

**Elucidation of High Yielding Soybean Characteristics through
Comparison of Biomass Production Dynamics between Japanese and
US Cultivars**

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Contents

Summary	1
Chapter 1 Introduction	
1.1 Increase in soybean production and future demand	5
1.2 Difference in soybean productivity between US and Japan	5
1.3 Key factors causing improvement in productivity	6
1.4 The objectives of this study	7
Chapter 2 Yield and Dry Matter Productivity of Japanese and US Soybean Cultivars	
2.1 Introduction	9
2.2 Materials and methods	
2.2.1 Location and environments	11
2.2.2 Plant materials	12
2.2.3 Measurements	14
2.2.4 Analysis	15
2.3 Results	16
2.4 Discussion	24
2.5 Conclusions	33
Chapter 3 Yield and Dry Matter Productivity of Japanese and US Soybean Cultivars in Response to Drought	
3.1 Introduction	34
3.2 Materials and methods	35
3.3 Results and discussion	37
Chapter 4 Dry Matter Dynamics and Partitioning to Reproductive Organs during Seed Filling Period in Japanese and US Soybean Cultivars	
4.1 Introduction	43
4.2 Materials and methods	
4.2.1 Field experiment at Azuchi in 2011	44
4.2.2 Field experiment at Takatsuki in 2012 and 2013	45
4.3 Results	
4.2.1 Field experiment at Azuchi in 2011	46
4.2.2 Field experiment at Takatsuki in 2012 and 2013	51
4.4 Discussion	58
4.5 Conclusions	63

Chapter 5 General Discussion

5.1	Improvement in soybean yield	64
5.2	Possible plant traits for breeding suggested in this research	65
5.3	Subject for further study	66
5.4	Conclusions	67

Acknowledgements	68
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References	69
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List of Publications	82
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Summary

The difference in yields of cultivars may be causing difference in soybean yield between Japan and the United States (US). The objective of this study was to identify the effect of the cultivar on dry matter production and to reveal the key factors causing the differences in yield by focusing utilization of solar radiation in recent Japanese and US soybean cultivars. To evaluate the amount of solar radiation intercepted, digital image analysis was established. Field experiments were conducted during two seasons in Takatsuki, Japan (34°50'N), and in a single season in Fayetteville (36°04'N), AR, US. Five Japanese and ten US cultivars were observed under near optimal conditions in order to achieve yields as close to their physiological potential as possible. The seed yield and total above ground dry matter (TDM) were measured at maturity as long as radiation was intercepted by the canopy. The seed yield ranged from 3.10 t ha⁻¹ to 5.91 t ha⁻¹. Throughout the three environments, the seed yield of US cultivars was significantly higher than that of Japanese cultivars. The seed yield correlated with the TDM rather than the harvest index (HI) with correlation coefficients from 0.519 to 0.928 for the TDM versus 0.175 to 0.800 for the HI, for each of the three environments. The higher TDM of US cultivars was caused by a higher radiation use efficiency rather than higher total intercepted radiation throughout the three environments. The seasonal change in the TDM observed in four cultivars indicated that dry matter productivity was different between cultivars specifically during the seed filling period.

While the high yield ability of US cultivars was confirmed under optimum soil condition, it cannot say that these results reflecting the yielding ability in farmers' field. The drought was one of the most limiting factor of the productivity of soybean. Two

representative cultivars were tested under drought during reproductive stage and compared yield and yield components. Yield and TDM was higher in US cultivars not only in optimum condition but also in drought. A significant cultivar by environment interaction was observed in HI. The HI of tested US cultivar did not tend to decrease under drought.

During seed filling period, soybean abscises almost all of the leaves and petioles. Considering abscised leaves and petioles, the actual dry matter production and dry matter distribution was analyzed. Two Japanese and two US cultivars were cultivated at Shiga Prefecture Agriculture Promoting Center in two different sowing dates. And seven Japanese and eight US cultivars were tested in Takatsuki in two years. Litter trap was settled between the plants and abscised leaves and petioles were collected. No significant difference was observed between US and Japanese cultivars in actual TDW (TDM accumulation at maturity including abscised leaves and petioles). On the other hand, actual HI (including abscised leaves and petioles) was significantly higher in US cultivars and the extent of the difference between US and Japanese cultivars was larger than apparent HI (not including abscised leaves and petioles). In Takatsuki the change in crop growth rate (CGR) and dry matter distribution ratio to pods were analyzed. The difference in CGR from R5 to 30d after R5, US cultivar group showed greater value of average than Japanese cultivar group. However, CGRs for the periods from emergence to R5 and from 30d after R5 to R8 did not differ between cultivar groups. The effect of cultivar group significant for pod distribution ratio from emergence to R5 and pod growth rate from R5 to 30d after R5 in which US cultivar group showed greater value of average than that of Japanese cultivar group. No significant difference was observed in pod distribution ratio from R5 to 30d after R5 between cultivar groups.

Across all environments, the US cultivar group exhibited greater yielding ability than Japanese cultivar group. Under optimum soil condition, high yield of US cultivars related to the amount of total above ground dry matter. Under drought, however, high yield of US cultivar related to stability of HI. To narrow the breeding target, “actual HI” including abscised leaves and petioles collected during seed filling period was investigated. US cultivars showed greater actual HI than Japanese cultivars. These results indicate that the US cultivars are genetically improved in yielding ability for a range of environments. This also suggests that Japanese soybean cultivars would possibly be improved introducing plant traits from US cultivars.

Chapter1

Introduction

1.1 Increase in soybean production and future demand

Soybeans (*Glycine max* (L.) Merrill) are an important crop for protein and oil. Soybean originated from east Asia (Kokubun, 2001), and now widely cultivated all over the world. The amount of global soybean production constantly increased and reached to 300 million metric tons, and most of them are produced in the United States (US), Brazil, Argentina and China (USDA-FAS, 2016). At the same time, the demand of soybean increased due to the increasing in human population, dietary changes, and industrial consumption (Foley et al., 2011). However, the land area suitable for cultivating soybean is limited and further improvement in yield is required (Ainsworth et al., 2012). The global rate of yield increase in soybean will need to almost double to meet the population demands predicted for 2050 (Ray et al., 2013).

1.2 Difference in soybean productivity between US and Japan

US is the largest country in soybean production (USDA-FAS, 2016). The productivity of soybeans, soybean production per unit area in the US has increased steadily over the last 50 years, and the average rate of yield increase was 31.4 kg ha⁻¹ year⁻¹ (Specht et al., 1999). On the other hand, soybean productivity in Japan is stagnating and the yield gap between Japan and the US is increasing (Katsura et al., 2009). The increase of soybean productivity is explained by both genetic and management improvement (Specht et

al.,1999; Salvagiotti et al., 2008). However, the information which can explain the difference of productivity between Japan and US is quite limited. The management could be one reason to explain the difference between US and Japanese soybean productivity. In mid-southern US, early soybean production system (ESPS) contributed to stabilize the yield through avoidance of summer drought (Bowers, 2013). In Japan, more than 80% of soybean is grown at converted paddy field and tends to suffer from excess moisture injury in early growing season and drought in reproductive stage (Shimada et al., 2012). That may be causing fluctuation in soybean production in Japan. The commercial use of gene modified cultivars also could be an important factor of difference between US and Japan. Gene modified cultivars are mainly used commonly in US and countries in South America (Ainsworth et al., 2012; Xu et al., 2013). More than 90% of gene modified soybean cultivars are tolerant to herbicide (Ainsworth et al., 2012). The combination of herbicide use and no-till plant management prevented field from soil erosion and herbicide tolerant soybean cultivars helped farmers to reduce labor and management (Dill et al., 2008). However in US, non-Gene modified cultivars are still cultivated because gene modified soybean is generally used as forage crop and is not accepted to consumers as food crop. In Japan soybean is cultivated for food, but more than 75% is imported in 2012 (Ministry of Agriculture, Forestry and Fisheries, 2015). Improvement in productivity of soybean in Japan is necessary for food security.

1.3 Key factors causing improvement in productivity.

To reveal the key factor causing improvement in productivity, a number of studies which compared old and new soybean cultivars were conducted. Voldeng et al. (1997)

compared old and new cultivars and reported the improvement in lodging tolerance. Soybean yield can be explain by multiplication of harvest index and total dry matter as a yield components. Morrison et al. (1999) reported the increase in seed yield with year of release was significantly correlated with an increase in harvest index, photosynthesis, stomatal conductance. Kumudini et al. (2001) quantified the contribution of the effect of improvement in harvest index and total dry matter in the maturity group (MG) 00 and MG0 in Canada, and reported that the increased dry matter accumulation contributed 78% and increased harvest index (HI) contributed 22% towards the genetic gains in yield. De Bruin and Pedersen (2009) compared the change in total above ground dry weight between old and new cultivars and found that the difference in total above ground dry weight occurred in the seed filling stage. In Japan, Shiraiwa et al. (1994), compared old and new cultivars in Japan and reported improvement in solar radiation use efficiency in seed filling period. Jin et al. (2010) compared old and new cultivars in north east China and reported improvement in photosynthesis and harvest index.

1.4 The objectives of this study

The objective of this study was to identify the key factor which plays an important role for improving the productivity of soybean. To achieve this objective, recent representative US and Japanese soybean cultivars were tested and compared.

In chapter 2, productivity of US and Japan in worm region was compared in terms of solar radiation use using recent representative US and Japanese soybean cultivars. The cross-location experiment was conducted between Fayetteville, AR, US and Takatsuki, Osaka, Japan. The growth condition was adjusted to near optimum condition to get

potential seed yield. Then the potential productivity was compared.

In chapter 3, seed yield and dry matter production of US and Japanese soybean cultivars was compared under drought environment. It is reported that recent US soybean cultivars were tend to have higher stomatal density and higher potential stomatal conductance (Tanaka et al., 2008). The comparison in chapter 2 was conducted only under optimum condition and still not enough to explain the gap of soybean productivity between US and Japan because farmers' fields tend to suffer from drought stress due to economical reason. The hypothesis that US cultivars lost more water as compared with Japanese soybean cultivars and less tolerant to drought was tested.

Based on the result of chapter 2, US soybean cultivars showed higher yield and dry matter productivity than that of Japanese soybean cultivars. In chapter 4, to look for the key factor causing the difference of the yield of Japanese and US soybean cultivars, dry matter dynamics during seed filling period was measured. Abscised leaves and petioles after initial seed filling period (R5 stage) were collected. The ratio of seed yield and total above ground dry matter including abscised leaves and petioles was measured (Actual HI). And crop growth rate from emergence to R5 stage, from R5 stage to 30d after R5stage and from 30d after R5 stage to maturity were measured.

In chapter 5, all the results of experiment were integrated and the important trait as a breeding target to achieve high yield was discussed.

Chapter 2

Yield and Dry Matter Productivity of Japanese and US Soybean Cultivars

2.1 Introduction

Soybean productivity in Japan is stagnating and the yield gap between Japan and the US is increasing (Katsura et al., 2009). In this chapter, the limiting factor of soybean productivity in Japan was discussed.

Genetic improvement could be an important factor for the increasing productivity gap between Japan and the US. Improvements in soybean yields are explained by greater TDM accumulation or an increase in the HI (Morrison et al., 1999; Kumudini, 2002; Jin et al., 2010). Kumudini et al. (2001) compared new and old soybean cultivars in the MG00 and MG0 in Canada, and reported that the increased dry matter accumulation contributed 78% and increased HI contributed 22% towards the genetic gains in yield. De Bruin and Pedersen (2009) compared new and old soybean cultivars in Iowa and reported that new cultivars produced higher yields as a result of improved TDM accumulation. In Japan also dry matter productivity differs among cultivars (Shiraiwa et al., 2004), but improvement of seed yield has not been clearly demonstrated. In a study (Okabe et al. 2006), though the lodging resistance of recently released cultivars was significantly improved, no advantage in yield was recognized in recently released cultivars as compared with old cultivars.

The meteorological environment could also be an important factor for high yields. TDM correlates with solar radiation (Shibles and Weber, 1966; Monteith, 1977).

Katsura et al. (2008) compared rice productivity between Yunnan, China and Kyoto, Japan through a cross-location experiment and revealed that the high potential yield of irrigated rice in Yunnan is achieved mainly by the intense incident solar radiation. Katsura et al. (2013) compared the meteorologically possible yields of soybean at four locations between the US and Japan, and reported that the potential yields of soybean in Illinois, Arkansas, Hokkaido and Shiga were 7 t ha⁻¹, 8 t ha⁻¹, 5 t ha⁻¹ and 6 t ha⁻¹, respectively. High potential yields estimated in two locations in the US are mainly due to higher solar radiation. Solar radiation in Illinois and Arkansas is over 30% higher than that in Hokkaido and Shiga. The amount of solar radiation intercepted during the seed filling period is important for seed yield, especially in soybeans (Board, 2004; Shiraiwa et al., 2004). However, information on the direct comparison of yield and dry matter production during growing season between US and Japanese soybean cultivars is very limited.

The radiation use efficiency (RUE), the amount of dry matter produced per unit of solar radiation intercepted, is a good trait to express dry matter productivity (Sinclair and Horie, 1989; Shiraiwa and Hashikawa, 1993; Loomis and Amthor, 1999; Sinclair and Muchow, 1999). The effects of the cultivar and the solar radiation environment can be distinguished by measuring the RUE. Shiraiwa et al. (1994) found a considerable variability of RUE among old and new Japanese cultivars. There is a possibility that differences in the RUE may exist between US and Japanese recent cultivars. As a trait related to photosynthesis, Tanaka et al. (2010) reported the diversity in the potential stomatal conductance of soybeans calculated from morphological traits of leaves. The morphologically determined potential of stomatal conductance is higher in US cultivars than in Japanese cultivars, and this result suggests that US soybean cultivars have a

greater capacity for photosynthesis and dry matter production. Direct comparison of solar radiation use is lacking for recent commercial cultivars, regardless of the great need to understand the physiological potential of soybean productivity in Japan and the US.

