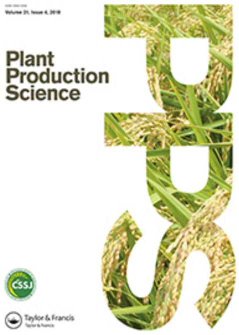

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# Yield and dry matter dynamics of vegetative and reproductive organs in Japanese and US soybean cultivars

Yohei Kawasaki[a,b], Keisuke Katsura[b,c] and Tatsuhiko Shiraiwa[b]

[a]Western Region Agricultural Research Center, National Agriculture and Food Research Organization (NARO), Fukuyama, Japan; [b]Graduate School of Agriculture, Kyoto University, Kyoto, Japan; [c]Graduate School of Agriculture, Tokyo University of Agriculture and Technology, Fuchu, Japan

**ABSTRACT**

Recently, US soybean cultivars have exhibited higher yields than Japanese soybean cultivars. To identify the determinants for this yield difference in reference to dry matter dynamics, recently developed US cultivars and Japanese commercial cultivars were cultivated in drained paddy fields in 2012 and 2013. The total dry matter (TDM) of each cultivar was measured at the initial seed-filling stage (R5), at 30 d after R5, and at maturity (R8). From R5 to R8, the DM of abscised leaves and petioles were measured. The actual HI (with abscised leaves and petioles) and apparent HI (without abscised leaves and petioles) were determined at R8. US soybean cultivars showed higher yields and apparent TDM (without abscised leaves and petioles) than did Japanese cultivars at R8. However, the difference in actual TDM (with abscised leaves and petioles) production was not significant between US and Japanese cultivars at R8. On the other hand, the actual HI was higher in US cultivars than in Japanese cultivars. US cultivars exhibited a higher TDM distribution to the pod before R5 and a higher pod growth rate from R5 to 30 d after R5. US cultivars tended to show greater crop growth rates (CGRs) from R5 to 30 d after R5. The higher yield in US cultivars was associated with the higher actual HI, which was considered attributable to a greater TDM productivity during the seed-filling period and higher DM distribution in the pod before R5.

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Dry matter production; harvest index; soybean; seed-filling stage; yield

**ABBREVIATIONS**
CGR: crop growth rate; HI: harvest index; LAI: leaf are index; TDM: total dry matter

## 1. Introduction

Soybean (*Glycine max* [L.] Merr.) is an important crop for its oil and protein content. The authors have previously found that recent US cultivars tended to exhibit higher seed yields than did Japanese commercial cultivars (Kawasaki, Tanaka, Katsura, Purcell, & Shiraiwa, 2016). It is necessary to determine key traits affecting seed yield to increase Japanese cultivar seed yields. The seed yield is the product of HI and total (aboveground) dry matter (TDM) at maturity. In Kawasaki et al. (2016), Japanese and US soybean cultivar seed yields correlated to a greater extent with DM at maturity than with HI. It was also found that the difference in DM between US and Japanese cultivars occurred after the initial seed-filling stage (R5; Fehr, Caviness, Burmood, & Pennington, 1971). These findings coincided with those of Cregan and Yaklich (1986), Kumudini, Hume, and Chu (2001), and De Bruin and Pedersen (2009), who reported the contribution of DM production to seed yield. However, most of the leaves and petioles were typically abscised during the late seed-filling period, and were not added into the measurement of DM at maturity in these experiments. Thus, the differences in HI and DM at maturity among cultivars in the previous experiments were 'apparent' and may not necessarily represent DM productivity and partitioning. Although measuring actual DM and actual HI is labor intensive (it entails frequent collection of abscised leaves and petioles), the relationship between seed yield and actual DM production is important to detect key traits for high yields in reference to the production and partitioning of DM.

