

Evaluation of High-Yielding Canadian Soybean Cultivars Suited to Japanese Growing Conditions

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Core Ideas

- Five Canadian soybean cultivars achieved high yields in Hokkaido, northern Japan, in screening tests.
- OAC Dorado soybean produced a significantly greater yield than a Hokkaido's leading cultivar.
- OAC Dorado soybean had six characteristics that were distinct from the Hokkaido cultivars.
- OAC Dorado soybean is an important germplasm for high-yield breeding.

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Received 6 Dec. 2018.

Accepted 30 Jan. 2019.

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Agrosyst. Geosci. Environ. 2:180061 (2019)
doi:10.2134/age2018.12.0061

ABSTRACT

The broadening of genetic diversity is essential to improving soybean [*Glycine max* (L.) Merr.] seed yields, and exotic germplasms can be a source of new alleles that improve yield. The stem termination habit is an important trait affecting seed yield in soybean, and this habit can be used to classify soybean into indeterminate, semi-determinate, and determinate phenotypes. The genetic background and environment determine whether indeterminate phenotypes have a higher yield than determinate phenotypes. Most soybean cultivars developed in high latitude countries such as Canada, Switzerland, and Poland have an indeterminate growth habit, but this is not found in any of the commercial Japanese cultivars. This study investigated high-yielding Canadian soybean cultivars growing in Hokkaido, northern Japan. Five Canadian cultivars, Haroson, RCAT Angora, Block, RCAT Alliance, and OAC Dorado, produced significantly greater than Hokkaido's leading cultivar Yukihomare in the preliminary screening tests. OAC Dorado also produced a significantly greater yield than Yukihomare in the trials (116%). OAC Dorado had six characteristics that were distinct from the Hokkaido cultivars: an indeterminate growth habit; high pod number, especially on branches; high seed number per pod; long reproductive period; low protein content; and short lower internodes. Our findings indicate that OAC Dorado is an important germplasm for high-yield breeding and suggest that it may be possible to breed a high-yielding cultivar with an indeterminate growth habit in Hokkaido.

Abbreviations: ANOVA, analysis of variance; DR, soybean cultivar OAC Dorado; TM, soybean cultivar Toyomusume; YH, soybean cultivar Yukihomare.

The broadening of genetic diversity is essential to improving the seed yield of soybean [*Glycine max* (L.) Merr.], and exotic germplasms can be a source of new alleles that improve yield (Kim et al., 2012; Li et al., 2008; Palomeque et al., 2009a, 2009b). The development of high-yielding lines derived from exotic germplasms may provide new genetic diversity to enrich the gene pool, which theoretically could increase the rate of yield increases in soybean cultivars (Nelson and Johnson, 2012).

Seed yields of late-maturing soybean isolines can be greater than seed yields of early maturing isolines (Cober et al., 2010; Yamada et al., 2012). In Hokkaido, northern Japan, the growing period of soybean is restricted because of a short fall season and early snowfall (Yamaguchi et al., 2015). In North America, soybean cultivars have been categorized into 13 maturity groups based on the climate and latitude to which they are adapted (Jia et al., 2014; Zhang et al., 2007). Maturity groups range from 000 for the very early maturing cultivars to X for the latest maturing cultivars. The leading cultivars in Hokkaido belong to maturity groups 0 to I (Yamaguchi et al., 2018). Late-maturing soybean belonging to maturity group I to II are damaged frequently by frost in Hokkaido. In years when the weather is cold, soybean frequently reach maturity later than under normal growth conditions. For example, Hagihara et al. (2003) reported that in 2003 it took an additional 19 to 22 d for soybean to reach maturity compared with warmer years. Therefore, early maturity is an important trait for soybean grown in Hokkaido.

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The stem termination habit is an important trait affecting seed yield in soybean, and this habit can be used to classify soybean into indeterminate, semi-determinate, and determinate phenotypes (Bernard, 1972). The genetic background and environment determine whether indeterminate phenotypes have a higher yield than determinate phenotypes (Cober and Morrison, 2010; Kato et al., 2015). Most soybean cultivars developed in high latitude countries such as Canada, Switzerland, and Poland have an indeterminate growth habit, but this is not found in any of the commercial Japanese cultivars.

We previously reported on Canadian cultivars belonging to maturity groups 00 to I maturing in fields in Hokkaido (Yamaguchi et al., 2018). However, the evaluation of high-yielding Canadian cultivars in Hokkaido has not been performed. Therefore, the objective of this study was to evaluate and identify high-yielding Canadian cultivars growing in Hokkaido.

