). qSI13-1 was detected between SSR markers Sat_375 and Satt657. The Y2 allele of qSI13-1 was partially dominant, resulting in shorter plant heights and AILs. The r² values (proportion of total phenotypic variance explained) of qSI13-1 for plant height and AIL were 0.40 and 0.46, respectively. No QTL for number of main stem nodes or flowering date were detected on chromosome 13. Other QTLs for plant height and number of main stem nodes were detected at a similar position as the QTL for days to flowering on chromosome 12 (Table 2).

**Confirmation of the effects of qSI13-1 on inter-node length and plant height**

The genotypes of qSI13-1 of F2 individuals investigated using two SSR markers, Sat_375 and Satt657, revealed that 12 and 14 plants possess homozygous allele of Fukuyutaka and Y2, respectively. The inter-node lengths of F2 individuals with Y2 allele were shorter than those of Fukuyutaka allele regardless of node positions, and significant differences between Y2 and Fukuyutaka were detected in all inter-nodes, except for 8th node (Fig. 3).

We developed F3 lines with homozygous allele of qSI13-1 derived from F2 individuals. AILs and plant heights of the F3 lines with Y2 allele of qSI13-1 were significantly shorter than those of Fukuyutaka allele (Fig. 4). No significant difference was detected between the F3 lines of different qSI13-1 alleles in number of main stem nodes and days to flowering (Fig. 4).

We introduced the Y2 allele of qSI13-1 to Fukuyutaka through five recurrent backcrosses that developed NILs
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(Fig. 5, Table 3). Genotypes of BC₃F₂ seeds were investigated and two NILs, NIL1-Y and NIL2-Y, were developed that harbored the Y2 allele of qSI13-1. Additionally, two NILs, NIL1-F and NIL2-F, which harbor the Fukuyutaka allele of qSI13-1 were also developed. NIL1-Y and NIL1-F were developed from the same BC₃F₁ individual, while NIL2-Y and NIL2-F were developed from another BC₃F₁ individual.

These NILs and Fukuyutaka flowered on the same date, August 23, and no significant differences were observed among the numbers of main stem nodes. The heights of NIL1-Y and NIL2-Y plants were nearly 10 cm less than those of Fukuyutaka, NIL1-F and NIL2-F, and significant differences between the alleles of qSI13-1 were confirmed (Fig. 5, Table 3). The AILs of NIL1-Y and NIL2-Y were approximately 0.5 cm less than those of Fukuyutaka, NIL1-F and NIL2-F, and significant differences were detected between the alleles of qSI13-1. No significant differences were detected among the seed yields and 100 seed weights of the NILs and Fukuyutaka.

Discussion

Clarifying the genetic basis of soybean plant height is important for developing lodging-tolerant cultivars, because large plants tend to be susceptible to lodging (Lee et al. 1996, Mansur et al. 1993, Orf et al. 1999, Specht et al. 2001). The development of cultivars with short heights is expected to be beneficial for achieving high yield through increased fertilization, because nitrogen fertilization can result in excessive vegetative growth and lodging (Salvagiotti et al. 2008, Wallace et al. 1990). The inter-node length of the semi-dwarf Japanese soybean Y2 was distinctively short regardless of node positions (Fig. 1), and we believe that this trait will be useful in developing cultivars with short heights and increased lodging tolerance levels. A QTL analysis was conducted for AIL, plant height and days for flowering using an F₂ population derived from a cross between Fukuyutaka and Y2. A QTL for AIL and plant height, qSI13-1, was identified on chromosome 13 (Table 2). The Y2 allele of qSI13-1 shortened inter-nodes regardless of node positions, revealing that the effect of qSI13-1 is not restricted by node positions (Fig. 3). In contrast, a QTL for plant height, number of main stem nodes, and days to flowering was detected on chromosome 12. The latter was not investigated further, because it was clearly related to days to flowering and had no effect on AIL. Kuroda et al. (2013) detected a QTL for days to flowering in the same region using a population of RILs derived from a cross between a wild soybean (JP110755) and Fukuyutaka. We expected that this is the same locus.

The Y2 allele of qSI13-1 was introduced into Fukuyutaka by recurrent backcrossing to develop NILs. The AILs and plant heights of the NILs harboring the Y2 allele of qSI13-1 were significantly less than those of Fukuyutaka and the NILs harboring the Fukuyutaka allele of qSI13-1 (Fig. 5,
fect not only lodging tolerance but also the number of nodes, which is an important yield component (Egli 2013).