Several reports have indicated that dry matter production during the seed-filling period is important for seed yield (Kumudini et al., 2001; Shiraiwa & Hashikawa, 1995; Shiraiwa, Ueno, Shimada, & Horie, 2004; Specht, Hume, & Kumudini, 1999). Wells, Schulze, Ashley, Boerma, and Brown (1982) and Boerma and Ashley (1988) reported that seed yield correlated with canopy photosynthesis during the seed-filling period. If this is true for the genotypic variation in DM productivity between US and Japanese soybean cultivars, information about photosynthesis during the seed-filling period would be necessary to narrow the breeding target for high yield cultivars. For example, Jin et al. (2010)

**CONTACT** Yohei Kawasaki kawasakiy566@affrc.go.jp

reported an increase in photosynthetic rate correlating to the year of release in Northeast China. Tanaka, Fujii, and Shiraiwa (2010) found that recent US soybean cultivars showed higher leaf stomatal densities and potential stomatal conductances than did Japanese cultivars at the seed-filling stage, which suggests that US cultivars have higher gas exchange capacities. Keep et al. (2016) observed a decrease in canopy temperature during reproductive growth correlating to the year of release in US cultivars; this indirectly suggests the possibility of improvement in gas change activity and photosynthetic activity, because canopy temperature is generally used as a proxy of stomatal conductance since the stomata opening promoted transpiration and thereby provided the heat removal canopy. And Tanaka, Shiraiwa, Nakajima, Sato, and Nakazaki (2008) pointed the relationship between photosynthetic rate and stomatal conductance from the observation of the progeny derived from US and Japanese cultivars. This information encourages physiological studies for increasing the photosynthetic rate and therefore obtaining a higher DM productivity. However, the direct association of actual DM productivity with yield is essential for this research direction, and has not yet been examined between US and Japanese soybean cultivars. On the other hand, Morisson, Voldeng, and Cober (1999) compared old and new cultivars in Canada, and found that an improvement in actual HI could be attributed to an improvement in seed yield. Although the study found improvements in photosynthetic rate and stomatal conductance, the correlation between the seed yield and actual HI was higher than that between the seed yield and actual TDM. This suggests that partitioning to seed yield, as well as actual DM production, is a key trait.

The objectives of the present study were to confirm the change in TDM during the seed-filling period, evaluate the effect of actual TDM productivity on seed yield, and identify the key trait that differentiates seed yield among cultivars. To achieve these objectives, US cultivars and Japanese cultivars were grown in drained paddy fields at Takatsuki in 2012 and 2013. The abscised leaves and petioles were collected during seed filling to measure the actual HI and actual DM production.

## 2. Materials and methods

In 2012 and 2013, field experiments were conducted at the Experimental Farm, Kyoto University, Takatsuki, Osaka, Japan (34°50′N). For both years, the seeds were sown in a drained paddy field (clay loam soil, Eutric Fluvisols) after adding fertilizers ($N:P_2O_5:K_2O$ = 3:10:10 g $m^{-2}$). Eight recently developed US cultivars (Athow, Omaha, LD00-3309, UA 4805, 5002T, Osage, Ozark, and 5601T) and six major Japanese cultivars (Ohsuzu, Enrei, Tachinagaha, Otsuru, Tamahomare, and Sachiyutaka), which were able to grow in warm regions of Japan with conventional planting dates and densities, were used in the experiment (Table 1). The planting density was 0.7 m by 0.15 m in 2012 and 0.8 m by 0.15 m in 2013. The dates of sowing were June 28 in 2012 and July 2 in 2013. Three replicates were arranged in a completely randomized block design. The single plot size was 2.8 m by 4.65 m in 2012 and 3.2 m by 4.65 m in 2013. Furrow irrigation was conducted to avoid drought. Weeding and agrochemical sprayings were conducted to maintain optimal conditions.