The objective of this study is to compare the potential productivity of soybean cultivars derived from the US and Japan under optimum growing conditions in reference to yield and dry matter production. If they differed, we then tried to note the key factor related to the difference in the yield and dry matter productivity in reference to solar radiation utilization.

2.2 Materials and methods

2.2.1 Location and environments

Field experiments were conducted at two locations in 2009: the Experimental Farm, Kyoto University, Takatsuki, Osaka, Japan (34°50'N) and the Experimental Farm, University of Arkansas, Fayetteville, AR, US (36°04' N). In 2010, the experiment was repeated only in Takatsuki. The experimental plots were managed under conventional conditions, with which soybean performance had been observed at the respective sites. Soybean seeds were sown in a converted paddy field (a clay loam soil, Eutric Fluvisols) after adding fertilizers (NH_4 : P_2O_5 : K_2O = 3: 10: 10 g m⁻²) in Takatsuki in both years, and in an upland field (fine-silty, mixed, active, mesic Mollic Paleudalfs) after fertilization (Zn: P: K = 1.12: 4.9: 14.9 g m⁻²) according to the soil test in Fayetteville. The planting density was 0.7 by 0.15 m in Takatsuki and 0.15 to 0.20 by 0.19 m in Fayetteville. There were 3 replications in Takatsuki and 4 in Fayetteville, which were

arranged in a completely randomized block design. Furrow irrigation was used to avoid drought stress. Weeding and the spraying of agrochemicals were conducted to maintain optimal conditions.

2.2.2 Plant materials

The cultivars were chosen from recent major non-GM cultivars in both regions. The cultivar entries and year of release, stem growth habit type were shown in Table 2.1 (Buss et al., 1988; Kenworthy et al., 1996; Wilcox and Abney, 1997; Nickell et al., 1998; Pantalone et al., 2003; Chen et al., 2004; Pantalone et al., 2004; Chen et al., 2006; Diers et al., 2006; Chen et al., 2007; Rincker et al., 2015; Ministry of Agriculture, Forestry and Fisheries, 2015). In 2009, five Japanese cultivars (Suzukari, Suzuyutaka, Enrei, Tachinagaha and Tamahomare) and ten US cultivars (Athrow, Omaha, LD00-3309, Manokin, 5002T, UA-4805, Osage, 5601T, Ozark and Hutcheson) were grown in Takatsuki. In Fayetteville, two Japanese cultivars (Tachinagaha and Tamahomare) and seven US cultivars (Manokin, 5002T, UA-4805, Osage, 5601T, Ozark and Hutcheson) were grown. The sowing date was 16th June in Takatsuki and 2nd June in Fayetteville. In 2010, 5 Japanese cultivars (Suzukari, Suzuyutaka, Enrei, Tachinagaha and Tamahomare) and the same 10 US cultivars were sown on July 7th in Takatsuki.

Table 2.1.Cultivar entries, year of release and stem growth habit type.

	Cultivar	Year of release	Stem growth habit type
Jpn cvs.	Enrei	1971	Determinate
	Suzukari	1985	Determinate
	Suzuyutaka	1982	Determinate
	Tachinagah	1986	Determinate
	Tamahomai	1980	Determinate
US cvs.	Athow	1996	Indeterminate
	Omaha	1996	Indeterminate
	LD003309	2005	Indeterminate
	Manokin	1991	Determinate
	5002T	2002	Determinate
	UA-4805	2005	Determinate
	Osage	2007	Determinate
	5601T	2001	Determinate
	Ozark	2004	Determinate
	Hutcheson	1987	Determinate

2.2.3 Measurements

Meteorological data (daily solar radiation and temperature) were recorded. In 2009, daily solar radiation and daily temperature were measured by QMS101 and QMH101 (VAISALA, Tokyo), respectively. In 2010, solar radiation meter (LI200X Pyranometer, Li-COR, Lincoln, NE) was used to estimate daily solar radiation and daily temperature was measured by HMP45C (Campbell Scientific, INC., Logan, UT). Growth stages (R1, R5, R7 and R8) were recorded according to Fehr et al. (1971). Canopy coverage was measured following Purcell (2000) to estimate the fraction of radiation intercepted. Canopy coverage was measured one or two times a week.

The seed yield (Yield), TDM and HI were measured at R8. Seed moisture content was measure and converted into 14%. 1.26 m² was harvested from one replication in Takatsuki and 4.35 m² was harvested from one replication in Fayetteville. If leaves and petioles were attached to the plant at R8, they were included in the TDM. The dry matter was measured after drying with the oven for 72 hr at 80°C.

The change in the TDM during growing season was measured in Takatsuki in 2009 and 2010. Two Japanese cultivars (Tachinagaha and Tamahomare) and two US cultivars (UA-4805 and 5601T) were harvested in 2009 as the representatives of each groups. Plant materials were harvested at R5, 20 d after R5 of the respective cultivars in 2009. In addition, simultaneous sampling of four cultivars was done 33, 52 and 75 d after emergence (DAE). At the 33DAE sampling, four plants per replication were harvested. After 33DAE sampling, six plants per replication were harvested. In 2010, only Tachinagaha and UA-4805 were harvested at 35, 47, 61 and 74DAE. 12 plants per replication were harvested in 2010.

2.2.4 Analysis

The equation shown below was used to analyze the yield formation.

$$\begin{aligned} Y &= HI \times TDM \\ &= HI \times \overline{RUE} \times \bar{F} \times I \end{aligned}$$

Y, HI and TDM are the seed yield (g m^{-2}), harvest index and total aboveground dry matter (g m^{-2}) at R8, respectively. $\overline{RUE}$, $\bar{F}$ and I are the mean solar radiation use efficiency of the whole growth duration (from emergence to physiological maturity, R7) (g MJ^{-1}), the mean fraction (mean F) of radiation intercepted during the whole growth duration, and the incident accumulated solar radiation (MJ). The mean fraction of radiation intercepted ($\bar{F}$) during whole growth duration was estimated by digital images taken above the canopy (Purcell, 2000) two times a week during growing season. Then the daily fraction of the solar radiation was estimated by interpolation and averaged. The incident accumulated solar radiation (I) was calculated from daily meteorological data. The mean solar radiation use efficiency ($\overline{RUE}$) of the whole growth duration was estimated by TDM, $\bar{F}$, I, and Y.

The effect of the cultivar group (2 Japanese cvs. vs 7 US cvs.) and environment were analyzed for 9 medium maturing cultivars in three environments, Takatsuki in 2009 and 2010 and Fayetteville in 2009 using analysis of variance (ANOVA). In addition, the effect of the cultivar group (3 Japanese cvs. vs 3 US cvs.) and the environment were analyzed separately for 6 early maturing cultivars in Takatsuki in 2009 and 2010 using ANOVA. All these statistical analysis were conducted using Microsoft Excel (Microsoft, Redmond, WA, US).

2.3 Results

Table 2.2 shows the daily average temperature and solar radiation. The average daily radiation of the whole growth duration was larger in Fayetteville ($17.8 \text{ MJ m}^{-2}\text{d}^{-1}$) relative to Takatsuki (17.0 and $17.0 \text{ MJ m}^{-2}\text{d}^{-1}$ in 2009 and 2010, respectively). In the early growth stage, from June to July, the daily solar radiation in Takatsuki is lower than in Fayetteville over the two years because of the rainy season in Japan. The average daily temperature throughout the whole growth duration was 23.6°C and 25.2°C in Takatsuki in 2009 and 2010, respectively, and 21.9°C in Fayetteville in 2009. These averages of whole growing season were similar between three environments, although the monthly averages somewhat differed with higher temperature in June at Fayetteville in 2009 and July and August at Takatsuki in 2010. However, the temperature in Fayetteville decreased rapidly from September to October compared to Takatsuki.

Table 2.2. Air temperature and solar radiation by month.

	2009		2010
	Takatsuki	Fayetteville	Takatsuki
Daily average radiation ($\text{MJ m}^{-2} \text{d}^{-1}$)			
Jun	20.0	21.7	17.9
Jul	17.0	21.1	18.6
Aug	18.1	19.8	20.4
Sep	17.1	14.6	16.0
Oct	13.0	11.8	12.2
Whole	17.0	17.8	17.0
Daily average temperature ($^{\circ}\text{C}$)			
Jun	23.3	25.9	23.7
Jul	26.6	25.5	27.6
Aug	27.3	24.7	29.8
Sep	23.3	20.3	25.7
Oct	17.7	13.1	18.9
Whole	23.6	21.9	25.2
Daily maximum temperature ($^{\circ}\text{C}$)			
Jun	28.3	31.2	28.5
Jul	30.5	30.8	32.2
Aug	31.8	30.3	34.7
Sep	28.1	24.8	31.0
Oct	22.7	17.6	23.9
Whole	28.3	26.9	30.1
Daily minimum temperature ($^{\circ}\text{C}$)			
Jun	18.7	20.6	19.4
Jul	23.4	20.2	23.7
Aug	23.4	19.2	25.6
Sep	18.7	15.7	21.0
Oct	13.3	8.6	14.7
Whole	19.5	16.8	20.9

Table 2.3 shows the growth stage measured in Takatsuki in 2009 and 2010, and Fayetteville in 2009 based on Fehr et al. (1971). The beginning of the flowering (R1) stage ranged from 16th July (Athrow) to 3rd August (Osage and Hutcheson) at Takatsuki, from 22nd July (Tachinagaha) to 1st August (Tamahomare) in Fayetteville in 2009, and from 8th August (Suzukari and Tachinagaha) to 17th August (Osage) at Takatsuki in 2010. The physiological maturity (R7) stage ranged from 22nd September (Suzukari) to 19th October (Hutcheson) in Takatsuki, from 27th September (5002T) to 8th October (Tamahomare) in Fayetteville, and from 13th October (Enrei) to 28th October (Tamahomare) at Takatsuki in 2010. The growth stage in 2010 is later than in 2009 in Takatsuki because of delayed sowing due to continuous heavy rain. However, the order was quite consistent among the three environments.

Table 2.3. Growth stage of Japanese and US soybean cultivars measured at Takatsuki and Fayetteville.

Cultivar	Takatsuki (2009)					Fayetteville (2009)				Takatsuki (2010)			
	R1	R5	R7	R8		R1	R5	R7	R8	R1	R5	R7	R8
Jpn cvs.	Enrei	19-Jul	11-Aug	23-Sep	8-Oct					9-Aug	25-Aug	13-Oct	19-Oct
	Suzukari	18-Jul	11-Aug	22-Sep	8-Oct					8-Aug	21-Aug	15-Oct	23-Oct
	Suzuyutaka	22-Jul	16-Aug	25-Sep	9-Oct					9-Aug	28-Aug	15-Oct	21-Oct
	Tachinagaha	18-Jul	11-Aug	9-Oct	22-Oct	22-Jul	21-Aug	28-Sep	-	8-Aug	26-Aug	17-Oct	4-Nov
	Tamahomare	25-Jul	20-Aug	17-Oct	28-Oct	1-Aug	1-Sep	8-Oct	-	12-Aug	5-Sep	28-Oct	9-Nov
US cvs.	Athow	16-Jul	11-Aug	23-Sep	4-Oct					6-Aug	26-Aug	15-Oct	20-Oct
	Omaha	17-Jul	13-Aug	29-Sep	10-Oct					6-Aug	26-Aug	17-Oct	23-Oct
	LD003309	18-Jul	13-Aug	25-Sep	18-Oct					6-Aug	27-Aug	15-Oct	23-Oct
	Manokin	25-Jul	23-Aug	9-Oct	18-Oct	26-Jul	21-Aug	1-Oct	-	14-Aug	2-Sep	20-Oct	27-Oct
	5002T	27-Jul	23-Aug	9-Oct	19-Oct	26-Jul	22-Aug	27-Sep	-	14-Aug	2-Sep	20-Oct	28-Oct
	UA-4805	1-Aug	22-Aug	9-Oct	20-Oct	27-Jul	24-Aug	29-Sep	-	15-Aug	28-Aug	20-Oct	2-Nov
	Osage	3-Aug	29-Aug	17-Oct	24-Oct	27-Jul	28-Aug	28-Sep	-	17-Aug	3-Sep	24-Oct	6-Nov
	5601T	27-Jul	23-Aug	17-Oct	27-Oct	-	28-Aug	2-Oct	-	14-Aug	2-Sep	27-Oct	10-Nov
	Ozark	30-Jul	27-Aug	17-Oct	27-Oct	30-Jul	28-Aug	28-Sep	-	14-Aug	5-Sep	24-Oct	6-Nov
	Hutcheson	3-Aug	27-Aug	19-Oct	29-Oct	30-Jul	26-Aug	29-Sep	-	15-Aug	1-Sep	27-Oct	9-Nov

Based on Fehr et al. (1971).

Table 2.4 shows the yield and its components for the medium maturing cultivars observed in 2009 in Takatsuki and Fayetteville and in 2010 in Takatsuki. The seed yield ranged from 3.10 t ha⁻¹ (Tachinagaha) to 5.50 t ha⁻¹ (5601T) in Takatsuki in 2009 and from 3.44 t ha⁻¹ (Tachinagaha) to 5.73 t ha⁻¹ (5002T) in Fayetteville in 2009. It ranged from 3.77 t ha⁻¹ (Tachinagaha) to 4.97 t ha⁻¹ (5601T) in Takatsuki in 2010. While the effect of the cultivar group on the seed yield was significant throughout the three environments, the effect of the environment was not significant. The total dry matter at maturity ranged from 6.73 t ha⁻¹ to 9.66 t ha⁻¹ and 6.22 t ha⁻¹ to 7.40 t ha⁻¹ in Takatsuki in 2009 and 2010, and from 6.34 t ha⁻¹ to 9.62 t ha⁻¹ in Fayetteville in 2009. A significant difference was observed in the environment, cultivar group, and interaction. HI ranged from 0.40 to 0.51 and from 0.52 to 0.58 in Takatsuki in 2009 and 2010, respectively, and from 0.42 to 0.52 in Fayetteville in 2009. A significant difference was observed in the environment and cultivars; however, no significant interaction was observed. The total intercepted solar radiation ranged from 1402 to 1556 MJ and from 1225 to 1331 MJ in Takatsuki in 2009 and 2010, respectively, and from 1439 to 1616 MJ in Fayetteville. The RUE ranged from 0.47 to 0.63 g MJ⁻¹ and 0.50 to 0.58 g MJ⁻¹ in Takatsuki in 2009 and 2010, respectively, and from 0.41 to 0.63 g MJ⁻¹ in Fayetteville.

