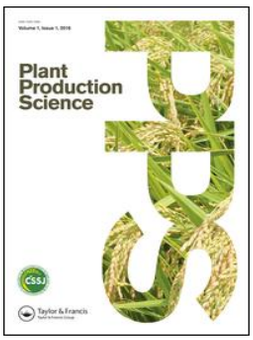

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Branch development responses to planting density and yield stability in soybean cultivars

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ABSTRACT

The objective of this study was to elucidate variability among soybean cultivars in yield response at different planting densities in reference to branch development. We investigated the main stem and branch seed yield and the branching characteristics of determinate Hokkaido and indeterminate US cultivars at the Rakuno Gakuen University in Ebetsu. In 2009 and 2010, two Japanese and two US cultivars were grown at three densities from 9.5 to 20 plants m^{-2}. In 2011 and 2012, three cultivars from each region were cultivated at three densities from 8.3 to 22.2 plants m^{-2}. The seed yields of the US cultivars at densities of 16.7 plants m^{-2} or less were markedly higher than those of the Hokkaido cultivars, showing that their yield is less sensitive to lower planting density than Hokkaido cultivars. The difference in yield in response to planting density among cultivars was closely associated with a larger increase in branch seed yield with lower planting density, which effectively compensated for the decrease in main stem number per unit land area. The variability of branch development in response to planting density (branching plasticity) was quantified by correlating branch performance with plant spacing (land area per plant). Some US cultivars exhibited greater branching plasticity than Japanese cultivars with similar growth duration. Results of this study suggest soybean cultivar differs in responsiveness to varied planting density through different branching plasticity.

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Branching plasticity; Japanese cultivar; land area per plant; planting density; seed yield; soybean (*Glycine max* (L.) Merrill); US cultivar

Crop yield typically increases with plant density until a particular density threshold is reached, after which any further increase in density will likely have a negative effect on yield. Crop management to achieve optimal plant density is important for stabilizing seed yield in different crop species (Donald, 1963). A broader range of desirable plant density in terms of seed productivity will be advantageous for better crop compensation for yield loss due to a non uniform crop stand (Carpenter & Board, 1997a, 1997b), for flexibility in planting date, and for reducing seed cost by lowering the sowing rate (Rigsby & Board, 2003).

In Japan, numerous studies have been conducted on the effect of planting density on soybean yield. In general, dense planting increases yield (Ikeda, 2000; Miura & Gemma, 1986; Nakaseko & Goto, 1986) and high-density or narrow-row planting has been recommended in various regions in Japan (Matsunaga et al., 2003). But due to the incidence of lodging and branch breakage (Kamiya et al., 1980), adoption of narrow-row/high-density cultivation is limited (Hamaguchi, 2011; Takahashi, 2011), with the standard soybean planting density being less than 20 plants m^{-2} (Tsuchiya, 1986; Uchikawa et al., 2004).

In the USA, on the other hand, narrow-row/high-density planting is broadly practiced with a plant density exceeding 25 plants m^{-2} and interrow spacing being 40–50 cm (Heatherly & Elmore, 2004), and this cultivation techniques is based on numerous studies of planting density in soybean production (e.g. Cooper, 1971a, 1971b; Duncan, 1986; Spaeth et al., 1984; Wilcox, 1977). At the same time, plant traits that also lead to better adaptation at lower plant density are being investigated to reduce seed cost and avoid disease and lodging. In addition, Board and Kahlon (2013) recently reported a considerable variation in yield under lower plant density among US soybean cultivars and they attributed the difference to branch development. Thus, it may also be assumed that, if there is variation in response to planting density among cultivars, it is related to the development of branches. Considering the situation in Japan and the USA, it may be assumed that US cultivars are adapted to a wider planting density than Japanese cultivars.

Yield stability to planting density is expected to be supported by the magnitude of the response of the planting density in terms of branch seed yield, branch pod number,

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and branch length. In this study, we defined branching plasticity as the branch characteristics that decreases branch development under dense planting and increases branch development in response to increasing land area per plant. For this we evaluated branching plasticity with the ratio of branch performance under low plant density to that under high plant density.

The objective of this study was to elucidate variability among soybean cultivars in yield in response to planting density and yield stability across different planting densities by branching plasticity value. We examined main stem and branch seed yields and clarified the branching characteristics of three Japanese cultivars and three US cultivars.