Meteorological data (daily solar radiation and temperature) were recorded. The growth stages (initial flowering stage [R1], R5, initial maturity stage [R7], and R8) based on Fehr et al. (1971) were recorded in both years. Twelve plants were harvested at the R5 stage and at 30 d after R5 from one replication of the experiment. The TDM, leaf DM, and pod DM were weighed after oven-drying for 72 h

**Table 1.** Cultivar entries, year of release, maturity group, and stem growth habit type.

| Cultivar | Year of release | Maturity group | Stem growth habit type | References |
|---|---|---|---|---|
| Japanese cvs. | | | | |
| Ohsuzu | 1998 | 3 | Determinate | Tabuchi et al. (1999) |
| Enrei | 1971 | 4 | Determinate | Ude, Kenworthy, Costa, Cregan, and Alvernaz (2003) |
| Otsuru | 1988 | 4 | Determinate | Ude et al. (2003) |
| Tachinagaha | 1986 | 5 | Determinate | Ude et al. (2003) |
| Tamahomare | 1980 | 6 | Determinate | Fatichin et al. (2013) |
| Sachiyutaka | 2001 | 6 | Determinate | Fatichin et al. (2013) |
| US cvs. | | | | |
| Athow | 1996 | 3 | Indeterminate | Wilcox and Abney (1997) |
| Omaha | 1996 | 4 | Indeterminate | Nickell, Bachman, Thomas, and Cary (1998) |
| LD00-3309 | 2005 | 4 | Indeterminate | Diers, Cary, Thomas, and Nickell (2006) |
| UA 4805 | 2005 | 4 | Determinate | Chen, Sneller, Rupe, Riggs, and Robbins (2006) |
| 5002T | 2002 | 5 | Determinate | Pantalone, Allen, and Landau-Ellis (2004) |
| Osage | 2007 | 5 | Determinate | Chen, Sneller, Mozzoni, and Rupe (2007) |
| Ozark | 2004 | 5 | Determinate | Chen, Sneller, Rupe, and Riggs (2004) |
| 5601T | 2001 | 5 | Determinate | Pantalone, Allen, and Landau-Ellis (2003) |

at 80°C. The CGR and pod growth rate were calculated from the change in DM. After R5, a black net was applied to a 1.26 $m^2$ area (1.4 m by 0.9 m) in 2012 and a 1.44 $m^2$ area (1.6 m by 0.9 m) in 2013, completely covering two inter-rows. The abscised leaves and petioles were periodically collected and weighed. The seed yield and TDM were measured in 12 plants at R8. The apparent HI and actual HI were calculated using the apparent and actual TDM, respectively. To evaluate the DM dynamics after R5 in detail, the ratio of change in DM in the leaves and petioles from R5 to R8 (ΔLDM) was calculated by following equation:

$$(\Delta \mathrm{LDM}) = \frac{(LDMR5) - (LDMR8)}{LDMR5}$$

,

where *LDWR5* is the DM of the leaves and petioles attached at R5, and *LDWR8* is the sum of the DM of the leaves and petioles attached at R8 and abscised after R5.

The effect of the cultivar group (six Japanese cvs., eight US cvs.) and year were analyzed for the Takatsuki 2012 and 2013 experiments using analysis of variance (ANOVA). All statistical analyses were conducted using Microsoft Excel (Microsoft, Redmond, WA, US).

## 3. Results

### 3.1. Meteorological data

The meteorological data recorded at Takatsuki in 2012 and 2013 are shown in Table 2. The daily solar radiation during the whole growing season (June to November) was slightly higher in 2013, due to higher solar radiation from July to September. The maximum, minimum, and daily average temperatures were higher in 2013. Although the meteorological data differed between the two years, the meteorological trends in Takatsuki in 2012 and 2013 were quite similar.