MATERIALS AND METHODS

Plant Materials

The cultivars used in this study are shown in Table 1. All of the Japanese cultivars had a determinate growth habit, whereas all of the Canadian cultivars had an indeterminate growth habit. Two Japanese cultivars—Yukihomare (YH) and Toyomusume (TM)—were used as control cultivars for early and middle maturity, respectively. Both cultivars were bred at Tokachi Agricultural Experiment Station (Sasaki et al., 1988; Tanaka et al., 2003). The Canadian cultivar

OAC Dorado (DR) was bred at the University of Guelph, Canada (Beversdorf et al., 1991). The seeds of Canadian cultivars were supplied from breeders at Ottawa Research and Development Centre and the University of Guelph.

Field Experiments

Field tests were performed in the fields of Memuro (experimental fields of Tokachi Agricultural Experiment Station; northern latitude of 42°89') and Ebetsu (experimental fields of Rakuno Gakuen University; northern latitude of 43°07') in Hokkaido, Japan. Ebetsu has a warmer climate than Memuro, based on a 30-yr average, with accumulated temperatures from June to September of 2187 and 2087°C, respectively. Both fields had dry Andosol soils, and fertilizer was applied according to Hokkaido fertilization standards (<http://www.pref.hokkaido.lg.jp/ns/shs/clean/sehiguide2015.htm>). At both sites, when the first trifoliate leaves of the seedlings emerged, the seedlings were thinned or transplanted to missing plants to ensure ideal plant stands. The plant population density was 17 plants m⁻². Seed yield was assessed by hand harvest per plot and adjusted to 15% moisture.

In Experiment 1, the field tests were conducted in Ebetsu in 2016 and 2017. Seeds were planted on 13 May 2016 and 15 May 2017. Each cultivar was planted in 2.0-m rows with 60 cm between rows. Each plot had four rows. A randomized complete block design with three replicates was used.

Experiment 2 included yield trials of the three cultivars, YH, TM, and DR, in Memuro in 2015 and 2016. Seeds were planted

Table 1. Preliminary screening of high-yielding cultivars in Experiment 1 (Ebetsu in 2016 and 2017).

Cultivar	USDA no.	Year of release	Maturity group	2016		2017		Mean	
				Maturity d	Seed yield g plant ⁻¹	Maturity d	Seed yield g plant ⁻¹	Maturity d	Seed yield g plant ⁻¹
Japan									
Toyomusume	PI 594301	1985	I	136	20.7	134	23.4	135.3 cd†	22.1 abcd
Yukihomare	–	2001	0	131	18.1	128	18.0	130.0 efg	18.1 defg
Canada									
Haroson	PI 548641	1987	I	140	25.8	132	29.4	136.0 bcd	27.6 a
RCAT Angora	PI 572242	1991	II	150	25.6	132	28.0	141.2 ab	26.8 a
Brock	PI 572241	1991	I	144	24.5	132	28.0	138.2 bc	26.3 ab
RCAT Alliance	PI 548646	1987	I	141	24.4	135	25.4	138.2 bc	24.9 abc
OAC Dorado	PI 567782	1988	I	139	22.6	129	26.8	134.2 cde	24.7 abc
RCAT Persian	PI 548647	1989	I	149	18.9	139	26.4	144.2 a	22.7 abcd
Maple Arrow	PI 548593	1976	00	128	18.9	119	25.5	123.7 hijk	22.2 abcd
Maple Donovan	PI 548642	1986	0	134	17.8	123	25.3	128.7 fgh	21.5 abcd
AC Proteus	–	1993	00	130	20.0	121	20.6	125.7 fghi	20.3 bcd
AC Bravor	–	1990	0	135	18.1	123	21.4	129.2 efg	19.7 cde
Maple Glen	PI 548643	1987	00	130	21.4	119	17.4	124.7 ghij	19.4 cdef
Maple Belle	–	1989	00	130	21.1	131	16.1	131.0 def	18.6 cdef
OAC Scorpio	PI 548640	1986	00	133	16.7	119	19.2	126.2 fghi	18.0 defg
Maple Isle	PI 548595	1984	00	126	16.7	113	16.0	119.7 jk	16.3 defg
Maple Presto	PI 548594	1979	000	117	15.9	108	11.6	112.5 l	13.7 efg
Maple Ridge	PI 548596	1984	00	124	14.4	113	10.4	118.8 k	12.4 fg
AC Harmony	–	1992	00	130	14.6	113	9.7	121.7 ijk	12.2 g
			F value	–	–	–	–	63.10***	13.76***
			Mean	134	19.8	124	21.0	129.1	20.4
			CV, %	6.2	18.0	7.2	29.7	6.5	22.7