The first study (experiment 1) was performed in the field over two years (2009 and 2010) at five different plant densities to establish the evaluation method of yield response and branching performance. The second study (experiment 2) was performed in the field over two years, using six cultivars in 2011 and four cultivars in 2012, with a reduced number of plant density treatments to examine variability among cultivars in branching performance.

2. Materials and methods

2.1. Planting density and cultivars

Both experiments were conducted in experimental fields at Rakuno Gakuen University in 2009 and 2010 (experiment 1) and in 2011 and 2012 (experiment 2). When conducting a planting density experiment, the range of density is extremely important. Taking into consideration the results of experiments by Lee et al. (2008) and Parvez et al. (1989), we determined that the greatest variation in soybean yield occurs over a planting density range from 8 to 25 plants m^{-2}. Therefore, in this experiment, we established planting density treatments, which fall in the above range. Soybean cultivars were planted at three plant densities (50 cm × 10 cm, 60 cm × 10 cm, 70 cm × 15 cm), with values given as row width × intrarow spacing in each case in experiment 1 and three densities (60 cm row width × 7.5 cm, 10 cm, and 20 cm intrarow spacing) in experiment 2.

In 2009, the US cultivar 'Athow' and the Japanese cultivar 'Toyomusume' were used. In 2010, the US cultivar 'LD00-3309' and the Japanese cultivar 'Toyoharuka' were tested in addition to the two cultivars used in 2009. In 2011, the US cultivar 'Jack' and the Japanese cultivar 'Yuzuru' were added to the cultivars tested (Tables 2 and 3). 'Toyomusume', 'Athow', 'Jack', and 'Yuzuru' were grown in 2012 under the varying planting densities mentioned above.

'Toyomusume' is known for its stable and high yields, while 'Toyoharuka' is used in Hokkaido Prefecture because of its lodging resistance. The maturity group (MG) of both cultivars is I. 'Athow' and 'LD00-3309' are new high-yielding cultivars used in the midwestern USA (MG III, IV respectively). 'Yuzuru' and 'Jack' were selected because of their similar maturation rates (MG II). 'Yuzuru' is cultivated in southern Hokkaido and bears large seeds. 'Jack' is a traditional soybean cultivar cultivated in the midwestern USA. These three Japanese cultivars were determinate type and the three US cultivars were indeterminate type.

2.2. Field management and measurements

The soybean cultivars (two in 2009, four in 2010, six in 2011, and four in 2012) were planted (two seeds per hill) on 24 May 2009, 15 May 2010, 27 May 2011, and 14 May 2012. When the first trifoliolate leaves of the seedlings emerged, the seedlings thinned to one plant per hill were planted on the same hill. Seedlings were transplanted from adjacent hills to vacant hills to ensure a complete plant community.

Basic fertilizer containing 2 g m^{-2} N (as ammonium sulfate), 12 g m^{-2} P_2O_5 (as calcium superphosphate), and 8 g m^{-2} of K_2O (as potassium sulfate) was applied in accordance with standard practices in Hokkaido. In all four years, weeds were removed manually up to the flowering stage.

Thiamethoxam was applied to the seeds to prevent pest damage (such as by seed-corn flies, aphids, and cutworms) to the plants. A mixture of metalaxyl and fludioxonil emulsions was applied in late July and early August on a required basis to protect the plants from Japanese beetles and aphids.

To evaluate soybean yield, 20 medium-sized plants were harvested at maturity (stage R8) from each plot by hand. After the harvested plants had been air-dried for three or four weeks, the number of nodes and pods on the main stems and branches was counted. After threshing by hand, the seed number and 100 seed weight of main stems and branches were recorded. Seed yield was adjusted to a 130 g kg^{-1} on the basis of the moisture content.

Branch seed yield per branch elongation period to R5 (BSY/R5) was calculated in comparison to branch seed yield in order to compensate for earliness of soybean cultivars, because the branch elongation period was longer and branch seed yield was higher in late cultivars than in early cultivars and indeterminate types, like US cultivars, continue to develop branches until R5 (Agudamu et al., 2013).

2.3. Statistical analyses

In Experiments 1 and 2, the cultivars were arranged in a split-plot design with three replications, with planting density levels as main plots and cultivars as subplots. Analyses of variance (ANOVA) were performed to evaluate treatment differences in seed yield.