**Table 2.** Solar radiation and air temperature by month at Takatsuki (34°50′N).

| | 2012 | 2013 |
|---|---|---|
| Daily average solar radiation (MJ $m^{-2}$ $d^{-1}$) | | |
| Jun | 15.3 | 17.1 |
| Jul | 18.9 | 19.8 |
| Aug | 19.5 | 19.8 |
| Sep | 15.1 | 16.0 |
| Oct | 13.0 | 11.0 |
| Nov | 8.3 | 9.4 |
| Whole | 15.0 | 15.5 |
| Daily average air temperature (℃) | | |
| Jun | 23.0 | 24.3 |
| Jul | 27.8 | 28.5 |
| Aug | 29.4 | 30.0 |
| Sep | 26.0 | 25.1 |
| Oct | 19.3 | 20.8 |
| Nov | 12.4 | 12.9 |
| Whole | 23.0 | 23.6 |
| Daily maximum air temperature (℃) | | |
| Jun | 27.4 | 28.9 |
| Jul | 32.0 | 32.9 |
| Aug | 34.3 | 34.8 |
| Sep | 30.7 | 30.0 |
| Oct | 23.9 | 24.6 |
| Nov | 15.9 | 17.0 |
| Whole | 27.4 | 28.0 |
| Daily minimum air temperature (℃) | | |
| Jun | 19.8 | 21.0 |
| Jul | 24.8 | 25.3 |
| Aug | 25.8 | 26.6 |
| Sep | 22.7 | 21.4 |
| Oct | 15.5 | 17.8 |
| Nov | 9.3 | 9.2 |
| Whole | 19.6 | 20.2 |

### 3.2. Field experiments in 2012 and 2013

The growth stages of the Japanese and the US soybean cultivars measured at Takatsuki in 2012 and 2013 are shown in Table 3. R1 ranged from July 29 (Athow) to August 12 (Osage) in 2012, and from July 27 (Athow) to August 13 (Osage) in 2013. R5 ranged from August 20 (Ohsuzu) to September 8 (Osage) in 2012 and from August 18 (Ohsuzu) to September 16 (5601T) in 2013. R7 ranged from October 5 (Ohsuzu) to October 28 (5601T) in 2012 and from October 4 (Ohsuzu) to November 1 (5601T) in 2013. R8 ranged from October 12 (Ohsuzu) to November 5 (5601T) in 2012 and from October 12 (Ohsuzu) to November 9 (5601T) in 2013. The trends were similar for 2012 and 2013.

The results for the seed yield, actual and apparent TDM, and DM of abscised leaves and petioles measured at Takatsuki in 2012 and 2013 are shown in Table 4. (Tamahomare was excluded from the analysis because of poor emergence.) The seed yield ranged from 254 g $m^{-2}$ (Tachinagaha) in 2013 to 581 g $m^{-2}$ (5601T) in 2012. The apparent TDM at R8 ranged from 585 g $m^{-2}$ (Ohsuzu) in 2012 to 931 g $m^{-2}$ (5601T) in 2012. The actual TDM ranged from 757 g $m^{-2}$ (Ohsuzu) in 2012 to 1,109 g $m^{-2}$ (5601T) in 2012. The DM of abscised leaves and petioles ranged from 124 g $m^{-2}$ (LD00-3309) in 2012 to 369 g $m^{-2}$ (Tamahomare) in 2013. The seed yield was significantly greater in 2012 than in 2013. The seed yield and apparent TDM in the US cultivars were significantly greater than those in the Japanese cultivars. The difference in actual TDM between the Japanese and the US cultivar groups was not significant. The DM of the abscised leaves and petioles was significantly higher in 2013 than in 2012, and was significantly higher in the Japanese cultivar group than in the US cultivar group. Though three indeterminate cultivars were applied in this experiment, the differences in seed yield, apparent TDM and actual TDM between indeterminate cultivar group and determinate cultivar group were not significant (data not shown). The effects