Table 2.4. Yield and yield components of Japanese and US soybean cultivars for medium maturing cultivars.

			Seed yield (t ha ⁻¹) ¹⁾	TDW (t ha ⁻¹) ²⁾	HI ²⁾	meanF (%) ³⁾	Solar radiation intercepted (MJ) ⁴⁾	Incident solar radiation (MJ) ⁴⁾	RUE (g MJ ⁻¹) ⁵⁾	
2009										
Takatsuki	(Emergence : 21 st June)									
	Jpn cvs.	Tachinagaha	3.10	6.73	0.40	78.2	1446	1850	0.47	
		Tamahomare	3.44	6.97	0.43	79.0	1560	1976	0.45	
	US cvs.	Manokin	5.23	8.87	0.51	75.7	1404	1855	0.63	
		5002T	4.69	8.76	0.46	75.9	1402	1847	0.63	
		UA-4805	5.15	8.70	0.51	76.5	1416	1850	0.61	
		Osage	5.19	9.60	0.47	78.1	1535	1965	0.63	
		5601T	5.50	9.66	0.49	79.0	1552	1965	0.62	
		Ozark	5.19	9.75	0.46	79.1	1554	1965	0.63	
		Hutcheson	5.03	9.15	0.47	78.0	1556	1995	0.59	
	Average	Whole	4.72	8.69	0.47	77.7	1492	1918	0.58	
		Jpn cvs.	3.27	6.85	0.41	78.6	1503		0.46	
		US cvs.	5.14	9.21	0.48	77.5	1488		0.62	
	Fayetteville	(Emergence : 12 th June)								
		Jpn cvs.	Tachinagaha	3.44	6.34	0.47	76.5	1528	1997	0.41
Tamahomare			3.48	7.23	0.42	79.9	1636	2049	0.44	
US cvs.		Manokin	4.70	8.69	0.47	78.3	1557	1989	0.56	
		5002T	5.73	9.62	0.52	78.6	1616	2057	0.60	
		UA-4805	4.44	8.38	0.46	72.1	1439	1994	0.58	
		Osage	4.72	8.58	0.48	74.5	1540	2067	0.56	
		5601T	5.42	9.91	0.46	77.4	1562	2018	0.63	
		Ozark	4.23	7.81	0.47	75.8	1511	1994	0.52	
		Hutcheson	4.85	8.99	0.47	75.6	1506	1993	0.60	
Average		Whole	4.56	8.40	0.47	76.5	1544	2018	0.54	
		Jpn cvs.	3.46	6.79	0.45	78.2	1582		0.43	
		US cvs.	4.87	8.85	0.48	76.0	1533		0.58	
2010										
Takatsuki		(Emergence : 12 th July))								
	Jpn cvs.	Tachinagaha	3.77	6.22	0.52	72.9	1233	1690	0.50	
		Tamahomare	4.37	7.01	0.54	75.4	1331	1765	0.53	
	US cvs.	Manokin	4.39	6.62	0.57	72.4	1240	1712	0.53	
		5002T	4.76	7.05	0.58	72.5	1241	1712	0.57	
		UA-4805	4.84	7.12	0.58	71.7	1225	1708	0.58	
		Osage	4.90	7.36	0.57	73.0	1264	1732	0.58	
		5601T	4.97	7.40	0.58	73.8	1296	1756	0.57	
		Ozark	4.95	7.30	0.58	73.5	1275	1735	0.57	
		Hutcheson	4.70	7.06	0.57	74.5	1313	1763	0.54	
	Average	Whole	4.63	7.02	0.57	73.3	1269	1730	0.55	
		Jpn cvs.	4.07	6.61	0.53	74.2	1282		0.52	
		US cvs.	4.79	7.13	0.58	73.0	1265		0.56	
	Analysis of variance ⁶⁾									
	Environment			0.53NS	27.34***	60.31***	17.09***	52.42***		6.27**
Cultivar group			68.79***	48.36***	32.37***	3.59NS	0.93NS		113.82***	
Environment×Cultivar group			4.36*	5.80**	1.57NS	0.20NS	0.15NS		10.23***	

¹⁾ Seed weight with a 14% moisture content.²⁾ Including leaves and petiole attached at R8.³⁾ MeanF: Fraction of light intercepted in the average of the whole growth duration (from emergence to R7).⁴⁾ Assessed for the period from emergence to R7.⁵⁾ Radiation use efficiency is the value of the total above ground dryweight at R7 divided by cumulative solar radiation intercepted.⁶⁾ *, **, *** *F* values significance at 0.05, 0.01 and 0.001 probability levels, respectively. NS means non-significant at *P*=0.05 level.

Table 2.5 shows the result of the comparison between early maturing US and Japanese cultivars in Takatsuki in 2009 and 2010. The seed yield ranged from 3.64 to 5.91 t ha⁻¹ in 2009 and from 3.69 to 4.88 t ha⁻¹ in 2010. While the difference in year was not significant, the difference in cultivar was significant. The total dry matter ranged from 5.96 to 9.89 t ha⁻¹ in 2009 and from 5.92 to 7.34 t ha⁻¹ in 2010. The HI ranged from 0.50 to 0.58 in 2009 and from 0.54 to 0.61 in 2010. The total intercepted solar radiation ranged from 1206 to 1313 MJ in 2009 and from 1168 to 1203 MJ in 2010. The RUE ranged from 0.48 to 0.75 g MJ⁻¹ in 2009 and from 0.50 to 0.61 g MJ⁻¹ in 2010. The difference in cultivar group was significant and a significant interaction was observed.

Table 2.5. Yield and yield components of Japanese and US soybean cultivars for early maturing cultivars.

			Seed yield (t ha ⁻¹) ¹⁾	TDW (t ha ⁻¹) ²⁾	HI ²⁾	meanF (%) ³⁾	Solar radiation intercepted (MJ) ⁴⁾	Incident solar radiation (MJ) ⁴⁾	RUE (g MJ ⁻¹) ⁵⁾
2009									
Takatsuki	(Emergence : 21 st June)								
	Jpn cvs.	Suzukari	3.64	5.96	0.52	74.0	1244	1681	0.48
		Suzuyutaka	4.13	6.78	0.52	74.2	1286	1732	0.53
		Enrei	3.93	6.65	0.51	74.2	1254	1690	0.53
	US cvs.	Athow	5.07	7.57	0.58	71.1	1206	1695	0.63
		Omaha	5.91	9.89	0.51	74.0	1313	1774	0.75
		LD003309	5.06	8.69	0.50	69.4	1207	1741	0.72
	Average	Whole	4.62	7.59	0.53	72.8	1252	1719	0.61
		Jpn cvs.	3.89	6.46	0.52	74.2	1261		0.51
		US cvs.	5.35	8.72	0.53	71.5	1242		0.70
2010									
Takatsuki	(Emergence : 12 th July)								
	Jpn cvs.	Enrei	4.41	6.33	0.60	72.2	1178	1631	0.54
		Suzuyutaka	4.23	6.00	0.61	71.3	1181	1656	0.51
		Suzukari	3.69	5.92	0.54	71.8	1189	1656	0.50
	US cvs.	Athow	4.61	6.92	0.57	70.8	1168	1650	0.59
		Omaha	4.88	7.34	0.57	71.7	1203	1678	0.61
		LD00-3309	4.60	6.80	0.58	69.0	1141	1652	0.60
	Average	Whole	4.40	6.55	0.58	71.2	1177	1654	0.56
		Jpn cvs.	4.11	6.09	0.58	71.8	1183		0.52
		US cvs.	4.70	7.02	0.58	70.5	1171		0.60
Analysis of variance ⁶⁾									
Year		1.22NS	7.72*	10.42*	4.48NS	12.97**		5.17NS	
Cultivar group		26.63***	18.16**	0.03NS	6.21*	0.58NS		39.71***	
Year × Cultivar group		4.78NS	3.12NS	0.20NS	0.79NS	0.03NS		5.68*	

¹⁾ Seed weight with a 14% moisture content.²⁾ Including leaves and petiole attached at R8.³⁾ MeanF: Fraction of light intercepted in the average of the whole growth duration (from emergence to R7).⁴⁾ Assessed for the period from emergence to R7.⁵⁾ Radiation use efficiency is the value of the total above ground dryweight at R7 divided by cumulative solar radiation intercepted.⁶⁾ **, ***, *** *F* values significance at 0.05, 0.01 and 0.001 probability levels, respectively. NS means non-significant at *P*=0.05 level.

2.4 Discussion

In Japan, record yields, as high as 5 t ha⁻¹ or more, have been reported in converted paddy fields (Nakaseko et al., 1984; Shimada et al., 1990). The average seed yield in our study was 4.67 t ha⁻¹ and 4.58 t ha⁻¹ in Takatsuki in 2009 and 2010, respectively, and the conditions were thought to be close to optimal. In Fayetteville in 2009, the average seed yield was 4.46 t ha⁻¹ and twice as large as the average seed yield in Arkansas (Katsura et al., 2009). Compared to the field experiment conducted in Arkansas by related authors, however, the value was in the range of the previous observations under favorable conditions (Purcell et al., 2002.). A significant difference in yield was not found among the three environments. On the other hand, differences in seed yield among cultivars were evident. The seed yield of Japanese cultivars, Tachinagaha and Tamahomare, were lower than the US cultivars. The comparison of early maturing cultivars in Takatsuki in 2009 and 2010 also coincided with the comparison of mid maturing cultivars. Combining these results with meteorological records suggests that, although this study provides only limited information, the difference in climate factors between Takatsuki and Fayetteville is not large to cause considerable differences in soybean productivity under well-managed conditions (Table 2.2). Therefore, at least for the cultivars commercially cultivated in recent years, US cultivars are better yielding than Japanese cultivars. This is the first direct comparison between US and Japanese soybean cultivars. In this experiment, tested US cultivars are relatively new (released from 1987 to 2005) as compared with Japanese cultivars (released from 1971 to 1986). Rincker et al. (2015) examined genetic yield gain per year in US soybean cultivars during past 80 yr and reported acceleration of improvement in yield released after 1960s.

Considering the recent yield difference, our result may contain the difference of release years. Therefore it may be worth trying to compare US cultivars with Japanese cultivars developed very recently. In this study, the only cultivars dominant in commercial production in Japan were studied.

The TDM (including the attached leaves and petiole) at maturity was higher in US cultivars. The seed yield correlated with the TDM rather than the HI with correlation coefficients from 0.519 to 0.928 for the TDM versus 0.175 to 0.800 for the HI, for each of the three environments. The relationship between the seed yield and TDM was quite significant throughout the three environments with the R^2 of linear regression for every environment ranging from 0.81 to 0.93 (data not shown). This means that the contribution to yield variation of the other component, HI, was limited. As the result, the contribution to yield was thought to be large from the TDM compared to that of HI (Fig. 2.1a and 2.1b).

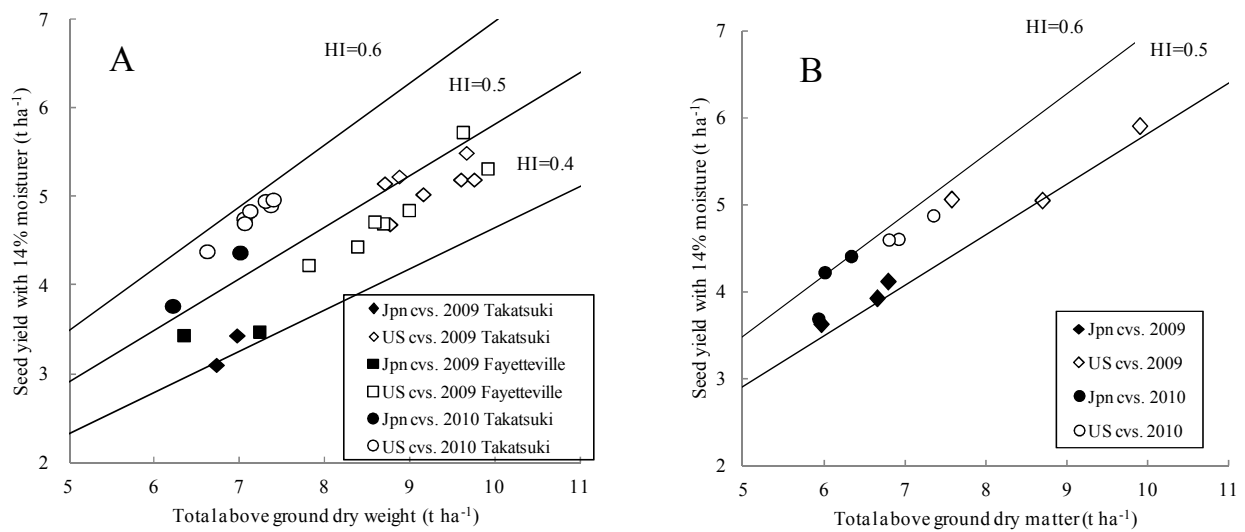


Fig. 2.1. (A) Relationship between total above ground dry matter and seed yield of medium maturing two Japanese and seven US cultivars at three environments. (B) Relationship between total above ground dry matter and seed yield of early maturing three Japanese and three US cultivars at Takatsuki in 2009 and 2010. Reference lines presented in the figure show the value of Harvest Index, respectively.