Table 1. Average air temperature and precipitation during the growing seasons in 2009–2012.

	Average air temperature (℃)					Precipitation (mm)				
Month	2009	2010	2011	2012	2003–2012*	2009	2010	2011	2012	2003–2012*
May	12.5	11.0	10.3	12.5	11.1	37	58	69	62	69
June	16.0	17.6	16.1	16.0	14.7	94	67	40	77	47
July	18.5	21.0	21.4	20.5	19.3	206	176	141	81	101
August	20.3	23.4	22.8	22.9	20.3	49	190	137	205	150
September	16.6	18.6	18.7	21.8	16.8	40	106	231	196	151
October	11.4	11.3	11.6	12.4	10.7	105	75	145	116	93
Total	2,904	3,135	3,067	3,247	2,834	529	671	762	736	610

*Indicates mean value of 2003–2012.

Branching plasticity was evaluated with the ratio of branch performances, seed yield, pod number, and total length, under sparse planting to those under dense planting. We hereafter refer to these ratios as branching plasticity value.

3. Results

3.1. Climatic conditions

Table 1 shows the mean temperature and precipitation in 2009–2012. The cumulative temperature during the soybean growth period was highest in 2010 and lowest in 2009. The accumulated precipitation was highest in 2011 and lowest in 2009.

Average air temperature in July, which is considered a primary meteorological factor for branch length in the central Hokkaido area, was lower in 2009 than in 2010 (experiment 1) and lower in 2012 than in 2011 (experiment 2).

In 2010–2012, the ambient temperature was slightly elevated during the first half of the seed filling period. In 2012, the temperature was elevated during the second half of the seed filling period as well. Based on this, we concluded that climatic conditions in 2009 were not suitable for branch development, whereas they were suitable in 2010–2012, promoting the formation of dense vegetation, resulting in the branches becoming thinner and longer.

3.2. Development, seed yield and related plant characteristics

Table 2 shows seed yield and related plant characteristics for experiment 1 (2009–2010). It was found that, among the cultivars grown in 2009 and 2010, the US cultivars reached R1 approximately one week later and R8 approximately three weeks later than the Hokkaido cultivars.

In 2009, the interaction of cultivar and planting density had a significant impact on total seed yield and branch characteristics except branch number. Total seed yield was significantly higher in Athow than in Toyomusume at sparse plant densities (70 × 15), while this was not true at higher plant densities. Athow exhibited generally higher branch seed yield, branch pod number, and total branch length than Toyomusume. No significant interaction of cultivar and planting density on main stem length, pod number of the main stem, or lodging score was observed. BY/R5, which was proposed by Board and Kohlan (2013) as an indicator of adaptation ability of genotype to low density, was higher in Athow than Toyomusume in all treatments.

In 2010, similarly to 2009, the interaction of cultivar and planting density had a significant impact on plant characteristics except main stem length. Total seed yield, branch seed yield, branch pod number, and total branch length were found to be higher for the two US cultivars tested (Athow and LD00-3309) than for the Japanese cultivars (Toyomusume and Toyoharuka).

Table 3 shows seed yield and related plant characteristics for experiment 2 (2011–2012). Jack, the earliest maturing of the US cultivars tested in 2011 reached R1 and R8 at approximately the same time as Yuzuru, the latest maturing of the Hokkaido cultivars. In both the years, total seed yield, branch seed yield, BY/R5, branch pod number, and total branch length were substantially higher for the US cultivars than for the Japanese cultivars. Those varietal differences were larger in sparse plantings than dense plantings. The interaction of cultivar and planting density had a significant impact on total seed yield, pod number, and stem length of branches, with the effect on seed yield and branch pod number being the most significant ($p = 0.01$) over the four-year period, including 2009 and 2010.

The total branch length was divided into branch number and average length of a single branch (one average branch). The interaction between cultivars and planting density in branch number was not significant except for 2010. On the other hand, the interaction in one average branch length was significant ($p = 0.001$) over four years.

3.3. Responses to planting density (land area per plant)

Table 4 shows the ratio of branch performances in sparse planting to that in dense planting (branching plasticity value) in experiments 1 and 2 (2009–2012). The ratios WWWWWUS cultivars were generally higher than those for

Table 2. Seed yield and the related chracteristics (Exp1, 2009–2010).