**Table 3.** Growth stage of Japanese and US cultivars.

| | 2012 | | | | 2013 | | | |
|---|---|---|---|---|---|---|---|---|
| | R1 | R5 | R7 | R8 | R1 | R5 | R7 | R8 |
| Japanese cvs. | | | | | | | | |
| Ohsuzu | Aug 2 | Aug 20 | Oct 5 | Oct 12 | Aug 1 | Aug 18 | Oct 4 | Oct 12 |
| Enrei | Aug 4 | Aug 24 | Oct 11 | Oct 20 | Aug 3 | Aug 22 | Oct 7 | Oct 21 |
| Otsuru | Aug 5 | Aug 27 | Oct 17 | Oct 28 | Aug 7 | Aug 29 | Oct 20 | Oct 31 |
| Tachinagaha | Aug 3 | Aug 24 | Oct 16 | Oct 29 | Aug 2 | Aug 21 | Oct 8 | Oct 28 |
| Tamahomare | Aug 7 | Aug 31 | Oct 17 | Oct 25 | Aug 8 | Sep 7 | Oct 31 | Nov 6 |
| Sachiyutaka | Aug 8 | Sep 1 | Oct 21 | Oct 27 | Aug 8 | Sep 4 | Oct 21 | Nov 1 |
| US cvs. | | | | | | | | |
| Athow | Jul 29 | Aug 23 | Oct 8 | Oct 15 | Jul 27 | Aug 20 | Oct 6 | Oct 13 |
| Omaha | Jul 30 | Aug 24 | Oct 10 | Oct 19 | Jul 30 | Aug 25 | Oct 9 | Oct 21 |
| LD00-3309 | Jul 28 | Aug 25 | Oct 10 | Oct 20 | Jul 29 | Aug 23 | Oct 9 | Oct 29 |
| UA 4805 | Aug 10 | Aug 31 | Oct 19 | Oct 28 | Aug 11 | Sep 3 | Oct 19 | Oct 31 |
| 5002T | Aug 10 | Aug 30 | Oct 13 | Oct 25 | Aug 10 | Sep 2 | Oct 19 | Oct 31 |
| Osage | Aug 12 | Sep 8 | Oct 20 | Oct 28 | Aug 13 | Sep 10 | Oct 26 | Nov 3 |
| Ozark | Aug 9 | Sep 3 | Oct 22 | Oct 30 | Aug 10 | Sep 2 | Oct 27 | Nov 4 |
| 5601T | Aug 9 | Sep 3 | Oct 28 | Nov 5 | Aug 11 | Sep 12 | Nov 1 | Nov 9 |

**Table 4.** Yield, total DMs, and DM of abscised leaves and petioles at maturity of Japanese and US soybean cultivars.

| | | | Seed yield (g $m^{-2}$)[1] | Apparent TDM (g $m^{-2}$) | Actual TDM (g $m^{-2}$) | DM of abscised leaves and petioles (g $m^{-2}$) |
|---|---|---|---|---|---|---|
| 2012 | Japanese cvs. | Ohsuzu | 383 | 585 | 757 | 172 |
| | | Enrei | 393 | 627 | 849 | 222 |
| | | Otsuru | 455 | 787 | 1007 | 220 |
| | | Tachinagaha | 342 | 675 | 848 | 173 |
| | | Sachiyutaka | 485 | 756 | 995 | 239 |
| | US cvs. | Athow | 482 | 739 | 884 | 145 |
| | | Omaha | 452 | 763 | 901 | 138 |
| | | LD00-3309 | 461 | 743 | 867 | 124 |
| | | UA 4805 | 498 | 794 | 975 | 181 |
| | | 5002T | 509 | 802 | 969 | 167 |
| | | Osage | 481 | 763 | 916 | 153 |
| | | Ozark | 500 | 795 | 965 | 170 |
| | | 5601T | 581 | 931 | 1109 | 178 |
| | Japanese cvs. mean | | 411 | 686 | 891 | 205 |
| | US cvs. mean | | 496 | 791 | 948 | 157 |
| | Whole mean | | 463 | 751 | 926 | 176 |
| 2013 | Japanese cvs. | Ohsuzu | 360 | 657 | 871 | 214 |
| | | Enrei | 270 | 601 | 829 | 228 |
| | | Otsuru | 297 | 657 | 1006 | 349 |
| | | Tachinagaha | 254 | 602 | 832 | 230 |
| | | Tamahomare | 387 | 686 | 1055 | 369 |
| | | Sachiyutaka | 422 | 694 | 963 | 269 |
| | US cvs | Athow | 378 | 709 | 862 | 153 |
| | | Omaha | 389 | 770 | 968 | 198 |
| | | LD00-3309 | 464 | 820 | 1005 | 185 |
| | | UA 4805 | 397 | 674 | 899 | 225 |
| | | 5002T | 410 | 723 | 943 | 220 |
| | | Osage | 411 | 695 | 923 | 228 |
| | | Ozark | 468 | 780 | 1000 | 220 |
| | | 5601T | 521 | 817 | 1073 | 256 |
| | Japanese cvs. mean | | 332 | 650 | 926 | 277 |
| | US cvs. mean | | 430 | 749 | 959 | 211 |
| | Whole mean | | 388 | 706 | 945 | 239 |
| ANOVA[2] | | | | | | |
| | Year | | 12.28** | 2.75NS | 0.47NS | 16.24*** |
| | Cultivar group | | 19.16*** | 18.28*** | 1.85NS | 13.54** |
| | Year × Cultivar group | | 0.12NS | 0.02NS | 0.13NS | 0.33NS |