*** Significant at $P < 0.001$.

† Means followed by a common letter are not significantly different according to Tukey's HSD test ($P \geq 0.05$).

on 20 May 2015 and 17 May 2016. Each cultivar was planted in 3.5-m (in 2015) or 2.8-m (in 2016) rows with 60 cm between rows, with two (in 2015) or four rows per plot (in 2016). A randomized complete block design with two replicates was used. At the time of maturity, the lodging score was recorded for each plot as: 0 (no lodging) to 4 (completely lodged). Six (in 2015) or eight central consecutive plants (in 2016) were selected from each plot for yield component measurements. Yield components on the main stem and branch were measured separately. The reproductive period was calculated as follows:

$$\text{Reproductive period} = \text{Day to maturity} - \text{Day to flowering}$$

The seed compounds, protein, sugar, and oil, were determined using a near-infrared spectrophotometer (Infratec 1241 Grain Analyzer; FOSS Tecator AB, Höganäs, Sweden).

For Experiment 3, the field tests were conducted in Memuro in 2017 and 2018. The internode lengths of four cultivars DR, Maple Presto, Maple Arrow, and TM were evaluated. Maple Presto and Maple Arrow were selected because their internodes appeared longer than the other indeterminate cultivars and lodged easily on field observations. Seeds were planted on 18 May 2017 and 22 May 2018. Each cultivar was planted in 1.2-m (in 2017) or 3.5-m (in 2018) rows with 60 cm between rows. Each plot had one row (in 2017) or two rows (in 2018). A randomized complete block design with two replicates was used. At the time of maturity, five central consecutive plants were selected from each plot. The first to sixth internode lengths on the main stems were measured, and each internode length was compared. Average internode lengths were calculated as follows:

$$\text{Average internode length} = \frac{\text{Main stem length}}{\text{No. of internodes on main stem}}$$

Statistical Analysis

A combined analysis of variance (ANOVA) was performed using the mixed model procedure of the JMP 10 statistical package (SAS, Cary, NC, USA). Statistical significance was evaluated at $P \leq 0.05$, unless otherwise stated. Years and replications within year were considered random effects, whereas cultivars were considered fixed effects in all experiments. In Experiment 3, the data of individual plants from each plot were treated as repeated measurements ($n = 5$). When the ANOVA showed a significant effect ($P \leq 0.05$), Tukey's HSD test at $P = 0.05$ was used to confirm the differences among cultivars.

RESULTS

Preliminary Screening for High-Yield Cultivars in Ebetsu (Experiment 1)

The field tests for preliminary screening were conducted in Ebetsu (Table 1). There were significant differences among the cultivars with respect to maturity and seed yield ($P < 0.001$). The five Canadian cultivars Haroson, RCAT Angora, DR, RCAT Alliance, and Brock produced significantly greater yield than YH (Table 1). No cultivars produced a significantly greater yield than TM, but the seed yields of these five cultivars were numerically higher than that of TM (Table 1). The cultivars that matured later than YH are frequently damaged by frost in Hokkaido (Yamaguchi et al., 2015). Haroson, RCAT Angora, RCAT Alliance, and Brock matured

significantly later than YH (Table 1). In contrast, DR consistently matured later than YH, but it was not statistically later (Table 1). Therefore, it was determined that DR had the most yield potential and it was advanced to the further trials in Memuro (Experiment 2). Further tests are needed to clarify whether the other four cultivars, Haroson, RCAT Angora, RCAT Alliance, and Brock, show high yields in Ebetsu.

Yield Trials for a High-Yielding Cultivar in Memuro (Experiment 2)

The yield trials of DR were conducted in Memuro. Representative plants from the yield trial in 2016 are shown in Fig. 1. There were significant differences in agronomic traits among cultivars, except for lodging score (Tables 2 and 3). The DR cultivar flowered significantly earlier than YH and TM, and matured significantly earlier than TM, but later than YH (Table 2). Therefore, the reproductive period was significantly longer in DR than in YH and TM (Table 2). The seed yield of DR was significantly greater than that of YH (Table 2). The yield of DR was 116% of that of YH, and 109% of that of TM. Focusing on yield components, DR had more branches than YH and TM (Table 2), and a significantly higher node number than YH and TM, especially on the branches (Table 3). The DR pod number was also significantly greater than that of YH (143%) and TM (137%) (Table 3). In particular, DR had more pods on its branches than YH (192%) and TM (147%). The seed number per pod was significantly greater in DR than in YH (132%) and TM (125%) (Table 3). In contrast, the 100-seed weight of DR was significantly less than those of YH (59%) and TM (55%) (Table 3). Thus, the high-yield performance of DR can be attributed to a high pod number, especially on branches, and a high seed number per pod.