Experimental year	Spacing (cm) × Row width (cm)	Plant density (m^{-2})	Land area per plant (100 × cm^2)	Cultivar	R1 stage (month / day)	R5 stage (month / day)	R8 stage (month / day)	Growth period (Sowing-R5) (day)	Total seed yield (g m^{-2})	Branch seed yield (g m^{-2})	Branch yield per growth period (Sowing-R5) (g m^{-2} day^{-1})	Branch pod number (m^{-2})	Total branch length (cm)	No. of branch pl^{-1})	Average branch length (cm pl^{-1})
2009	50 × 10	20	5	Toyomusume	25-Jul	1-Sep	1-Oct	100 a	340 a	91 a	0.91 a	208 a	126 a	2.2 a	57 b
				Athow	2-Aug	17-Sep	24-Oct	116 b	338 a	128 b	1.1 b	249 a	111 a	2.8 a	40 a
	60 × 10	16.7	6	Toyomusume	24-Jul	31-Aug	2-Oct	100 a	308 a	122 a	1.22 a	207 a	73 a	2.4 a	30 a
				Athow	1-Aug	15-Sep	22-Oct	114 b	335 b	144 b	1.26 a	264 b	112 b	3.3 b	34 a
	70 × 15	9.5	10.5	Toyomusume	21-Jul	29-Aug	29-Sep	97 a	275 a	127 a	1.3 a	283 a	135 a	3.2 a	42 a
				Athow	29-Jul	11-Sep	17-Oct	110 b	344 b	215 b	1.95 b	371 b	190 b	4.3 b	45 b
	Cultivar						**	**	**	**		**	***	**	*
	Density						ns	***	***	ns		***	***	**	**
	Cultivar × Density						ns	*	*	*		*	***	ns	**
2010	50 × 10	20	5	Toyomusume	18-Jul	21-Aug	17-Sep	98 a	346 a	124 b	1.26 b	292 b	131 b	3.7 a	36 b
				Toyoharuka	20-Jul	21-Aug	17-Sep	99 a	328 a	103 a	1.04 ab	234 a	136 b	3.1 a	44 b
				Athow	18-Jul	10-Sep	20-Oct	118 b	344 a	125 b	1.06 ab	276 b	88 a	3.7 a	24 a
				LD00-3309	25-Jul	14-Sep	24-Oct	122 c	374 a	117 ab	0.96 a	223 ab	95 a	3.5 a	27 a
	60 × 10	16.7	6	Toyomusume	18-Jul	20-Aug	17-Sep	98 a	321 a	147 b	1.5 b	406 c	173 b	4.6 b	38
				Toyoharuka	20-Jul	22-Aug	18-Sep	99 a	303 a	123 a	1.24 a	163 a	120 a	2.7 a	44 b
				Athow	21-Jul	8-Sep	18-Oct	116 b	343 a	163 bc	1.4 ab	342 b	119 a	4 b	30 a
				LD00-3309	26-Jul	14-Sep	22-Oct	123 c	353 a	182 c	1.48 b	420 c	162 b	4.4 b	37
	70 × 15	9.5	10.5	Toyomusume	14-Jul	17-Aug	12-Sep	95 a	266 a	167 b	1.77 b	254 b	203 b	5.1 b	40 b
				Toyoharuka	14-Jul	18-Aug	10-Sep	95 a	245 a	135 a	1.42 a	144 a	92 a	3.7 a	25 a
				Athow	18-Jul	7-Sep	14-Oct	115b	351 b	224 c	1.94 c	400 c	240 c	4.7 b	51 c
				LD00-3309	23-Jul	11-Sep	22-Oct	120 c	375 b	248 c	2.07 c	483 c	326 d	5.5 b	59 c
	Cultivar							***	*	**	**	**	***	**	**
	Density							ns	ns	**	*	***	***	**	*
	Cultivar × Density						ns	*	**	*	**	***	*	**	

Note: Means followed by the same letters in the same column are not significantly different at 5% level by Tukey-Kramer test.
*Indicate significant at the 5%;
**Indicate significant at the 1%;
***Indicate significant at the 0.1%.
nsIndicate significant at the nor significant,respectively.

Table 3. Seed yield and the related chracteristics (Exp 2, 2011–2012).