The mean F differed significantly among environments in medium maturing cultivars, while not significant in cultivar group and no interaction was observed (Table 2.4). In this analysis, mean F was assessed from emergence to R7 and the difference in mean F among environments caused by planting density or planting date became relatively smaller. Though the planting density was higher in Fayetteville, the mean F was lower than Takatsuki in 2009. There is a possibility that rainy season in Takatsuki provided more favorable soil moisture condition as compared with Fayetteville in early growth stage. On the other hand, significant difference in cultivar group was observed in early maturing cultivars (Table 2.5). The stem growth habit of early maturing US cultivars was indeterminate and different from Japanese cultivars (Table 2.1). The difference in stem growth habit may cause the difference in canopy coverage. However, the difference in mean F between cultivar groups was not large.

The total solar radiation intercepted differed significantly among environments, while the total solar radiation intercepted did not differ significantly in cultivar groups, and no significant interaction was observed. The response to temperature and day length of the early growth stage is related to the differentiated duration between sowing and flowering and hence, the total intercepted solar radiation. This difference of the total solar radiation among environments is thought to be caused by the difference in location, the sowing date.

The results of the RUE were consistent between Takatsuki and Fayetteville (Fig. 2.2). Purcell et al. (2002) reported that planting density does not affect the RUE in Fayetteville. US cultivars showed significantly higher values compared to Japanese cultivars (Table 2.3, 2.4). The observed range of the RUE in this study was 0.41 to 0.72 g MJ⁻¹ and quite low compared to prior reports (Sinclair and Horie, 1989; Shiraiwa et al.,

1994). One possible reason is the difference in solar radiation environment. Sinclair and Muchow (1999) reported that RUE increased when incident radiation was low and high-diffuse component condition as compared with high radiation and low-diffuse component condition. Nakaseko and Gotoh (1983) reported that RUE decreased curvilinearly with increase in light intensity. Takatsuki and Fayetteville are higher solar radiation environment, 19 to 24 MJ per day, compared to that in the measurement of Shiraiwa et al. (1994), 13 to 15 MJ per day. Actually, Ries et al. (2012) measured RUE at Fayetteville in the same way using digital image analysis and reported 0.85 to 1.60 g MJ⁻¹ based on photosynthetic active radiation (PAR) during vegetative growth. The calculation of the RUE is divided into two types, based on the photosynthetic active radiation and solar radiation (Bonhomme, 2000; Hatfield, 2014). Ries et al. (2012) estimated PAR as 50% of total incident solar radiation and the range of RUE based on total solar radiation was similar to our result. In addition, the duration of the measurement also can be a reason. Unlike previous studies, we assessed the intercepted solar radiation for the entire duration of growth, from emergence to physiological maturity. This measurement included the period from the late seed filling period to maturity when a decrease in the photosynthetic rate occurs. In addition, the abscission of the leaves and petioles was not included to the TDM at maturity. In the late seed filling period, the abscission of leaves and petioles occurred and the above ground dry weight of the canopy began to decrease. These factors may explain the incomparable values of RUE observed in this experiment.

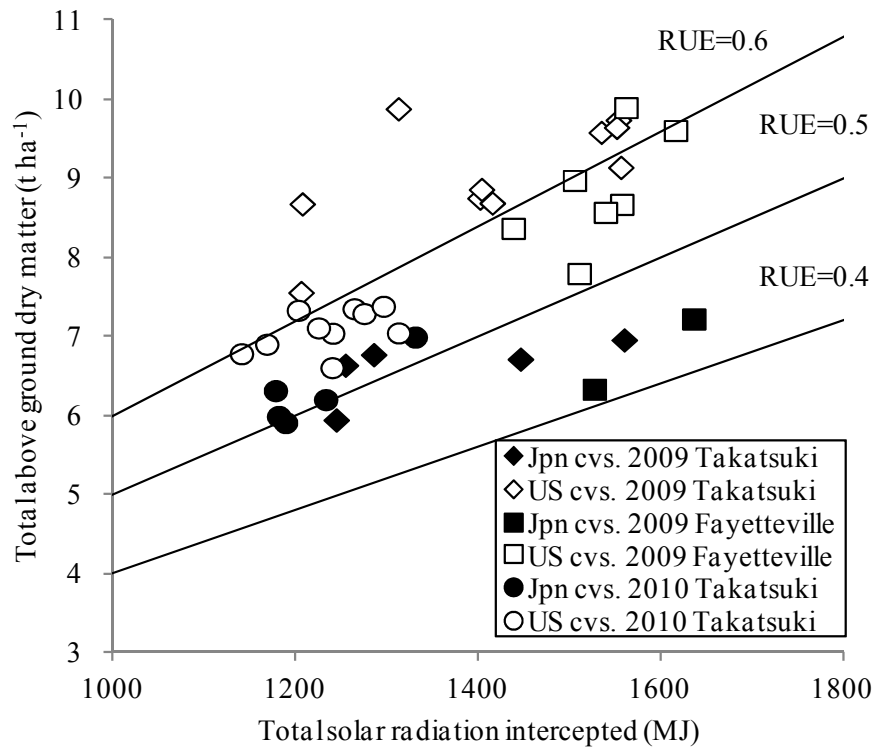


Fig. 2.2. Relationship between total radiation intercepted and total above ground dry matter at three environments. Reference lines presented in the figure show the value of Radiation Use Efficiency, respectively.

To look for key factors in the differences in TDM at maturity and the dry matter productivity, the change in the total dry weight of representative cultivars (Tachinagaha, Tamahomare, UA-4805 and 5601T) was measured in Takatsuki in 2009. The result was shown in Fig. 2.3a. The change in TDM of Tachinagaha and UA-4805 in Takatsuki in 2010 was shown in Fig. 2.3b. Before R5, the dry matter production did not differ between US cultivars (UA-4805, 5601T) and Japanese cultivars (Tachinagaha and Tamahomare). However, after R5, US cultivars tended to show higher dry matter production compared to Japanese cultivars. The amount of intercepted solar radiation during the seed filling period is said to be important in yield formation (Board, 2004). The seed filling period is important because there are reports that the canopy photosynthesis rate during the seed filling period correlates with seed yield (Wells et al., 1982; Ashley and Boerma, 1989), and dry matter production during the seed filling period correlates with seed yield (Shiraiwa and Hashikawa, 1995; Specht et al., 1999; Kumudini et al., 2001; Shiraiwa et al., 2004). There is a high probability that the higher total above ground dry matter of US cultivars at R8 is explained by higher dry matter production during seed filling.

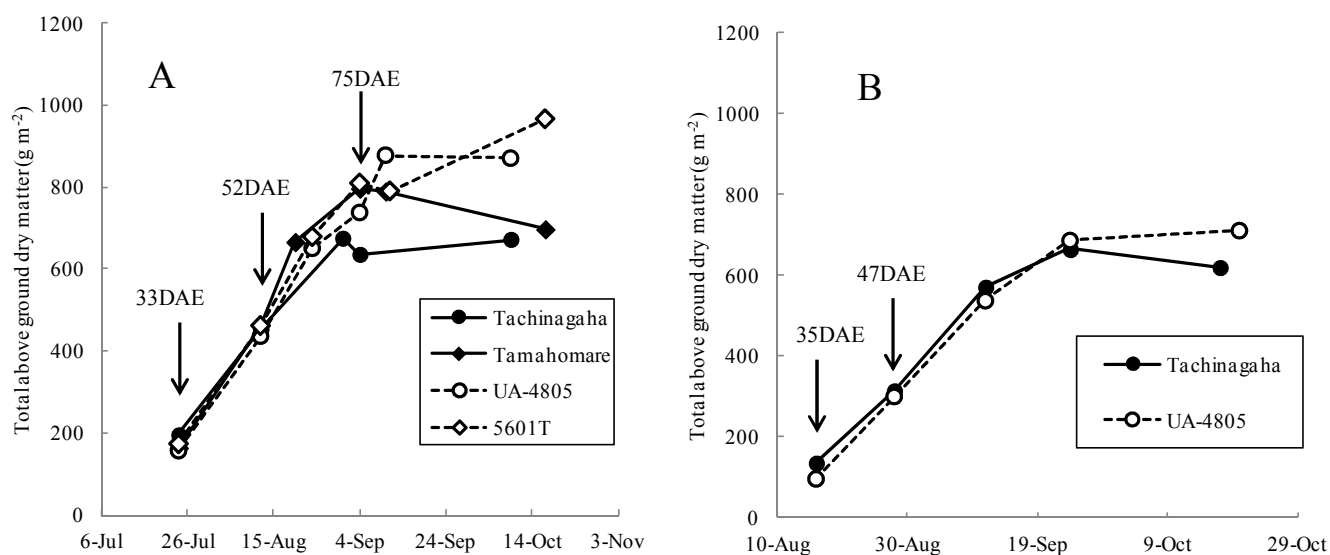


Fig.2.3. (A) Seasonal change of total above ground dry matter measured at Takatsuki in 2009. Arrows presented in the figure show the simultaneous sampling conducted at 33, 52 and 75 days after emergence. (B) Seasonal change of total aboveground measured at Takatsuki in 2010.

Tanaka et al. (2008) compared leaf photosynthetic rate of the top leaflet of US soybean cultivar 'Stressland' and Japanese soybean cultivar 'Tachinagaha' during seed filling period and reported that Stressland showed higher photosynthetic rate than that of Tachinagaha after R5. The high photosynthetic rate of Stressland was mainly explained by higher stomatal conductance. In addition, Tanaka et al. (2010) reported that the diversity in stomatal density measured at seed filling stage and the estimated potential stomatal conductance in US cultivars are higher than Japanese cultivars. The difference in potential stomatal conductance also suggested that the photosynthetic rate in US cultivars is higher than in Japanese cultivars. There is a possibility that the differences in the stem growth habit can be attributed to dry matter production in early maturing cultivars (Tanaka and Shiraiwa, 2009).

The analysis of dry matter production of the cross-location experiment between Takatsuki and Fayetteville was done at the R8 stage and the relationship between the total above ground dry matter and the seed yield in this experiment was 'apparent' HI. Apparent HI is calculated as the ratio of seed dry matter to above ground dry matter at harvest (Kumudini, 2002). In this analysis, the final above ground dry matter does not take into consideration dry matter lost as senescent leaves abscise prior to harvest. In general, it is difficult to detect the dry matter production during seed filling period because of the abscission of the leaves and petioles observed during this period. However, a high correlation was found in a previous study between an apparent HI and the true HI, which include abscised leaves and petioles (Schapaugh and Wilcox, 1980). In addition, there were several reports that the improvement in the apparent total dry matter at R8 contributed more than the improvement in the apparent HI (Cregan and Yaklich, 1986; Specht et al., 1999; Kumudini et al., 2001; De Bruin and Pederson,

2009) and our results coincide with those reports. To survey the key trait that can improve the yield of Japanese soybean cultivars, more attention must be paid to the seed filling period and focused on the traits related to dry matter dynamics.

2.5 Conclusions

The seed yield of US cultivars was higher than Japanese cultivars. When the fields were managed to optimal conditions as much as possible, the environmental factor did not cause a difference in the seed yield. The difference in yield was closely associated with the difference in the TDM rather than a difference in HI. The apparent dry matter production per unit of intercepted solar radiation was higher in US cultivars. These results suggest that a difference in yield exists between US and Japanese soybean cultivars that can be attributed to crop biomass productivity. Traits related to canopy photosynthesis or information about the contribution of abscised leaves to dry matter production is needed to further understand the difference in true dry matter productivity.

Chapter 3

Yield and Dry Matter Productivity of Japanese and US Soybean Cultivars in Response to Drought Stress

3.1 Introduction

The author compared yield and dry matter production of US and Japanese cultivars and found that US cultivars tended to show high yield and dry matter production as compared to Japanese cultivars under near optimum condition in Chapter 2. However, the farmers' fields are not always maintained in optimum condition as compared to experimental field because of economic reasons, such as infrastructure and high labor cost for management. Drought is one of the most serious problems in soybean production. And it is true for production in Japan with wet climate due to water deficit in the mid summer after rainy season (Hirasawa et al., 1994). Evaluation under different soil moisture conditions may give us detailed information about productivity of US and Japanese soybean cultivars. In this chapter, yield and dry matter production of Japanese and US soybean cultivars under drought stress was focused.

The author found US cultivars tend show higher dry matter production during seed filling period under near optimum condition. Our results coincide with Kumudini et al.(2002) and De Bruin and Peterson (2009) in terms of contribution of dry matter production to seed yield. Shiraiwa et al. (2004) reported dry matter production during seed filling period played an important role to seed yield. Tanaka and Shiraiwa (2009) reported diversity in stomatal density among soybean cultivars and found that morphological potential of stomatal conductance in US cultivars is higher than that of

Japanese cultivars. Higher dry matter production of US cultivar under optimum condition might be explained by higher stomatal conductance and photosynthesis rate of US cultivars and suggested that US cultivars were genetically improved indirectly in stomatal conductance through selection in yield (Roche, 2015). However, the higher stomatal density and potential stomatal conductance of US cultivars suggests that US cultivars tend to consume more water than Japanese cultivars. King et al. (2009) pointed out soil water conservation as an important trait for drought tolerance. In this context, US cultivars can be less tolerant to drought than Japanese cultivars. On this subject, report from field experiment of drought stress is quite limited as compared to pot experiment due to the difficulty in environmental management.

In this chapter, yield and dry matter productivity of US and Japanese soybean cultivars under drought were compared, and G x E interaction was tested. Japanese cultivar ‘Tachinagaha’ and US cultivar ‘UA4805’ were evaluated under two different soil moisture environments during reproductive period. Seed yield, total dry matter at maturity, HI, and RUE during whole growth period were measured in 2009 and 2010 at Takatsuki, Japan. Volumetric soil water content and stomatal conductance were measured to evaluate the environment.

3.2 Materials and methods

The two cultivars were grown on a drained paddy field in the Experimental Farm of Kyoto University (Takatsuki, Japan, Eutric Fluvisols) located at 34°50'N and 135°37'E. The cultivars were chosen from recent major non-GM cultivars in both regions with near maturity groups. One Japanese cultivar (Tachinagaha) and one US cultivar

(UA-4805) were grown in Takatsuki with three replications. The sowing date was 16th June in Takatsuki in 2009 and 7th July in 2010. Plant spacing was 0.7 by 0.15m. Fertilizers of N, P₂O₅, K₂O were incorporated into the soil before sowing at 3, 10 and 10 g m⁻², respectively.