The main stem length of DR was significantly longer than those of YH and TM, but their lodging scores were similar (Table 2). The control of soybean internode extension is important to avoid seed yield reduction caused by lodging (Oki et al., 2018; Umezaki and Yoshida, 1992). In the next field experiment, internode lengths of DR were compared with other indeterminate cultivars (Experiment 3).

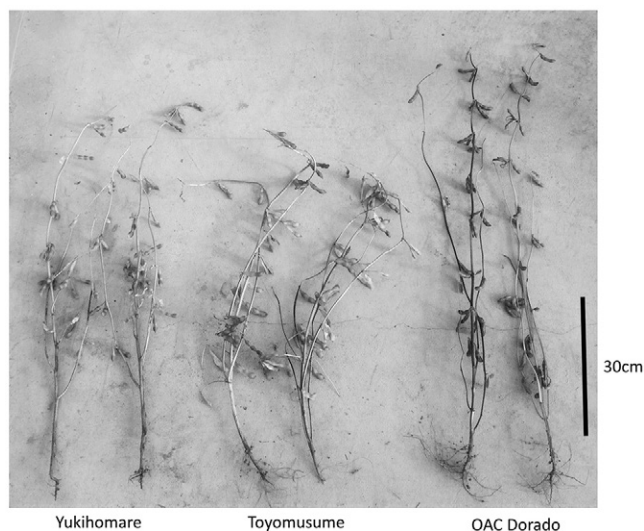


Fig. 1. Representative plants from the yield trial at Memuro in 2016 (Experiment 2). The photograph was taken after harvesting.

Comparison of Lower Internode Lengths between Four Cultivars (Experiment 3)

The results of Experiment 3 are shown in Fig. 2. There were significant differences among cultivars for the first to third internode lengths, whereas there were no significant differences for the fourth to sixth internode lengths. The first internode length of DR was significantly shorter than those of the other three cultivars, Maple Presto, Maple Arrow, and TM. The second and third internode lengths of DR were significantly shorter than those of Maple Arrow and TM. The average internode length of DR was significantly shorter than those of Maple Presto and Maple Arrow. Thus, there are varietal differences in internode lengths, especially for the first and third internodes, among indeterminate cultivars.

DISCUSSION

In the yield trials in Ontario, Canada, the DR yield was greater, at 105 to 108%, than those of the control cultivars (Beverdorsdorf et al., 1991). In this study, the seed yield of DR was significantly greater than that of YH (116%), and the high-yield performance of DR could be attributed to a high pod number, especially on branches, and a high seed number per pod (Tables 2 and 3). In our previous study, US cultivars with indeterminate growth habits produced greater yield than Japanese cultivars, particularly under sparse planting densities in Hokkaido, and their high-yield performances were attributed to greater branch pod numbers (Agudamu et al., 2016). We speculate that branch pod number may be an important factor of high-yield performances in Hokkaido.

Table 2. Agronomic traits in the yield trails of Experiment 2 (Memuro in 2015 and 2016).

Cultivar	Time to flowering	Time to maturity	Reproductive period	Main stem length	Branch no. per plant	Lodging score†	Seed yield	Seed compounds		
								Protein	Sugar	Oil
	d			cm			t ha ⁻¹	%		
2015										
Yukihomare	55.0	123.0	68.0	63.5	3.2	0.0	3.69	41.1	23.2	19.9
Toyomusume	56.0	133.0	77.0	61.5	3.6	0.0	4.05	43.0	23.6	18.6
OAC Dorado	49.5	128.0	78.5	91.5	4.3	1.5	4.38	37.9	22.2	21.5
2016										
Yukihomare	64.0	136.0	72.0	81.5	2.5	3.0	3.17	44.0	22.2	19.8
Toyomusume	65.0	143.0	78.0	74.0	4.0	4.0	3.23	44.2	22.2	19.5
OAC Dorado	55.0	139.5	84.5	99.5	4.0	2.5	3.55	40.6	20.3	21.4
Mean‡										
Yukihomare	59.5 a	129.5 c	70.0 c	72.6 b	2.8 b	1.5	3.43 b	42.5 a	22.7 a	19.8 b
Toyomusume	60.5 a	138.0 a	77.5 b	67.7 b	3.8 a	2.0	3.64 ab	43.6 a	22.9 a	19.0 b
OAC Dorado	52.3 b	133.8 b	81.5 a	95.2 a	4.1 a	2.0	3.97 a	39.2 b	21.2 b	21.4 a
F value	49.47***	57.80***	42.31***	67.92***	15.97**	0.38 ns§	5.72*	38.41***	21.00**	32.58***

* Significant at $P < 0.05$.