$qSI13-1$ had no effect on flowering date and growth habit, and is clearly different from those reported QTLs. $qSI13-1$ is expected to be easily used in breeding programs, because its influence is limited to plant height.

Table 2. Quantitative trait loci for soybean plant height, number of main stem nodes, average inter-node length and days to flowering detected in an F2 population derived from a cross between Fukuyutaka and Y2

| Trait                                      | Chromosome | LOD$^d$ | $r^2$ $^b$ | $d^c$ | $d^d$ | Position (cM) | QTL region (cM) |
|--------------------------------------------|------------|---------|------------|-------|-------|---------------|-----------------|
| Plant height (cm)                          | 12         | 6.1     | 0.19       | −5.8  | −1.2  | 19.4          | GMES3950 (12.2)–Satt192 (19.4) |
|                                            | 13         | 9.1     | 0.40       | 6.6   | −4.9  | 78.7          | Sat.375 (58.6)–Satt657 (86.5) |
| Number of main stem nodes                  | 12         | 12.2    | 0.38       | −1.6  | −0.5  | 19.2          | GMES3950 (12.2)–Satt192 (19.4) |
| Average inter-node length (cm)             | 13         | 12.4    | 0.46       | 0.34  | −0.13 | 83.7          | Sat.375 (58.6)–Satt657 (86.5) |
| Days to flowering (d)                      | 12         | 28.4    | 0.73       | −3.1  | 0.18  | 18.2          | GMES3950 (12.2)–Satt192 (19.4) |

$^a$ Logarithm of odds.
$^b$ Proportion of variance explained.
$^c$ Additive effect of the Fukuyutaka allele.
$^d$ Dominance effect. If the locus is heterozygous, then the trait value increases through the dominance effect from the intermediate value of the parents.

Table 3). No significant differences between Fukuyutaka and the NILs were detected for seed yield, the flowering date, and 100 seed weight. Thus, $qSI13-1$ may be used to decrease plant height, without or with limited negative effects on seed yield, flowering date and 100 seed weight. However, the effect of $qSI13-1$ on lodging tolerance has not been confirmed because, in the investigation conducted in 2017, almost no lodged plants were observed in Fukuyutaka nor the NILs. In south western Japan, severe lodging damages are frequently occurred by typhoons. However, no severe lodging damage was occurred by typhoon in 2017, and this is the main reason why no difference of lodging extent was observed among Fukuyutaka and the NILs. We are planning to confirm the effect of $qSI13-1$ on lodging tolerance using Fukuyutaka and the NILs under enhanced lodging conditions by increasing plant density. In addition, yield potential and other important agronomic traits of the NILs will be compared with those of Fukuyutaka in large-scale experiments to clarify the effects of $qSI13-1$.

In the previous studies, QTLs for lodging tolerance were frequently related to early flowering time and determinate habit (Lee et al. 1996, Mansur et al. 1993, Orf et al. 1999, Specht et al. 2001). These traits reduce plant heights, resulting in low lodging scores. However, these traits usually affect not only lodging tolerance but also the number of nodes, which is an important yield component (Egli 2013). $qSI13-1$ had no effect on flowering date and growth habit, and is clearly different from those reported QTLs. $qSI13-1$ is expected to be easily used in breeding programs, because its influence is limited to plant height.
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Yamaguchi et al. (2014) reported a lodging-tolerance QTL, \( qLS19-1 \) from the lodging-tolerant cultivar Toyoharuka. The lodging scores of the NILs harboring the resistance allele of \( qLS19-1 \) were lower than those harboring the susceptible allele. The resistance allele of \( qLS19-1 \) should be useful in developing elite lodging-tolerant cultivars, because negative influences on yield and other agronomic traits are rarely observed. The integrated effect of \( qSI13-1 \) and \( qLS19-1 \) must be confirmed for practical use in the breeding program.

Another lodging tolerance QTL, \( qLS13-1 \), was reported in the vicinity of \( qSI13-1 \) by Yamaguchi et al. (2014). The Toyomusume allele of \( qLS13-1 \) reduces plant height, but exhibits a negative effect on seed yield. The peak position of \( qLS13-1 \) was approximately 10 cM upstream from the SSR marker \( Sat_{313} \) and that of \( qSI13-1 \) was more than 20 cM downstream from the SSR marker \( Sat_{375} \). According to Soybase (https://www.soybase.org/), \( Sat_{313} \) and \( Sat_{375} \) are only 4 cM apart, and the estimated length between the peak positions of \( qSI13-1 \) and \( qLS13-1 \) was more than 25 cM. Therefore, these QTLs are probably different loci, although the fine mapping of these QTLs is necessary owing to the lack of common markers in their vicinities.