The treatments with irrigation (Control) and without irrigation (Drought) were started at 20DAE. In the Control, irrigation water was evenly applied using the plastic tube (Sumisansui, SUMIKA AGROTECH CO. LTD.) extended on the ground in every other interrow. Irrigation was conducted when the soil matric potential declined lower than 50 kPa. In 2009, the all Drought plots were covered with a half transmittable sheet that is water-proof but transmittable to water vapor to develop soil water deficit in Drought. The volumetric soil water content was measured using Time-domain reflectometry method described by Topp et al. (1980). TDR cable tester 1502C (Tektronix, Tokyo) was used to measure once a week in 2009 and twice a week using EC-5 (Decagon Devices, Inc. WA) in 2010.

The canopy coverage was measured by the digital image analysis using ImageJ (NIH, US) (Purcell, 2000; Shiraiwa et al., 2011) to estimate radiation use efficiency. In 2010, change in the total above-ground dry matter was measured. Plants were harvested at 35, 47, 61, and 74DAE from a 1.26 m² land area and the dry matter was determined after drying at 80°C for 72hr. The LAI was estimated by measuring leaf area of representative plants. In 2010, leaf stomatal conductance was measured by polometer AP-4 (Delta-T Devices, London) on 28th August and 11th September to evaluate the stress. Seed yield and total above ground dry weight was measured at maturity in both years.

3.3 Results and discussion

The treatment for Drought was commenced on 16th August in 2009 and 3rd August in 2010. The volumetric soil water content was on average 7.3% lower in 2009 and 8.4% in 2010 in the Drought than in the Control (Fig 3.1).

In 2009, seed yield and HI decreased significantly under drought (Table 3.1). UA4805 showed higher yield, total above ground dry weight, HI and RUE. A significant G x E interaction was observed in HI and Tachinagaha (Tc) tended to decrease more than UA4805 (UA).

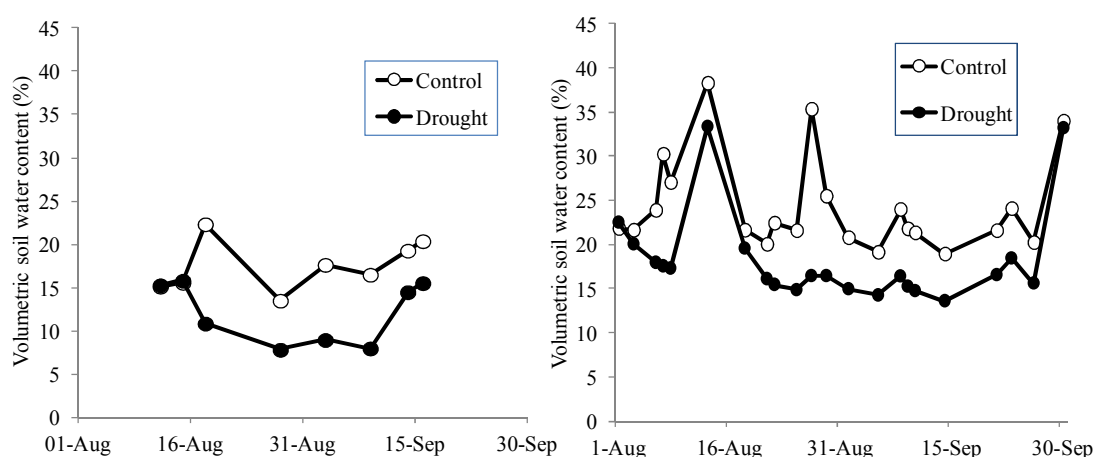


Fig. 3.1. Changes in volumetric soil water content measured in 2009 (A) and 2010 (B).

Table 3.1. Yield and yield components of field experiment in 2009.

Cultivar	Environment	Seed yield (t ha ⁻¹) ¹⁾	HI	TDW (t ha ⁻¹) ²⁾	Solar radiation intercepted (MJ) ⁴⁾	meanF (%) ³⁾	RUE (g MJ ⁻¹) ⁵⁾
Tachinagaha	Control	3.10	0.398	6.73	1446	78.2	0.47
Tachinagaha	Drought	2.16	0.270	6.83	1462	79.0	0.47
UA4805	Control	5.15	0.509	8.70	1416	76.5	0.61
UA4805	Drought	4.78	0.475	8.66	1455	78.9	0.59
Analysis of variance ⁶⁾							
Cultivar		98.26***	112.40***	23.25**	2.69NS	3.22NS	28.72***
Environment		7.82*	29.46***	0.01NS	5.55*	11.35**	0.13NS
Cultivar x Environment		1.45NS	9.82*	0.03NS	1.09NS	2.83NS	0.17NS

¹⁾ Seed weight with a 14% moisture content.

²⁾ Including leaves and petiole attached at R8.

³⁾ MeanF : Fraction of light intercepted in the average of the whole growth duration (from emergence to R7).

⁴⁾ Assessed for the period from emergence to R7.

⁵⁾ Radiation use efficiency is the value of the total above ground dryweight at R7 divided by cumulative solar radiation intercepted.

⁶⁾ *, **, *** , F values significance at 0.05, 0.01 and 0.001 probability levels, respectively. NS means non-significant at $P=0.05$ level.

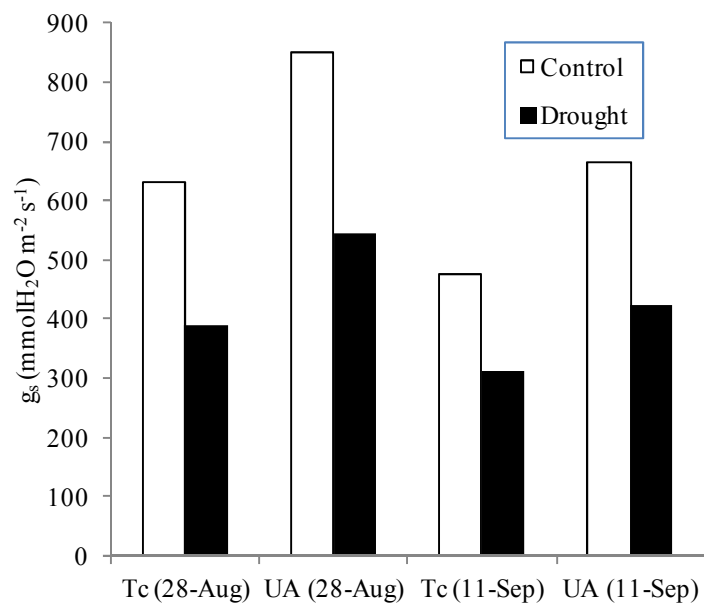


Fig. 3.2 Stomatal conductance measured in 2010.

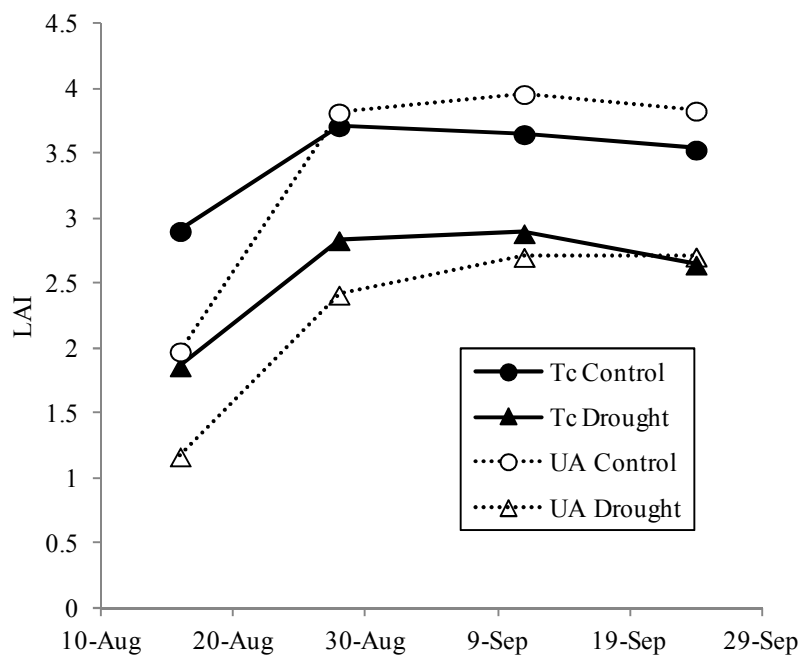


Fig. 3.3. Change in Leaf Area Index measured in 2010.

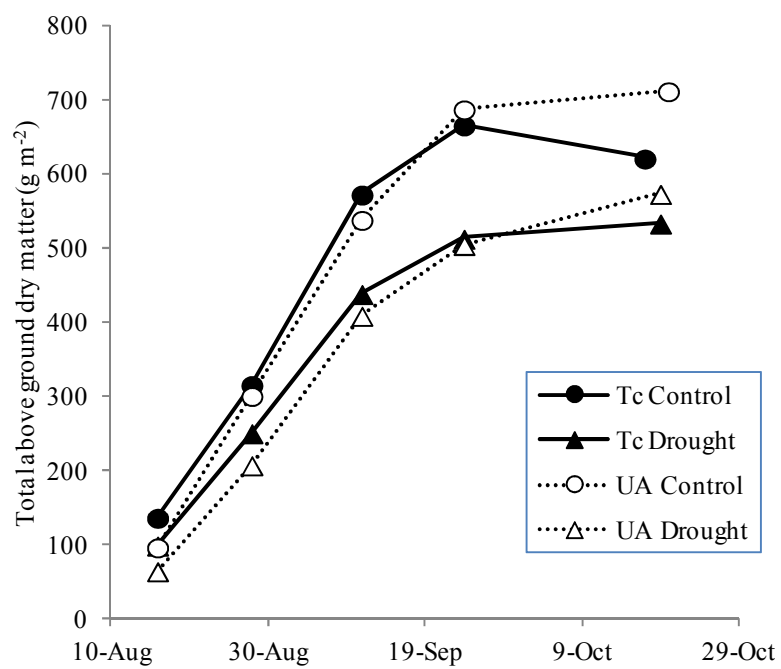


Fig. 3.4. Change in total above ground dry weight measured in 2010.

Table 3.2. Yield and Yield components of field experiment in 2010.

Cultivar	Environment	Seed yield (t ha ⁻¹) ¹⁾	HI	TDW (t ha ⁻¹) ²⁾	Solar radiation intercepted (MJ) ⁴⁾	meanF (%) ³⁾	RUE (g MJ ⁻¹) ⁵⁾
Tachinagaha	Control	3.77	0.521	6.22	1233	72.9	0.50
Tachinagaha	Drought	2.17	0.341	5.34	1170	69.2	0.46
UA4805	Control	4.84	0.585	7.12	1225	71.7	0.58
UA4805	Drought	3.65	0.531	5.74	1000	58.6	0.57
Analysis of variance ⁶⁾							
Cultivar		29.75**	32.50**	19.65*	8.84*	13.87*	46.75**
Environment		35.49**	27.49**	58.79**	23.13**	28.33**	4.16*
Cultivar x Environment		0.77NS	8.14*	2.98NS	7.33NS	8.72*	1.98NS

¹⁾ Seed weight with a 14% moisture content.

²⁾ Including leaves and petiole attached at R8.

³⁾ MeanF : Fraction of light intercepted in the average of the whole growth duration (from emergence to R7).

⁴⁾ Assessed for the period from emergence to R7.

⁵⁾ Radiation use efficiency is the value of the total above ground dryweight at R7 divided by cumulative solar radiation intercepted.

⁶⁾ **, ***, **** *F* values significance at 0.05, 0.01 and 0.001 probability levels, respectively. NS means non-significant at *P*=0.05 level.

The stomatal conductance was higher in UA than in Tc and it decreased in both cultivars by 34~38%. The leaf area development was inhibited only in UA under Drought (Fig. 3.3). UA showed a greater mean seed yield and harvest index in both of Control and Drought in 2010. Drought reduced mean seed yield and total dry weight of two cultivars. The yield reduction by drought in UA was associated with reduced radiation intercepted, while yield reduction in Tc was associated with reduced radiation use efficiency and harvest index. The significant G x E interaction was detected in harvest index and mean fraction of radiation intercepted (Table 3.2).

Across two years, a significant G x E interaction was observed in HI. HI in Tc decreased more than UA under drought. The seed yield was more stable in UA. The high yield in US cultivars is thought to be related to stable HI in addition to total DM accumulation. The irrigation is supposed to be critical in Japanese cultivars during reproductive stage to achieve high yield.

Chapter 4

Dry Matter Dynamics and Partitioning to Reproductive Organs during Seed Filling Period in Japanese and US Soybean Cultivars

4.1 Introduction

In Chapter 2, the author found recent US cultivars tended to show higher seed yield as compared with Japanese commercial cultivars. The seed yield of Japanese and US soybean cultivars correlated with total above ground dry matter at maturity to a great extent compared to HI. Our results coincide with Kumudini (2002) and De Bruin and Peterson (2009) who reported the contribution of dry matter production to seed yield. However, the total above ground dry matter observed in this experiment and examined its relation with seed yield was of ‘apparent’ above ground dry matter. And thus the HI in Chapter 2 was ‘apparent’. An ‘actual’ HI should be calculated based on TDM that include abscised leaves and petioles. A high correlation was found in a previous study between the apparent HI and the actual HI (Schapaugh and Wilcox, 1980). For this, the author did not take into consideration dry matter lost as senescent leaves abscised prior to harvest in the prior analysis. But the relationship between seed yield and true above ground dry matter production including abscised leaves and petiole is important to detect the key trait for a high yield in reference to production and partitioning of dry matter.

Several reports indicated that dry matter production during seed filling period is important for seed yield (Shiraiwa and Hashikawa, 1995; Specht et al., 1999; Kumudini et al., 2001; Shiraiwa et al., 2004). If it is true for genotypic variation of seed yield, an effort to get information related to photosynthesis from leaf during seed filling period

would be demanded for narrowing the breeding target for high yield. In addition, re-translocation of the nutrition occurs from vegetative organs to seed during seed filling period. The contribution of re-translocation also could be an important factor.