** Significant at $P < 0.01$.

*** Significant at $P < 0.001$.

† Lodging score: 0 (no lodging) to 4 (completely lodged).

‡ Means followed by a common letter are not significantly different according to Tukey's HSD test ($P \geq 0.05$).

§ ns, not significant.

Table 3. Yield components in the yield trails of Experiment 2 (Memuro in 2015 and 2016).

Cultivar	Node no. per plant			Pod no. per plant			Seed no. per pod			100-seed wt.		
	Main stem	Branch	Total	Main stem	Branch	Total	Main stem	Branch	Mean	Main stem	Branch	Mean
	g											
2015												
Yukihomare	10.8	15.4	26.2	20.3	14.9	35.2	1.77	1.90	1.83	33.9	34.3	33.9
Toyomusume	9.7	16.3	25.9	15.5	15.0	30.5	2.06	1.88	1.97	40.1	39.2	39.7
OAC Dorado	14.2	23.1	37.3	20.0	27.0	47.0	2.64	2.36	2.48	21.1	19.6	20.3
2016												
Yukihomare	11.8	11.2	23.0	18.8	11.3	30.1	1.63	1.53	1.60	38.9	37.9	38.5
Toyomusume	10.4	18.0	28.4	18.5	19.4	37.9	1.64	1.62	1.63	38.8	37.2	38.0
OAC Dorado	14.3	21.9	36.2	23.0	23.7	46.7	2.09	1.96	2.02	23.0	21.5	22.3
Mean‡												
Yukihomare	11.3 b	13.3 b	24.6 b	19.6 ab	13.1 b	32.7 b	1.70 b	1.71 b	1.71 b	36.4 a	36.1 a	36.2 a
Toyomusume	10.0 c	17.2 b	27.1 b	17.0 b	17.2 b	34.2 b	1.85 b	1.75 b	1.80 b	39.4 a	38.2 a	38.8 a
OAC Dorado	14.3 a	22.5 a	36.7 a	21.5 a	25.3 a	46.8 a	2.36 a	2.16 a	2.25 a	22.0 b	20.6 b	21.3 b
F value	91.74***	24.95**	43.76***	7.44*	13.09**	13.84**	20.32**	29.98***	43.57***	62.42***	64.17***	60.75***

* Significant at $P < 0.05$.

** Significant at $P < 0.01$.

*** Significant at $P < 0.001$.

† Means followed by a common letter are not significantly different according to Tukey's HSD test ($P \geq 0.05$).

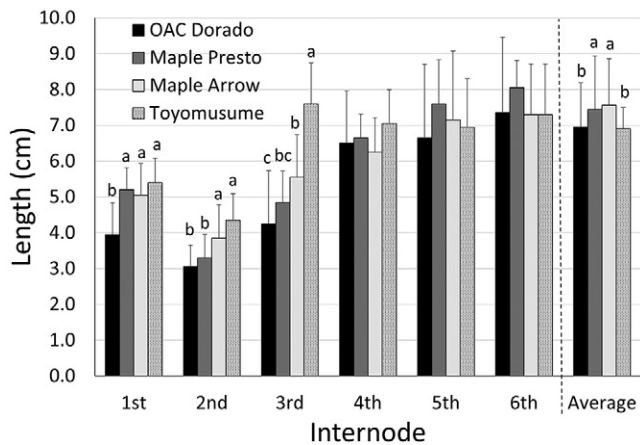


Fig. 2. Comparison of internode lengths among the four cultivars at Memuro in 2017 and 2018 (Experiment 3). The three Canadian cultivars OAC Dorado, Maple Presto, and Maple Arrow have indeterminate growth habits, whereas the Hokkaido cultivar Toyomusume has a determinate growth habit. The error bars indicate standard errors. Means for each internode followed by a common letter are not significantly different according to Tukey's HSD test ($P \geq 0.05$).