Experimental year	Spacing(cm) × Row width(cm)	Plant density (m-2)	Land area per plant (100 × cm2)	Cultivar	R1stage (month/day)	R5 stage (month/day)	R8stage (month/day)	Growth period (Sowing-R5) (day)	Total seed yield (g m-2)	Branch seed yield (g m-2)	Branch yield per growth period (Sowing-R5 (g m-2 day-1)	Branch pod number (m-2)	Total branch length (cm)	No. of branch (pl-1)	Average branch length (cm pl-1)
2011	60 × 7.5	22.2	4.5	Toyomusume	15-Jul	31-Aug	30-Sep	97 a	324 ab	86 ab	0.89 b	184 bc	55 a	2 a	28 a
				Toyoharuka	18-Jul	1-Sep	28-Sep	97 a	315 a	57 ab	0.58 ab	171 b	69 a	1.5 a	26 a
				Yuzuru	17-Jul	7-Sep	9-Oct	104 bc	312 a	48 a	0.46 a	78 a	87 ab	2.1 a	27 a
				Athow	21-Jul	10-Sep	15-Oct	106 c	344 b	94 b	0.88 b	123 ab	115 b	3.3 b	21 a
				LD00-3309	28-Jul	19-Sep	25-Oct	115 d	353 b	166 c	1.44 c	249 c	141 c	4.9 c	36 a
				Jack	18-Jul	6-Sep	8-Oct	102 b	323 ab	87 ab	0.85 b	74 a	112 b	2.4 a	35 a
	60 × 10	16.7	6	Toyomusume	13-Jul	29-Aug	30-Sep	95 a	208 a	70 a	0.74 a	230 b	37 a	2.8 b	41 ab
				Toyoharuka	15-Jul	30-Aug	28-Sep	95 a	299 b	98 b	1.03 ab	206 b	56 a	1.9 a	30 a
				Yuzuru	18-Jul	7-Sep	10-Oct	104 bc	284 b	53 a	0.51 a	43 a	71 ab	2.3 ab	43 ab
				Athow	20-Jul	9-Sep	15-Oct	105 c	345 c	188 d	1.78 c	448 c	101 b	4 cd	28 a
				LD00-3309	29-Jul	18-Sep	25-Oct	115 d	342 c	205 d	1.79 c	558 d	225 c	4.7 d	47 b
				Jack	19-Jul	6-Sep	9-Oct	102 b	302 b	136 c	1.34 b	394 c	224 c	3.5 c	45 ab
	60 × 20	8.3	12	Toyomusume	13-Jul	27-Aug	28-Sep	93 a	189 a	105 a	1.13 b	358 a	78 a	2.9 a	29 a
				Toyoharuka	13-Jul	27-Aug	28-Sep	93 a	210 a	91 a	0.98 ab	373 a	69 a	2.6 a	27 a
				Yuzuru	19-Jul	6-Sep	10-Oct	103 b	258 *ab*	88 a	0.86 a	282 a	81 a	2.3 a	36 ab
				Athow	20-Jul	8-Sep	15-Oct	105 c	319 c	212 c	2.02 d	664 b	195 b	4.7 bc	42 b
				LD00-3309	29-Jul	18-Sep	25-Oct	115 d	323 c	213 c	1.86 c	760 b	301 c	5.8 c	53 c
				Jack	20-Jul	5-Sep	8-Oct	101 b	287 b	178 b	1.76 c	698 b	285 c	4.3 b	48 bc
	Cultivar							**	***	***	***	***	***	**	**
	Density							ns	ns	ns	*	**	***	**	*
	Cultivar × Density							ns	***	***	*	***	***	ns	**
2012	60 × 7.5	22.2	4.5	Toyomusume	26-Jul	2-Sep	29-Sep	111 a	325 a	101 a	0.91 a	295 a	104 b	2.6 b	40 a
				Yuzuru	26-Jul	12-Sep	12-Oct	121 b	316 a	105 a	0.87 a	207 a	80 a	1.2 a	50 b
				Athow	30-Jul	17-Sep	20-Oct	126 c	366 b	115 b	1.07 b	301 a	113 bc	3.7 c	30 a
				Jack	27-Jul	11-Sep	11-Oct	120 b	352 ab	110 ab	0.91 a	339 b	123 c	3.5 bc	36 a
	60 × 10	16.7	6	Toyomusume	26-Jul	1-Sep	29-Sep	111 a	307 b	119 a	1.07 a	478 b	189 bc	4.1 b	46 ab
				Yuzuru	26-Jul	12-Sep	12-Oct	121 b	263 a	137 ab	1.13 ab	249 a	130 a	3 a	43 ab
				Athow	30-Jul	16-Sep	20-Oct	125 c	354 c	155 b	1.24 b	399 b	158 b	3.7 ab	42 a
				Jack	27-Jul	11-Sep	11-Oct	121 b	324 bc	151 b	1.25 b	470 b	197 c	4.1 b	48 b
	60 × 20	8.3	12	Toyomusume	26-Jul	2-Sep	29-Sep	112 a	260 a	160 b	1.43 b	402 ab	217 a	5.5 b	40 a
				Yuzuru	30-Jul	11-Sep	12-Oct	121 bc	299 b	105 a	0.87 a	295 a	201 a	4.1 a	50 b
				Athow	30-Jul	15-Sep	19-Oct	124 c	334 c	202 bc	1.62 c	462 b	416 b	4.4 ab	71 c
				Jack	30-Jul	10-Sep	12-Oct	120 b	317 c	228 c	1.9 c	604 c	444 c	5 ab	88 d
	Cultivar							**	*	**	**	***	***	***	*
	Density							ns	ns	***	ns	***	***	**	**
	Cultivar × Density							ns	*	***	*	**	***	ns	**