The objective of this Chapter is to confirm the change in total above ground dry matter during seed filling period and to evaluate the effect of dry matter productivity including abscised leaves and petioles on seed yield and identify the key trait differentiates seed yield among cultivars in terms of leaf nitrogen utilization. To achieve these objectives, two US cultivars and two Japanese cultivars were grown on a drained paddy field at Azuchi in 2011 and eight US cultivars and seven Japanese cultivars were grown on a drained paddy field at Takatsuki in 2012 and 2013. The abscised leaves and petioles were collected during seed filling period.

4.2 Materials and methods

4.2.1 Field experiment at Azuchi in 2011

In 2011, a field experiment was conducted at the Shiga Prefecture Agricultural Technology Promotion Center at Azuchi, Japan (35°07'N). Two Japanese cultivars (Enrei and Tachinagaha) and two US cultivars (LD00-3309 and UA4805) were grown under optimum field condition. The seeds were sown on 14th June and 11th July. The planting density was 0.7 by 0.15 m. Fertilizers (N: P₂O₅: K₂O = 2: 6: 6 g m⁻²) were applied prior to sowing to the drained paddy field (a silty clay loam soil, Typic Hydraquent). The experimental field was irrigated with the Farm-Oriented Enhancing Aquatic System (FOEAS, Shimada et al., 2012). in Takatsuki and 0.15 to 0.20 by 0.19 m in Fayetteville. Three replications were arranged in a completely randomized block

design. Weeding and the spraying of agrochemicals were conducted to maintain optimal conditions.

Meteorological data (daily solar radiation and temperature) were recorded. The beginning of flowering stage (R1), initial seed filling stage (R5), physiological maturity stage (R7) and maturity (R8) were recorded based on Fehr et al. (1971). The total above ground dry matter was measured at R5, 15d after R5, 30d after R5 and maturity from a 1.26 m^2 area. Cultivars were divided into two sampling groups during seed filling period due to the difference of the growth stage. In June sowing, Enrei and LD00-3309 were harvested at 57, 71 and 87d after sowing, and Tachinagaha and UA4805 were harvested at 63, 84 and 92d after sowing. In July sowing, Enrei and LD00-3309 were harvested at 51, 64 and 80d after sowing, and Tachinagaha and UA4805 were harvested at 52, 66 and 85d after sowing. At R5 an area of 1.89 m^2 (3 inter-rows of 0.9 m length) was covered with a shade net for catchment of litter. And after R5 the abscised leaves and petioles were collected periodically and the dry matter was weighed. At maturity, the seed yield and total above ground dry matter were weighed.

4.2.2 Field experiment at Takatsuki in 2012 and 2013

In 2012 and 2013, field experiments were conducted at the Experimental Farm, Kyoto University, Takatsuki, Osaka, Japan ($34^{\circ}50'N$). The seeds were sown on a drained paddy field (a clay loam soil, Eutric Fluvisols) after adding fertilizers (N: P_2O_5 : K_2O = 3: 10: 10 g m^{-2}) in both years. Eight US cultivars (Athrow, Omaha, LD00-3309, 5002T, UA4805, Ozark, Osage and 5601T) and seven Japanese cultivars (Osuzu, Enrei, Tachinagaha, Otsuru, Tamahomare, Sachiutaka and Fukuyutaka) were grown. The planting density was 0.7 m by 0.15 m in 2012 and 0.8 by 0.15 m in 2013. Three

replicates were arranged in a completely randomized block design. Furrow irrigation was conducted to avoid drought. Weeding and the spraying of agrochemicals were conducted to maintain optimal conditions.

Meteorological data (daily solar radiation and temperature) were recorded. The growth stages (R1, R5, R7 and R8) were recorded in both years. Total above ground dry matter was weighed at R5 stage and 30 d after R5. CGR and pod growth rate were calculated from change in dry matter. After R5, black net was settled to a 1.26 m² land area (1.4 m by 0.9 m) in 2012 and 1.44 m² land area (1.6 m by 0.9 m) in 2013 completely covering two inter-rows. Abscised leaves and petioles were collected periodically and dry matter was weighed. The seed yield and total above ground dry matter was weighed at maturity. Apparent HI and actual HI were calculated combining dry matter of abscised leaves and petioles.

The effect of the cultivar group (2 Japanese cvs. vs 2 US cvs.) and sowing date were analyzed at Azuchi in 2011 using ANOVA. In addition, the effect of the cultivar group (7 Japanese cvs. vs 8 US cvs.) and year were analyzed at Takatsuki in 2012 and 2013 using ANOVA. A multiple regression analysis was conducted to explain the effect of CGR and dry matter distribution into pods and seeds. All these statistical analysis were conducted using Microsoft Excel (Microsoft, Redmond, WA, US).

4.3 Results

4.3.1 Field experiment in 2011

The growth stage of Japanese and US soybean cultivars measured at Azuchi in 2011 was shown in Table 4.1. Enrei was the earliest maturing cultivar in this experiment and

UA4805 was the latest. In both sowing environment, Japanese cultivars reached beginning of flowering stage (R1), initial seed filling stage (R5), physiological maturity stage (R7) and maturity stage (R8) earlier than US cultivars. In June sowing, R5 differed among cultivars with a range of 8 days and R8 did with a range of 11 days. In July sowing, R5 showed a range of 8 days and R8 showed a range of 17 days. Whole growth duration from emergence to maturity was shorter in July sowing than June sowing.

Table 4.1. Growth stage of Japanese and US cultivars grown at Azuchi in 2011.

		June sowing				July sowing			
		R1	R5	R7	R8	R1	R5	R7	R8
Japanese cvs.									
	Enrei	21-Jul	11-Aug	22-Sep	30-Sep	12-Aug	26-Aug	5-Oct	13-Oct
	Tachinagaha	21-Jul	11-Aug	29-Sep	6-Oct	13-Aug	27-Aug	12-Oct	24-Oct
US cvs.									
	LD00-3309	16-Jul	12-Aug	29-Sep	10-Oct	15-Aug	29-Aug	13-Oct	25-Oct
	UA-4805	1-Aug	19-Aug	4-Oct	11-Oct	19-Aug	3-Sep	23-Oct	31-Oct

The change in TDM was shown in Fig. 4.1. Throughout both growing seasons, Japanese cultivars were larger in TDM at R5 stage. However at 30d after R5 stage, US cultivars accumulated larger TDM than Japanese cultivars. The trend was similar in both growing seasons.

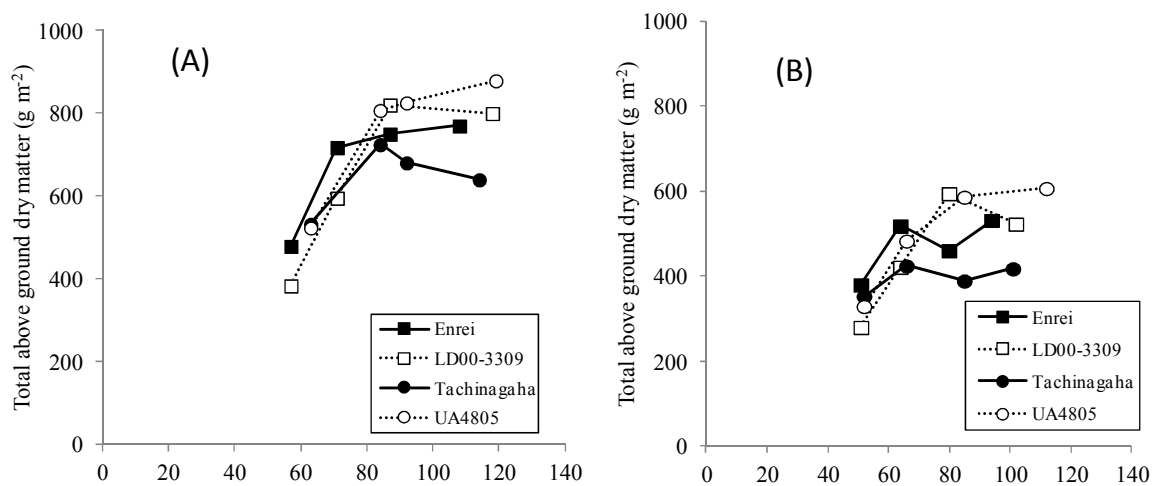


Fig. 4.1. Change in total above ground dry matter measured at Azuchi in 2011. (A) shows June sowing and (B) shows July sowing.

Table 4.2 shows the results of seed yield, TDW without and including the abscised leaves and petioles, apparent HI and actual HI. Throughout both growing seasons, LD00-3309 was the highest yielding cultivar and Tachinagaha was the lowest. A significant difference between June sowing and July sowing was observed in seed yield, TDM without abscised leaves and petioles, apparent harvest index, and total above ground dry matter including abscised leaves and petioles. But there was no difference between June and July sowing in actual harvest index. Seed yield, TDW without abscised leaves and petioles, and TDW including the abscised leaves and petioles were higher in June sowing, on the other hand, apparent HI was higher in July sowing. Significant differences between US and Japanese cultivar groups were observed in seed yield, TDW without abscised leaves and petioles and apparent harvest. US cultivars showed higher seed yield, TDW without abscised leaves and petioles, and apparent HI. No sowing date $\times$ cultivar group interaction was observed.

Table 4.2. Yield and yield components measured at Azuchi in 2011.

		Yield (g m ⁻²)	Total dry matter without abscised leaves and petiole (g m ⁻²)	Apparent HI	Total dry matter including abscised leaves and petiole (g m ⁻²)	Actual HI
June sowing						
Japanese cvs.	Enrei	384	652	0.510	770	0.429
	Tachinagaha	294	555	0.456	640	0.396
US cvs.	LD00-3309	439	703	0.536	800	0.472
	UA4805	432	733	0.507	879	0.422
July sowing						
Japanese cvs.	Enrei	274	421	0.560	532	0.444
	Tachinagaha	198	330	0.517	418	0.408
US cvs.	LD00-3309	349	477	0.629	523	0.574
	UA4805	309	441	0.605	607	0.438
Sowing date						
Cultivar group		11.38*	47.73**	14.78*	23.55**	0.89NS
Sowing date × Cultivar group		9.26*	7.89*	8.78*	4.68NS	2.25NS
		0.00NS	0.19NS	1.02NS	0.18NS	0.34NS

4.3.2 Field experiment in 2012 and 2013

The growth stages of Japanese and US soybean cultivars measured at Takatsuki in 2012 and 2013 were shown in Table 4.3. The R1 stage showed a range from 29th July (Athow) to 15th August (Fukuyutaka) in 2012, from 27th July (Athow) to 16th August (Fukuyutaka) in 2013. R5 stage showed a range from 20th August (Osuzu) to 11th September (Fukuyutaka) in 2012 and from 18th August (Osuzu) to 16th September (Fukuyutaka) in 2013. R7 stage showed a range from 5th October (Osuzu) to 28th October (5601T) in 2012 and from 4th October (Osuzu) to 1st November (5601T) in 2013. R8 stage showed a range from 12th October (Osuzu) to 5th November (5601T) in 2012 and from 12th October (Osuzu) to 9th November (5601T) in 2013. The trends were almost similar between 2012 and 2013.

Table 4.3. Growth stage of Japanese and US soybean cultivars grown at Takatsuki in 2012 and 2013.

	2012				2013			
	R1	R5	R7	R8	R1	R5	R7	R8
Japanese cvs.								
Osuzu	2-Aug	20-Aug	5-Oct	12-Oct	1-Aug	18-Aug	4-Oct	12-Oct
Enrei	4-Aug	24-Aug	11-Oct	20-Oct	3-Aug	22-Aug	7-Oct	21-Oct
Tachinagaha	3-Aug	24-Aug	16-Oct	29-Oct	2-Aug	21-Aug	8-Oct	28-Oct
Otsuru	5-Aug	27-Aug	17-Oct	28-Oct	7-Aug	29-Aug	20-Oct	31-Oct
Tamahomare	7-Aug	31-Aug	17-Oct	25-Oct	8-Aug	7-Sep	31-Oct	6-Nov
Sachiyutaka	8-Aug	1-Sep	21-Oct	27-Oct	8-Aug	4-Sep	21-Oct	1-Nov
Fukuyutaka	15-Aug	11-Sep	26-Oct	3-Nov	16-Aug	16-Sep	31-Oct	8-Nov
US cvs.								
Athow	29-Jul	23-Aug	8-Oct	15-Oct	27-Jul	20-Aug	6-Oct	13-Oct
LD00-3309	28-Jul	25-Aug	10-Oct	20-Oct	29-Jul	23-Aug	9-Oct	29-Oct
Omaha	30-Jul	24-Aug	10-Oct	19-Oct	30-Jul	25-Aug	9-Oct	21-Oct
5002T	10-Aug	30-Aug	13-Oct	25-Oct	10-Aug	2-Sep	19-Oct	31-Oct
UA4805	10-Aug	31-Aug	19-Oct	28-Oct	11-Aug	3-Sep	19-Oct	31-Oct
Osage	12-Aug	8-Sep	20-Oct	28-Oct	13-Aug	10-Sep	26-Oct	3-Nov
Ozark	9-Aug	3-Sep	22-Oct	30-Oct	10-Aug	2-Sep	27-Oct	4-Nov
5601T	9-Aug	3-Sep	28-Oct	5-Nov	11-Aug	12-Sep	1-Nov	9-Nov

The results of seed yield, TDM without abscised leaves and petioles, apparent HI, TDM including abscised leaves and petioles and actual HI measured at Takatsuki in 2012 and 2013 was shown in Table 4.4. Yield ranged from 254 g m⁻² (Tachinagaha) in 2013 to 581 g m⁻² (5601T) in 2012. TDM without abscised leaves and petioles ranged from 585 g m⁻² (Osuzu) in 2012 to 931 g m⁻² (5601T) in 2012. Apparent HI ranged from 0.363 (Tachinagaha) in 2013 to 0.552 (Sachiyutaka) in 2012. TDM including abscised leaves and petioles ranged from 757 g m⁻² (Osuzu) in 2012 to 1109 g m⁻² (5601T) in 2012. Actual HI ranged from 0.254 (Otsuru) to 0.457 (LD00-3309). The year effect was significant in yield, apparent HI and actual HI and these were greater in 2012 than 2013. The effect of cultivar group was significant in yield, TDM without abscised leaves and petioles, apparent HI and actual HI and US cultivar group was greater than Japanese cultivars in these traits. No significant difference was observed in TDM including abscised leaves and petioles between Japanese and US cultivar groups. No year × Cultivar group interaction was observed.