Appropriately balancing between pre- and post-flowering periods may result in a high-yield performance (Cober and Morrison, 2010). In this study, DR flowered significantly earlier than YH and TM, and matured significantly earlier than TM but later than YH (Table 2). The long reproductive period may be an important factor in the high-yield performance of DR. In total, 10 maturity genes *E1* to *E10* controlling flowering time and maturity have been identified in soybean (Bernard, 1971; Bonato and Vello, 1999; Buzzell, 1971; Buzzell and Voldeng, 1980; Cober and Voldeng, 2001; Cober et al., 2010; Kong et al., 2014; McBlain and Bernard, 1987; Samanfar et al., 2017). The *E2* and *Dt1* alleles delayed maturity compared with the *e2* and *dt1* alleles, respectively (Cober and Morrison, 2010; Yamada et al., 2012). The DR cultivar has the indeterminate allele *Dt1*, whereas TM has the determinate allele *dt1* based on phenotypic evaluation. Hokkaido cultivars, including TM, carry the recessive allele *e9*, which promotes late flowering, whereas Canadian cultivars carry the dominant allele *E9*, which promotes early flowering (Kong et al., 2014; Zhao et al., 2016). According to the web database SoySNP50K in SoyBase (<https://soybase.org/snps>; Song et al., 2013) and previous reports (Tsubokura et al., 2014; Zhao et al., 2016), the maturity genotypes of TM and DR were estimated as *e2/e9/dt1* and *E2/E9/Dt1*, respectively. The genotypes of the other major maturity genes *E1* and *E3* were estimated to be the same, *e1-ml/E3*, in TM and DR. Therefore, we hypothesize that *E2*, *E9*, and *Dt1* are involved in the long reproductive period of DR. More precise analyses of maturity genes in DR are required for future marker-assisted selection.

In the yield trials in Ontario, Canada, the DR lodging score was lower than those of the control cultivars (Beversdorf et al., 1991). The control of soybean internode extension is important to avoid lodging (Umezaki and Yoshida, 1992). In this study, the lodging scores of YH, TM, and DR were similar (Table 2), and the average internode length of DR was significantly shorter than those of the other indeterminate cultivars (Fig. 2). Shading treatments during the growth period promote internode extension (Umezaki and Yoshida, 1992). The number of solar irradiation hours in Hokkaido is less than that in Canada during the soybean growth period (Yamaguchi, 2017). The average accumulated solar irradiation hours from June to

September in Memuro and Ottawa, ON, Canada over a 30-yr period, were 545 and 1019 h, respectively. Therefore, the low solar irradiation intensity in Hokkaido may cause lodging by increasing the internode length. In this study, the first to third internode lengths of TM were significantly longer than those of DR (Fig. 2). This may indicate that vigorous early growth is an important factor for high-yielding determinate cultivars in Hokkaido. Conversely, we speculate that short lower internode lengths may be an important factor for high-yielding indeterminate cultivars in Hokkaido because the frequency of lodging is high in Hokkaido. Further studies are required to clarify the mechanism of DR lodging resistance.

Soybean seed protein content is an important trait in Japanese breeding programs because it is associated with the breaking stress of tofu (Toda et al., 2003). In this study, the protein and sugar contents of DR were significantly lower than those of YH and TM, whereas the oil content of DR was greater (Table 2). Previous studies reported that the protein content and yield were negatively correlated (Hartwig and Hinson, 1972; Wehrmann et al., 1987; Wilcox and Zhang, 1997). Therefore, we speculate that a low protein content may be a factor in the high-yield performance of DR.

Exotic germplasms can be sources of new alleles to improve yield (Kim et al., 2012; Li et al., 2008; Palomeque et al., 2009a, 2009b), and our results indicate that DR could be an important germplasm for high-yield breeding in Hokkaido. In conclusion, this study revealed that DR is a high-yield cultivar in Hokkaido. Our findings indicate that DR is an important germplasm for high-yield breeding and suggest that it may be possible to breed a high-yielding cultivar with an indeterminate growth habit in Hokkaido.

ACKNOWLEDGMENTS

We thank Dr. E.R. Cober from the Ottawa Research and Development Centre in Canada for helpful discussions, and Dr. H.D. Voldeng and Dr. J.W. Tanner for supplying the seeds of the Canadian cultivars. We thank Lesley Benyon, Ph.D., and Sarah Williams, Ph.D., from Edanz Group (www.edanzediting.com) for editing a draft of this manuscript.

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