Means followed by the same letters in the same column are not significantly different at 5% level by Tukey-Kramer test.
*Indicate significant at the 5%;
**Indicate significant at the 1%;
***Indicate significant at the 0.1%.
nsIndicate significant at the nor significant,respectively.

the Hokkaido cultivars in all the four years. The exception was branch yield for LD00-3309 in 2011. Seed yield of the latest cultivar, LD00-3309, was low due to a low percentage of ripened seed because of high precipitation and low solar radiation in autumn. Hence, the ratio of cultivar LD00-3309 in 2011 was as low as other determinate cultivars.

The ratio of branch length was significantly higher in the US cultivars than that in the Hokkaido cultivars in all the years. In addition, there was a significant varietal difference in branch length when comparison was made within Hokkaido cultivars (2009–2011) and within US cultivars (2010 and 2011).

Figure 1 shows the relationship between days from sowing to the beginning of seed filling stage (R5) and ratio of performance in sparse planting to that in dense planting in branch traits (branching plasticity value) in experiments 1 and 2 (2009–2012).The branching plasticity value for total branch length exhibited significant correlation with days from sowing to R5 ($r = 0.85^{***}$). The regression coefficient between days from sowing to R5 and this ratio tended to be higher in indeterminate US cultivars than that in determinate Japanese cultivars.

But the correlation coefficient between branching plasticity value for branch yield and branch pod number, and days from seeding to R5 were not significant ($r = 0.19, 0.15$). The higher branching plasticity values of US cultivars were attributable to a longer duration from sowing to R5 for US cultivars. Although Yuzuru and Jack require the same growth period to reach R5, the branching plasticity value for Jack was higher than for Yuzuru.

4. Discussion

This study was conducted to elucidate variability among soybean cultivars in yield across different planting densities in response to branch development. We hypothesized that US commercial cultivars can adapt to a wider planting density than Japanese cultivars. The interaction of cultivar and plant density was found to have a significant effect on total seed yield. The US cultivars exhibited greater yield than the Japanese cultivars under sparse planting conditions. The total seed yield of US cultivars was remarkably stable across different planting densities, while the total seed yield of Japanese cultivars declined with decreasing planting density.

As indicated in Tables 3 and 4, although variability in total seed yield across planting density was lower for the US cultivars than for the Japanese cultivars, the variability in branch seed yield was larger for the US cultivars than for the Japanese cultivars. Branch seed yield increased with increasing planting density in the US cultivars and this compensated for the decrease in main stem yield resulting from low planting density. The US cultivars exhibited greater variability in branch traits, including node number, pod number, and total branch length as a function of planting density than the Japanese cultivars. Board and Kahlon (2013) observed variation in soybean yield under lower plant density and attributed the difference to branch development. They also pointed out that the branch dry matter relative to days in R5 is a good indicator of the ability to adapt to low plant density. In this study, too, the branch seed yield relative to days in R5 (BY/R5) was greater in the US cultivars than the Japanese cultivars in over four years. Although it is generally assumed that a longer growing cultivar would adapt to lower density, the above finding suggests that yield response differs among the tested cultivars regardless of growth duration.