Table 4.5 shows CGR of Japanese and US cultivars measured at Takatsuki in 2012 and 2013. CGR from emergence to R5 ranged from 7.08 g m⁻² d⁻¹ (LD00-3309) in 2012 to 11.01 g m⁻² d⁻¹ (Sachiyutaka) in 2013. CGR from R5 to 30d after R5 ranged from 4.50 g m⁻² d⁻¹ (Fukuyutaka) in 2013 to 19.07 g m⁻² d⁻¹ (5601T) in 2012. CGR from 30d after R5 to R8 ranged from 0.23 g m⁻² d⁻¹ (Otsuru) in 2013 to 29.54 g m⁻² d⁻¹ (Fukuyutaka) in 2012. The year effect was significant only for CGR from emergence to R5 and it was greater in 2013 than in 2012. The effect of cultivar group was significant for CGR from R5 to 30d after R5 in which US cultivar group showed greater value of average than Japanese cultivar group. CGRs for the periods from emergence to R5 and from 30d after R5 to R8 did not differ between cultivar groups. Japanese cultivar ‘Fukuyutaka’ showed

different trend as compared with the other Japanese cultivars. This may be due to the difference in maturity. Fukuyutaka was late maturing cultivar among Japanese cultivars tested in this experiment and stem growth continued longer than the other cultivars. The lodging was observed between R5 and 30d after R5 in Fukuyutaka. This may caused the temporal decrease in crop growth rate between R5 and 30d after R5.

Table 4.6 shows pod distribution ratio and pod growth rate of Japanese and US cultivars measured at Takatsuki in 2012 and 2013. Pod distribution ratio from emergence to R5 ranged from 0.049 g g⁻¹ (Enrei) in 2013 to 0.154 g g⁻¹ (Osage) in 2012. Pod distribution ratio from R5 to 30d after R5 ranged from 0.665 g g⁻¹ (Fukuyutaka) in 2012 to 2.264 g g⁻¹ (Fukuyutaka) in 2013. Pod growth rate from R5 to 30d after R5 ranged from 7.43 g m⁻² d⁻¹ (Tachinagaha) in 2013 to 15.50 g m⁻² d⁻¹ (5601T) in 2012. The year effect was significant for pod growth rate from R5 to 30d after R5 and it was greater in 2012 than 2013. The effect of cultivar group significant for pod distribution ratio from emergence to R5 and pod growth rate from R5 to 30d after R5 in which US cultivar group showed greater value of average than that of Japanese cultivar group. No significant difference was observed in pod distribution ratio from R5 to 30d after R5 between cultivar groups.

Table 4.4. Yield and yield components measured at Takatsuki in 2012 and 2013.

			Yield (g m ⁻²)	Total dry matter without abscised leaves and petiole (g m ⁻²)	Apparent HI	Total dry matter including abscised leaves and petiole (g m ⁻²)	Actual HI
2012	Japanese cvs.	Osuzu	383	585	0.563	757	0.435
		Enrei	393	627	0.539	849	0.398
		Tachinagaha	342	675	0.436	848	0.346
		Sachiyutaka	485	756	0.552	995	0.419
		Otsuru	455	787	0.497	1007	0.389
		Fukuyutaka	484	858	0.485	1045	0.398
	US cvs.	Athow	482	739	0.561	884	0.469
		Omaha	452	763	0.510	901	0.432
		LD00-3309	461	743	0.533	867	0.457
		5002T	509	802	0.546	969	0.452
		UA4805	498	794	0.540	975	0.440
		Ozark	500	795	0.541	965	0.446
		Osage	481	763	0.542	916	0.451
		5601T	581	931	0.536	1109	0.451
	Japanese cvs. mean		424	715	0.512	917	0.398
	US cvs. mean		496	791	0.539	948	0.450
	Whole mean		465	758	0.527	935	0.427
2013	Japanese cvs.	Osuzu	360	657	0.472	871	0.356
		Enrei	270	601	0.386	829	0.280
		Tachinagaha	254	602	0.363	832	0.263
		Otsuru	297	657	0.389	1006	0.254
		Sachiyutaka	422	694	0.523	963	0.377
		Tamahomare	387	686	0.486	1055	0.316
		Fukuyutaka	473	825	0.493	1093	0.372
	US cvs.	Athow	378	709	0.458	862	0.377
		LD00-3309	464	820	0.486	1005	0.397
		Omaha	389	770	0.435	968	0.346
		5002T	410	723	0.488	943	0.374
		UA4805	397	674	0.506	899	0.379
		Ozark	468	780	0.516	1000	0.403
		Osage	411	695	0.508	923	0.382
		5601T	521	817	0.548	1073	0.417
	Japanese cvs. mean		352	675	0.445	950	0.317
	US cvs. mean		430	749	0.493	959	0.384
Whole mean		393	714	0.471	955	0.353	
ANOVA							
Year		9.83**	2.29NS	12.05**	0.38NS	37.52***	
Cultivar group		11.68**	7.44*	5.71*	0.35NS	25.80***	
Year × Cultivar group		0.02NS	0.00NS	0.46NS	0.11NS	0.44NS	

Table4.5. Crop growth rate of Japanese and US soybean cultivars measured at Takatsuki in 2012 and 2013.

			CGR (Emergence~R5) (g m ⁻² d ⁻¹)	CGR (R5~R5+30d) (g m ⁻² d ⁻¹)	CGR (R5+30d~R8) (g m ⁻² d ⁻¹)
2012	Japanese cvs.	Osuzu	8.31	10.47	2.74
		Enrei	8.98	10.59	3.25
		Tachinagaha	8.68	11.74	1.50
		Sachiyutaka	9.51	12.24	8.77
		Otsuru	8.86	8.21	6.90
		Fukuyutaka	7.88	4.68	29.54
	US cvs.	Athow	7.32	14.65	4.90
		Omaha	8.55	12.36	4.81
		LD00-3309	7.08	15.93	2.06
		5002T	8.86	10.92	9.02
		UA4805	9.44	11.56	2.95
		Ozark	7.80	11.63	6.14
		Osage	8.18	11.74	1.91
		5601T	7.78	19.07	2.88
	Japanese cvs. mean		8.70	9.66	8.78
	US cvs. mean		8.13	13.48	4.33
	Whole mean		8.37	11.84	6.24
2013	Japanese cvs.	Osuzu	9.95	13.43	2.28
		Enrei	10.03	7.70	8.75
		Tachinagaha	8.99	13.26	0.23
		Otsuru	10.08	10.46	7.19
		Sachiyutaka	11.01	9.05	3.26
		Tamahomare	10.64	8.14	6.41
		Fukuyutaka	9.37	4.50	17.94
	US cvs.	Athow	9.38	12.52	2.60
		LD00-3309	9.08	14.32	8.02
		Omaha	10.76	11.32	6.74
		5002T	9.79	10.62	4.47
		UA4805	9.83	9.25	3.73
		Ozark	9.99	10.69	4.03
		Osage	9.42	7.18	5.68
		5601T	9.51	12.13	4.40
	Japanese cvs. mean		10.01	9.51	6.58
	US cvs. mean		9.72	11.00	4.96
Whole mean		9.86	10.31	5.71	
ANOVA					
Year		36.40***	1.97NS	0.09NS	
Cultivar group		3.09NS	6.46*	1.93NS	
Year×Cultivar group		0.34NS	1.28NS	0.44NS	

Table 4.6. Dry matter distribution ratio to pod and pod growth rate of Japanese and US soybean cultivars.

			Pod distribution ratio (Emergence~R5) (g g ⁻¹)	Pod distribution ratio (R5~R5+30 d) (g g ⁻¹)	Pod growth rate (R5~R5+30 d) (g m ⁻² d ⁻¹)
2012	Japanese cvs.	Osuzu	0.094	1.016	11.63
		Enrei	0.071	1.060	10.57
		Tachinagaha	0.080	0.897	10.31
		Sachiyutaka	0.074	1.450	11.90
		Otsuru	0.077	1.114	12.27
		Fukuyutaka	0.091	0.665	8.12
		US cvs.	Athow	0.109	0.809
	Omaha		0.093	0.840	12.38
	LD00-3309		0.075	0.934	13.97
	5002T		0.088	1.258	13.39
	UA4805		0.117	1.207	12.95
	Ozark		0.121	0.628	8.30
	Osage		0.154	0.861	11.19
	5601T	0.144	0.724	15.50	
	Japanese cvs. mean		0.081	1.034	10.80
	US cvs. mean		0.113	0.908	12.65
	Whole mean		0.099	0.962	11.86
	2013	Japanese cvs.	Osuzu	0.064	0.646
Enrei			0.049	0.752	9.51
Tachinagaha			0.062	0.928	7.43
Otsuru			0.089	1.003	8.86
Sachiyutaka			0.091	0.952	10.13
Tamahomare			0.070	0.749	9.44
Fukuyutaka			0.066	2.264	10.40
US cvs.		Athow	0.102	0.758	10.38
		LD00-3309	0.111	0.825	11.84
		Omaha	0.125	0.841	9.93
		5002T	0.092	1.137	12.32
		UA4805	0.142	1.163	10.98
		Ozark	0.057	1.011	11.34
		Osage	0.087	1.519	11.19
5601T		0.101	1.133	13.41	
Japanese cvs. mean		0.070	1.042	9.39	
US cvs. mean		0.102	1.048	11.42	
Whole mean		0.087	1.045	10.47	
ANOVA					
Year		1.86NS	0.41NS	5.33*	
Cultivar group		15.69***	0.20NS	11.66**	
Year×Cultivar group		0.00NS	0.26NS	0.03NS	

4.4 Discussion

In Chapter 2, the author compared Japanese and US soybean cultivars and found that US soybean cultivars tend to show higher seed yield than that of Japanese cultivars. In the experiments of this Chapter, high yielding ability of US cultivars was confirmed again. The range of seed yield measured at Takatsuki was similar to the range of Chapter 2. But the seed yield and TDM weighed at Azuchi in 2011 were relatively lower than the value observed at Takatsuki in 2012 and 2013. Considering fairly high N fertility of the soils at those locations (Rajen et al., 2015), the difference in yield between Azuchi and Takatsuki may be caused by the difference in weather condition, particularly of solar radiation (Table 4.7). Across those different environments, however, the high yielding ability of US cultivars was observed. In addition, the results of TDM without abscised leaves and petioles and apparent HI were similar to the results in Chapter 2. These results suggest that better performance of US cultivars in growth and yield appeared quite consistent. Soybean had been improved typically in the improvement of lodging resistance, the consequent greater TDM, and increase in HI through the process of domestication and breeding (Egli, 2010). US cultivars tested in this experiment were relatively new cultivars as compared with Japanese cultivars. It is possible that US cultivars tend to show high harvest index as the result of selection pressure for yield to a greater extent compare to Japanese cultivars.

Table 4.7. Air temperature and solar radiation by month.

	Azuchi	Takatsuki	
	2011	2012	2013
Daily average radiation ($\text{MJ m}^{-2} \text{d}^{-1}$)			
Jun	14.0	15.3	17.1
Jul	15.7	18.9	19.8
Aug	15.9	19.5	19.8
Sep	11.8	15.1	16.0
Oct	10.3	13.0	11.0
Nov	6.9	8.3	9.4
Whole	12.5	15.0	15.5
Daily average temperature ($^{\circ}\text{C}$)			
Jun	22.7	23.0	24.3
Jul	26.5	27.8	28.5
Aug	27.0	29.4	30.0
Sep	23.2	26.0	25.1
Oct	17.0	19.3	20.8
Nov	12.4	12.4	12.9
Whole	21.5	23.0	23.6
Daily maximum temperature ($^{\circ}\text{C}$)			
Jun	26.9	27.4	28.9
Jul	31.0	32.0	32.9
Aug	32.0	34.3	34.8
Sep	28.0	30.7	30.0
Oct	22.1	23.9	24.6
Nov	16.9	15.9	17.0
Whole	26.2	27.4	28.0
Daily minimum temperature ($^{\circ}\text{C}$)			
Jun	19.3	19.8	21.0
Jul	22.8	24.8	25.3
Aug	23.2	25.8	26.6
Sep	19.2	22.7	21.4
Oct	12.3	15.5	17.8
Nov	8.2	9.3	9.2
Whole	17.5	19.6	20.2

The most important point of this experiment was comparison of “actual” dry matter production considering dry matter of abscised leaves and petioles between US and Japanese cultivars. Usually, the measurement of dry matter production does not contain abscised leaves and petioles for its easiness of measurement and existence of high correlation between apparent HI and actual HI (Kumudini, 2002). Only leaves and petioles attached to stems at maturity are measured. For this, it is difficult to detect the true dry matter production during seed filling period.

As mentioned above, the significant difference between US and Japanese cultivars was observed in seed yield across environments. However, no significant difference was observed between US and Japanese soybean cultivars in the TDW including abscised leaves and petioles at maturity. And significant differences in actual HI were observed in the experiments conducted in both 2012 and 2013. Importantly the difference between US and Japanese groups is considerably larger in actual HI than in apparent HI. Schapaugh and Wilcox (1980) reported a close relationship between actual HI and apparent HI. However, the correlation was relatively lower in the comparison of US and Japanese cultivar group than the value reported in Schapaugh and Wilcox (1980) (Fig. 4.2).