[1] Seed weight with a 14% moisture content.
[2] †, *,**,*** F values significance at 0.10, 0.05, 0.01 and 0.001 probability levels, respectively. NS means nonsignificant at $P = 0.10$ level.

**Table 5.** Crop growth rate from emergence to R5, dry matter distribution to pod and leaf, and LAI of Japanese and US cultivars at R5.

| | | | CGR (Emergence – R5) ($g\ m^{-2}\ d^{-1}$) | DM distribution to pod at R5 ($g\ g^{-1}$) | DM distribution to leaf at R5 ($g\ g^{-1}$) | LAI at R5 |
|---|---|---|---|---|---|---|
| 2012 | Japanese cvs. | Ohsuzu | 8.31 | 0.067 | 0.294 | 3.73 |
| | | Enrei | 8.98 | 0.079 | 0.274 | 4.19 |
| | | Otsuru | 8.86 | 0.088 | 0.266 | 4.93 |
| | | Tachinagaha | 8.68 | 0.104 | 0.280 | 4.18 |
| | | Sachiyutaka | 9.51 | 0.086 | 0.241 | 4.68 |
| | US cvs. | Athow | 7.32 | 0.118 | 0.282 | 3.46 |
| | | Omaha | 8.55 | 0.088 | 0.246 | 4.06 |
| | | LD00-3309 | 7.08 | 0.074 | 0.273 | 3.94 |
| | | UA 4805 | 9.44 | 0.130 | 0.225 | 4.37 |
| | | 5002T | 8.86 | 0.061 | 0.242 | 4.16 |
| | | Osage | 8.18 | 0.120 | 0.212 | 4.17 |
| | | Ozark | 7.80 | 0.095 | 0.218 | 4.17 |
| | | 5601T | 7.78 | 0.085 | 0.215 | 3.46 |
| | Japanese cvs. mean | | 8.87 | 0.085 | 0.271 | 4.34 |
| | US cvs. mean | | 8.13 | 0.096 | 0.239 | 3.97 |
| | Whole mean | | 8.41 | 0.092 | 0.251 | 4.12 |
| 2013 | Japanese cvs. | Ohsuzu | 9.95 | 0.064 | 0.364 | 5.33 |
| | | Enrei | 10.03 | 0.049 | 0.354 | 6.07 |
| | | Otsuru | 10.08 | 0.086 | 0.312 | 5.52 |
| | | Tachinagaha | 8.99 | 0.062 | 0.361 | 3.79 |
| | | Tamahomare | 10.64 | 0.070 | 0.287 | 6.11 |
| | | Sachiyutaka | 11.01 | 0.091 | 0.321 | 7.28 |
| | US cvs. | Athow | 9.38 | 0.102 | 0.323 | 5.30 |
| | | Omaha | 10.76 | 0.125 | 0.289 | 5.44 |
| | | LD00-3309 | 9.08 | 0.111 | 0.327 | 4.98 |
| | | UA 4805 | 9.83 | 0.142 | 0.278 | 5.28 |
| | | 5002T | 9.79 | 0.093 | 0.300 | 6.29 |
| | | Osage | 9.42 | 0.087 | 0.251 | 4.95 |
| | | Ozark | 9.99 | 0.058 | 0.271 | 6.18 |
| | | 5601T | 9.51 | 0.100 | 0.279 | 5.93 |
| | Japanese cvs. mean | | 10.11 | 0.070 | 0.333 | 5.68 |
| | US cvs. mean | | 9.72 | 0.102 | 0.290 | 5.54 |
| | Whole mean | | 9.89 | 0.089 | 0.308 | 5.60 |
| ANOVA[1)] | | | | | | |
| | Year | | 32.06*** | 0.26NS | 29.40*** | 30.91*** |
| | Cultivar group | | 5.14* | 6.70* | 13.10** | 0.9NS |
| | Year × Cultivar group | | 0.47NS | 0.24NS | 0.31NS | 0.19NS |