In contrast, the QTL for plant height reported by Kuroda et al. (2013) is in almost the same position as \( qSI13-1 \). However, the Fukuyutaka allele of the QTL decreased the plant heights in the RIL population derived from a cross between Fukuyutaka and Japanese wild soybean. Although the QTL may be the same, the genetic effect of the \( Y2 \) allele of \( qSI13-1 \) on plant height is clearly different from those of Fukuyutaka and Japanese wild soybean. In addition, Lee et al. (2015) detected a QTL for plant height using a RIL population derived from a cross between the cultivar Wyandot, developed in Ohio, and a Chinese germplasm, PI 567301B. This QTL was also identified in almost the same position as \( qSI13-1 \). The RILs were originally developed to identify aphid-resistance genes, and PI 567301B was highly susceptible to lodging (Jun et al. 2012). The plant height of PI 567301B was more than 160 cm, and the plants have more secondary and tertiary branches than Wyandot. These characteristics of PI 567301B are similar to those of wild soybean. PI 567301B could have the same allele as the Japanese wild soybean described above, while Wyandot shares a common allele with cultivated soybean and Fukuyutaka. An allelic test is necessary to determine whether previously reported QTLs and \( qSI13-1 \) represent the same locus. Nonetheless, this is the first report that developed NILs and confirmed that \( qSI13-1 \) can be used to decrease plant height without negative effects on seed yield and days to flowering.

The development of semi-dwarf rice and wheat cultivars resulted in prominent yield increases, known as the ‘green revolution’. The semi-dwarf traits of rice and wheat are controlled by \( sd1 \) and \( Rht1 \) loci, respectively (Ashikari et al. 2002, Hedden 2003, Monna et al. 2002, Peng et al. 1999). The semi-dwarf cultivars contribute to yield increases because the plant heights of semi-dwarf cultivars are not influenced by increased nitrogen fertilization. Our finding revealed that \( qSI13-1 \) decreased only plant height without affecting flowering date, number of main stem nodes and yield. Therefore, \( qSI13-1 \) may prevent excessive vegetative growth stimulated by a high nitrogen fertilization and contributes to yield increase through fertilization management. Global warming will cause serious yield losses by increasing lodging owing to strong winds and increased rain falls. We expect that \( qSI13-1 \) will play an important role in the development of high-yield soybean cultivars with lodging tolerance.

Table 3. Plant height, number of main stem nodes, average inter-node length, yield and 100 seed weight of the soybean NILs harboring the \( Y2 \) allele of \( qSI13-1 \) in the genetic background of Fukuyutaka

| Line     | Plant height (cm) | Number of main stem nodes | Average inter-node length (cm) | Yield (kg/a) | 100 seed weight (g) |
|----------|-------------------|---------------------------|--------------------------------|--------------|-------------------|
| Fukuyutaka | 58.4 ± 4.4a       | 14.6 ± 1.3a               | 4.0 ± 0.2a                     | 30.2 ± 7.4a  | 30.4 ± 0.3a       |
| NIL1-F    | 60.1 ± 5.2a       | 14.5 ± 1.3a               | 4.1 ± 0.2a                     | 25.4 ± 6.4a  | 30.4 ± 0.5a       |
| NIL1-Y    | 50.2 ± 1.8b       | 14.4 ± 2.1a               | 3.5 ± 0.2b                     | 27.1 ± 6.9a  | 30.1 ± 0.4a       |
| NIL2-F    | 58.3 ± 3.4a       | 14.9 ± 1.0a               | 3.9 ± 0.1a                     | 27.1 ± 6.0a  | 29.6 ± 0.6a       |
| NIL2-Y    | 51.4 ± 1.5b       | 15.0 ± 0.7a               | 3.4 ± 0.1b                     | 30.3 ± 10.3a | 30.0 ± 0.5a       |

\( ^a \) NIL1-F and NIL2-F harbor the Fukuyutaka allele of \( qSI13-1 \).

\( ^b \) NIL1-Y and NIL2-Y harbor the \( Y2 \) allele of \( qSI13-1 \).

Values followed by the same lowercase letters are not significantly different as assessed by Tukey’s multiple comparison test at the 5% level.
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