Morrison et al. (1999) compared 14 old and new soybean cultivars and reported that total dry matter at maturity was not significantly related to yield improvement but related to a corrected value of HI. In their study, total dry matter at maturity for calculation of HI was the sum of biomass at maturity plus leaf dry weight at R6. Though there is a possibility that estimation of true dry matter at maturity using leaf weight at R6 tend to overestimates because of ignoring remobilization (Kumudini, 2002), the result, a greater actual HI in higher yielding US cultivars, was quite similar.

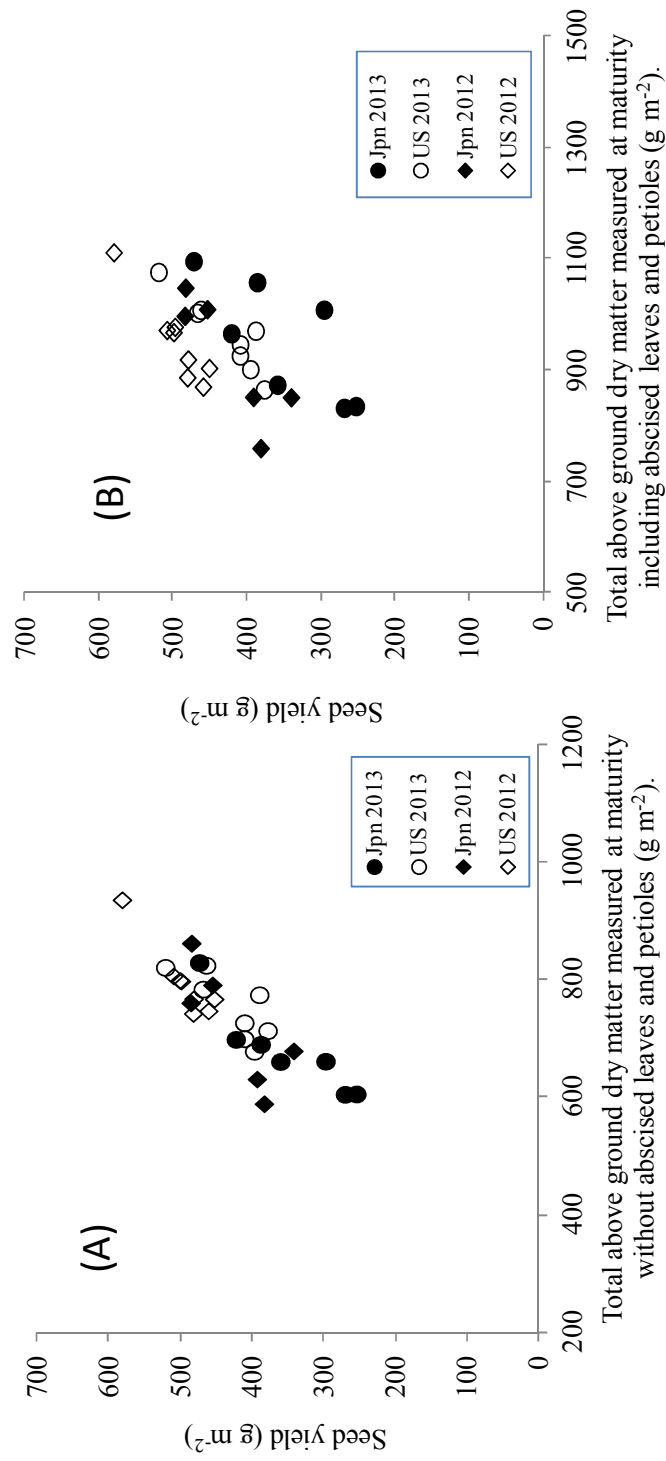


Fig. 4.2.(A) Relationship between seed yield and total above ground dry matter without abscised leaves and petioles.
(B) Relationship between seed yield and total above ground dry matter including abscised leaves and petioles.

As for the change in TDM, the relative dry matter production showed different tendency depending on growing stages. At Azuchi in 2011, Japanese cultivars tended to show similar or even greater dry matter production than US cultivars before R5. But US cultivars showed significantly higher dry matter productivity in the period from R5 to 30d after R5. In 2012 and 2013 also, throughout the comparison of eight US cultivars and seven Japanese cultivars, Japanese cultivars showed higher average values in the CGR from emergence to R5 and from 30d after R5 to R8. But in the period from R5 to 30d after R5, US cultivars showed a significantly higher CGR.

The dry matter accumulation before R5 occurs mainly in vegetative organs and the dry matter production after R5 in reproductive organs, typically in pod and seed growth. Actually, the pod growth rate from R5 to 30d after R5 was significantly higher in US cultivars and a high correlation was observed between pod growth rate and crop growth rate from R5 to 30d after R5.

From a comparison between a Japanese cultivar Tachinagaha and a US cultivar Stressland, Tanaka et al. (2008) reported that a higher photosynthetic activity of the uppermost leaves was maintained in Stressland during seed filling period. Thus it is very likely that the difference of dry matter productivity from R5 to 30d after R5 is attributable to leaf photosynthetic activity. The physiological factor of high and well sustained activity is not identified in this study. This would include high capacity of photosynthetic ability associated with stomatal conductance (Tanaka et al., 2010), sustained nitrogen (N) supply to plants by N fixation and consequent delay of leaf senescence (Sinclair and de Wit, 1976; Imsande, 1989), and/or absence of inhibitive factor of carbon fixation due to starch accumulation associated with insufficient sink

demand (Sincalir, 2004). Out of them, the difference of leaf photosynthetic capacity between US and Japanese cultivars has been evidenced (Tanaka et al., 2010). The other possibilities demand for further study.

Another significant difference was observed in DW distribution ratio to the pod before R5 between Japanese and US cultivar groups. Board and Harville (1993) reported the importance of CGR from R1 to R5 in terms of pod setting. However, CGR before R5 did not differ between US and Japanese cultivars. The difference in pod setting efficiency may exist between US and Japanese cultivars.

4.5 Conclusions

US soybean cultivars showed higher yields than Japanese cultivars. But, the difference in total dry matter at maturity including abscised leaves and petioles was not significant between US and Japanese cultivars. On the other hand, the actual HI including abscised leaves and petioles was higher in US cultivars as compared with Japanese cultivars. US cultivars showed a higher DM distribution ratio to the pod before R5 and pod growth rate from R5 to 30d after R5. CGR from R5 to 30d after R5 was greater in US cultivars and related to pod growth rate. The higher actual HI was associated with greater dry matter productivity during seed filling period and higher pod distribution before R5.

Chapter 5

General Discussion

5.1 Improvement in soybean yield

Soybean is currently a leading source of protein and oil for human food, animal feed, and industrial products. The future demand for soybeans will increase and the soybean yield must be improved to meet this demand (Kokubun, 2001; Ainsworth et al., 2012). Improvements in soybean yields are explained by greater TDM accumulation or an increase in the HI (Kumudini, 2002). Kumudini et al. (2001) compared old and new soybean cultivars in the MG00 and MG0 in Canada, and reported that the increased total dry matter accumulation contributed 78% and increased HI contributed 22% towards the genetic gains in yield. De Bruin and Peterson (2009) compared old and new soybean cultivars in Iowa and reported that new cultivars produced higher yields as a result of improved TDM accumulation. In Japan also dry matter productivity differs among cultivars (Shiraiwa et al., 2004), but improvement of seed yield has not been clearly demonstrated. Previous studies indicated that increased TDM accumulation contributed to improvement in yield relatively more than HI. In this study also, contribution of TDM accumulation to high yield of US cultivars was suggested in Chapter 2. However, the results of actual dry matter production and actual HI measured in Chapter 4 suggested the importance of higher actual HI. And higher actual HI was associated with higher partition of dry matter into pods before R5 and higher dry matter productivity after R5.

5.2 Possible plant traits for breeding suggested in this research

In this research, several possible plant traits for breeding high yield soybean were suggested. First, stability of pod or seed development was suggested. Board and Tan (1995) and Egli (1999) pointed the importance of pod setting before R5. In Chapter 4, the difference in dry matter distribution into pod at R5 was observed between US and Japanese cultivar group while no difference in CGR was observed. This means pod setting efficiency per dry matter accumulation largely differed between US and Japanese cultivars. Traits related to pod set, for example, node number, pod number per node and pod set ratio can be important. Dry matter productivity during early seed growth stage also can be important (Chapter 2 and Chapter 4). The author found the significant difference in CGR from R5 to 30d after R5 between US and Japanese cultivars (Chapter 4) and agreed with Shiraiwa et al. (2004). Shiraiwa et al. (2004) reported the importance of dry matter productivity from R5 to 20d after R5 for high yield. Narrowing the breeding target from CGR, leaf photosynthetic rate is an important and representative trait. Tanaka et al. (2008) found US cultivars tend to show higher potential stomatal conductance and stomatal density. The higher stomatal density often related to higher soil water consumption, however, the author found no interaction in the decrease in stomatal conductance between US and Japanese cultivar (Chapter 3). This suggested that there is a room in improving stomatal conductance at drained paddy field in Japan. As a trait related to photosynthesis, carbon fixation activity also can be important. Jiang et al. (1993) found relationship between photosynthetic rate and leaf Rubisco content. The author found diversity among cultivars in leaf Rubisco content during seed filling period. Sakoda et al. (2015) found some local cultivars showed

extremely high photosynthetic rate and related to leaf Rubisco content. Stomatal density and leaf Rubisco content can be measured from single leaf and these traits are genetically controlled. The investigation of Quantitative Trait Loci is supposed to be effective way to breed high yielding cultivar. Tanaka and Shiraiwa (2009) found *Dt1* had a positive effect on stomatal density and leaf gas change activity and discussed the possibility of introducing *Dt1*. In addition to stomatal density, *Dt1* has the great impact on the plant shape, stem length, and other agronomic traits (Heatherly and Elmore, 2004; Curtis et al. 2000). However, the effect on maturity is critical for field management and needs additional regulating genes.

5.3 Subject for further study

In Chapter 4, the difference of dry matter productivity from R5 to 30d after R5 is attributable to photosynthetic activity. However, still several possibilities remains. High capacity of photosynthetic ability associated with stomatal conductance (Tanaka et al., 2010), sustained nitrogen (N) supply to plants by N fixation and consequent delay of leaf senescence (Sinclair and de Wit, 1976; Imsande, 1989), and/or absence of inhibitive factor of carbon fixation due to starch accumulation associated with insufficient sink demand (Sincalir, 2004) was thought to be candidates. The measurement of the assimilate storage in the leaves and pod during seed filling period may give us detailed information. And if the results combined with of sink formation like pod setting, the traits related to photosynthesis can be useful indicator in breeding high yielding soybean.

In this study, almost all of the cultivars were supported artificially in order to prevent from lodging and measure potential biomass productivity. However, the improvement in lodging resistance in addition to yielding ability was observed in recent soybean cultivars (Luedders 1977; Boerma et al. 1979, Wilcox et al. 1979). Lodging resistance should be taken into consideration when breeding high yielding cultivar in Japan.

5.4 Conclusions

The author conducted cultivar comparisons under in total 8 environments differing year, location, planting date and soil moisture condition with special reference to the difference between Japanese and US cultivars. Across all environments, the US cultivar group exhibited greater yielding ability than Japanese cultivar group. Under optimum soil condition, high yield of US cultivars related to the amount of TDM(Chapter 2). Under drought, however, high yield of US cultivar related to stability of HI (Chapter 3). To narrow the breeding target, the author investigated “actual HI” including abscised leaves and petioles collected during seed filling period and found that US cultivars showed greater actual HI than Japanese cultivars (Chapter 4). These results indicate that the US cultivars are genetically improved in yielding ability for a range of environments. This also suggests that Japanese soybean cultivars would possibly be improved introducing plant traits from US cultivars.

Acknowledgments

At completing my seven years' work at Crop Science Laboratory, Graduate School of Agriculture, Kyoto University, I would like to acknowledge the following people for assisting my work. This could never be finished without their help. Above all, I would like to express my sincere gratitude to Professor Tatsuhiko Shiraiwa for his continuous direction and support throughout the long term study.

I am grateful to Dr. Tomoyuki Katsube-Tanaka, Dr. Koki Homma and Dr. Yu Tanaka for their insightful advice to this thesis. My appreciation also should be taken to Dr. Keisuke Katsura for his important contribution to the experiments at Takatsuki.

I am greatly appreciating to Dr. Larry C. Purcell (University of Arkansas) and Dr. Randall L. Nelson (University of Illinois) for cross location experiment in Chapter 2. A part of the experiment in Chapter 4 was supported by Hisanori Kawamura (Shiga Prefecture Agricultural Technology Promotion Center).

I never forget my special thanks to Dr. Custodio R. P. Tacarindua, Dr. Kenichiro Fujii, Dr. Sonia Hossain, Dr. Yasuko Fukuda, Mr. Yusaku Akamatsu, Mr. Rajen Bujgain, Mr. Keiichiro Nakashima, Mr. Akinori Yoshifuji, Mr. Kazuma Sakoda, Ms. Sanae Hane, Mr. Hiroto Katayama and other members of the Laboratory of Crop Science at Kyoto University, for their fruitful opinion on the study and for the collaborative work at the experimental field.

Finally, I deeply appreciate my parents for giving me the chance to study in the graduate school and mental and financial supports as well as encouragements.

January 2016

Yohei Kawasaki

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* In Japanese.

** In Japanese with English abstract.

*** In Japanese with English summary.

List of Publications

(Chapter 2)

Shiraiwa T., Kawasaki Y. and Homma K. 2011. Estimation of Crop Radiation Use Efficiency. *Jpn. J. Crop Sci.* 80: 360-364.

Kawasaki Y., Tanaka Y., Katsura K., Purcell L.C., and Shiraiwa T. 2016. Yield and Dry Matter Productivity of Japanese and US Soybean Cultivars. *Plant Prod. Sci.* (in press)

(Chapter 3)

Kawasaki Y., Tanaka Y., Katsura K., and Shiraiwa T. 2013. Yield and Dry Matter Production of Japanese and US Soybean Cultivars under Drought Stress. *Proc. the 7th Asian Crop Science Conference 2011* : 205-208.