Branch seed yield and related branch characteristics varied widely with land area per plant, compensating for the decrease in yield on the main stem under low planting density. The term 'branching plasticity' is used to refer to this phenotypic variability in branch development depending on plant density; the above cultivar difference in yield in response to planting density can be attributed to the branching plasticity.

A number of studies on dicotyledonous plants, trees in particular, have examined morphological responses as related to branching plasticity (Smith & Jordan, 1994; Steingraeber, 1982), in such aspects as branch to stem angle, branch length, differences in these values between tree species (Bisht et al., 1993), and shade tolerance (Banez et al., 1999). However, few studies have examined the relationship between branching plasticity and yield of soybeans. The results of the present study suggest there exists a substantial cultivar difference in the branching plasticity that is reflected in different yields in response to planting density.

All the US cultivars used in the present study were of the indeterminate type, while all of the Japanese cultivars were of the determinate type.

In general, branching behavior varies depending on the growth habit. Given that the branches of indeterminate cultivars continue to grow even after the beginning of flowering, it is assumed that indeterminate cultivars have a longer period over which they are able to adapt to their environment through branch development compared to determinate cultivars with a similar growth duration to beginning of flowering.

When branch length is divided into its components of branch number and average branch length, the interaction between branch number and planting density was not significant except for 2010. On the other hand, the interaction between average branch length and planting density was significant all four years. These observations suggest that high branching plasticity in US cultivars were more strongly associated with the effect of planting density

Table 4. Regression coefficient to the land area per plant in branch chracteristics (2009–2012).

Year	Cultivar	Branch yield	Branch pod number	Total branch length
2009	Toyomusume	1.39 ± 0.07 a	1.36 ± 0.05 a	1.07 ± 0.02 a
	Athow	1.69 ± 0.04 b	1.49 ± 0.04 b	1.71 ± 0.09 b
2010	Toyomusume	1.35 ± 0.01 a	0.87 ± 0.06 a	1.55 ± 0.21 b
	Toyoharuka	1.31 ± 0.04 a	0.61 ± 0.05 a	0.68 ± 0.15 a
	Athow	1.79 ± 0.02 ab	1.45 ± 0.10 b	2.72 ± 0.17 c
	LD00-3309	2.12 ± 0.02 b	2.17 ± 0.21c	3.42 ± 0.10 d
2011	Toyomusume	1.22 ± 0.10 a	1.94 ± 0.07 a	1.43 ± 0.09 ab
	Toyoharuka	1.60 ± 0.12 ab	2.19 ± 0.01 a	1.00 ± 0.14 a
	Yuzuru	1.84 ± 0.22 b	3.61 ± 0.02 b	0.93 ± 0.09 a
	Athow	2.26 ± 0.35 d	5.39 ± 0.05 c	1.70 ± 0.03 b
	LD00-3309	1.28 ± 0.07 a	3.05 ± 0.03 ab	2.14 ± 0.13 c
	Jack	2.05 ± 0.07 c	9.48 ± 0.03 d	2.54 ± 0.13 d
2012	Toyomusume	1.58 ± 0.12 b	1.36 ± 0.13 a	2.09 ± 0.06 a
	Yuzuru	1.00 ± 0.15 a	1.42 ± 0.18 a	2.51 ± 0.11 b
	Athow	1.76 ± 0.11 b	1.54 ± 0.11 b	3.67 ± 0.11 c
	Jack	2.08 ± 0.16c	1.78 ± 0.11 c	3.60 ± 0.20 c

Means followed by the same letters in the same column are not significantly different at 5% level by Tukey-Kramer test.

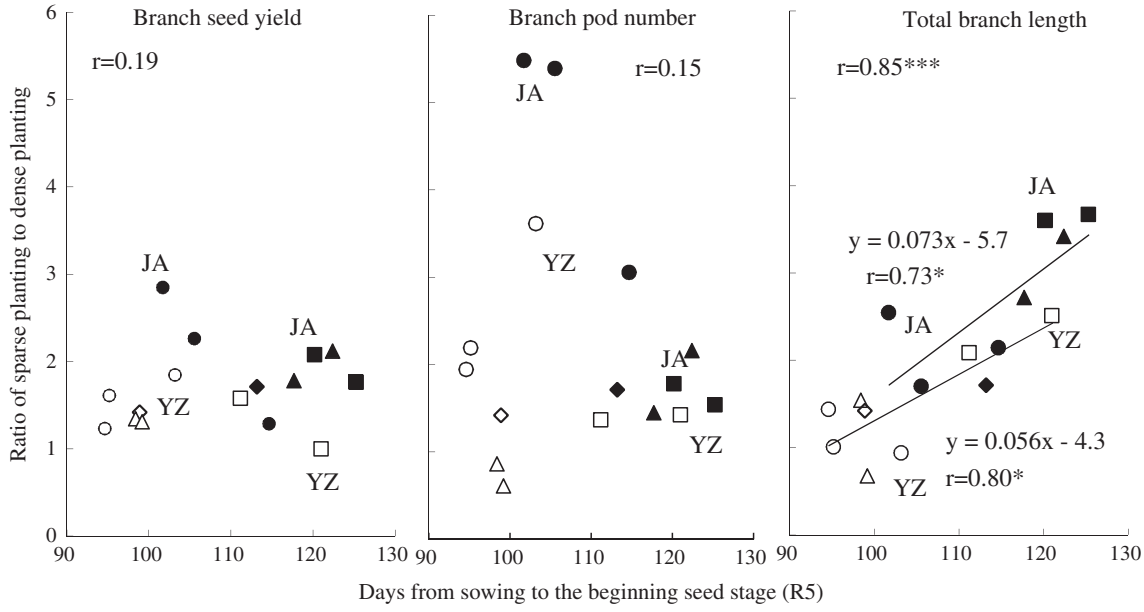

Figure 1. Relationship between days from sowing to the beginning seed filling stage (R5) and ratio of sparse planting to dense planting in branch traits (branching plasticity value) in Exp.1and 2 (2009-2012).
Notes: ◇ , ◆ , △ , ▲, ○, ●, □, ■ indicate Hokkaido, US cultivar in 2009–2012, respectively, †, *, *** indicate significant at the 10, 5, 0.1% levels, respectively. YZ: Yuzuru, JA: Jack.

on branch elongation than on branch occurrence. These results trended to be common as the other experiments on branching plasticity that compared with near isogenic lines of stem growth habit (Agudamu et al., 2015).

Miura and Gemma (1986) and Kuroda et al. (1992) reported varying responses to planting density among Japanese determinate cultivars related to seed size (Kousaka et al., 1995), leaf shape (Sanbuichi & Tsuchiya, 1975), and lodging resistance (Matsunaga et al., 2003). Various responses to planting density have also been reported for different determinate (Board et al., 1990) and indeterminate (Costa et al., 1980; Lehman & Lambert, 1960) cultivars.

The differences in branching plasticity between Japanese and US cultivars may be attributable to factors other than growth habit. This possibility warrants further investigation. Branching plasticity may be affected by a variety of factors including the ability to change branch number, the ability to adapt to different planting densities, the ability to compensate for decreases in yield due to drought stress, low temperatures, and water logging, and the continued suppression of branch growth after the improvement in environmental conditions. As suggested by this study, increasing the branching plasticity of soybean cultivars may enable more stable production. In order to realize future genetic improvements, there is a

need to rapidly assess the branching plasticity of numerous soybean cultivars. It is thus important to develop simple methods for assessing branching plasticity.

The US cultivars tested in this study produced higher yields than Japanese cultivars, particularly under sparse planting densities. This difference in yield response to planting density can be attributed to the fact that, in the US cultivars, branch seed yield increased to a greater degree in response to decreasing planting density, effectively compensating for the decrease in main stem seed yield per unit land area. We evaluated plasticity of branch development (branching plasticity) with the ratio of branch performances under sparse planting to those under dense planting. Although greater branching plasticity was observed in the late-maturing cultivar, some US cultivars exhibited greater branching plasticity even in comparison to Japanese cultivars with similar growth duration. The results of this study suggest that yields of the US cultivars were more consistent across planting densities than those of the Japanese cultivars, due in part to their greater branching plasticity.

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Disclosure statement

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*In Japanese

**In Japanese with English abstract