1) †, *,**,*** F values significance at 0.10, 0.05, 0.01 and 0.001 probability levels, respectively. NS means nonsignificant at $P = 0.10$ level.

of year × cultivar group interaction in the seed yield, apparent TDM, actual TDM, or DM of abscised leaves and petioles were not significant.

Table 5 shows the CGR from emergence to R5, DM distribution to pod at R5 (pod distribution ratio, pod dry matter at R5/TDM at R5), DM distribution to leaf at R5 (leaf distribution ratio, leaf DM at R5/TDM at R5) and leaf area index (LAI) of the Japanese and the US cultivars measured in 2012 and 2013. The 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. The effects of year and cultivar group on CGR from emergence to R5 were both significant. The CGR from emergence to R5 was greater in 2013 than in 2012. Japanese cultivars showed higher CGR from emergence to R5. The pod distribution ratio ranged from 0.049 (Enrei) in 2013 to 0.142 (UA 4805) in 2013. The US cultivars showed significantly higher pod distribution ratios at R5. The effects of year and year × cultivar group interaction on pod distribution were not significant. The leaf distribution ratio ranged from 0.212 (Osage) in 2012 to 0.364 (Ohsuzu) in 2012. Leaf distribution ratio at R5 was significantly higher in 2013 than in 2012. Japanese cultivars showed significantly higher leaf distribution ratio at R5. The LAI was significantly higher in 2013 than in 2012, and ranged from 3.46 (Athow and 5601T) in 2012 to 7.28 (Sachiyutaka) in 2013. The difference in LAI between the cultivar groups and the effect of year × cultivar group interaction on LAI were not significant.

Table 6 shows the CGRs after R5 (from R5 to 30 d after R5, from 30 d after R5 to R8), pod growth rate, and apparent and actual HIs. The CGR from R5 to 30 d after R5 ranged from 7.70 $g\ m^{-2}\ d^{-1}$ (Enrei) in 2013 to 19.07 $g\ m^{-2}\ d^{-1}$ (5601T) in 2012. The US cultivar group tended to show a higher CGR from R5 to 30 d after R5 than did the Japanese cultivar group ($P < 0.10$). The effects of the year and year × cultivar group interaction on the CGR from R5 to 30 d after R5 were not significant. The CGR from 30 d after R5 to R8 ranged from 0.23 $g\ m^{-2}\ d^{-1}$ (Otsuru) in 2013 to 9.02 $g\ m^{-2}\ d^{-1}$ (5002T) in 2012. The difference in CGR for the period from 30 d after R5 to R8 between the two cultivar groups was not significant. The effects of the year and

**Table 6.** Crop growth rates after R5, pod growth rate, ratio of DM in leaf and petiole changed from R5 to R8 (ΔLDM), apparent HI and actual HI of Japanese and US cultivars.

| | | | CGR (R5 − R5 + 30d) ($g\ m^{-2}\ d^{-1}$) | CGR (R5 + 30d − R8) ($g\ m^{-2}\ d^{-1}$)[1] | Pod growth rate (R5 − R5 + 30 d) ($g\ m^{-2}\ d^{-1}$) | ΔLDM ($g\ g^{-1}$) | Apparent HI | Actual HI[1] |
|---|---|---|---|---|---|---|---|---|
| 2012 | Japanese cvs. | Ohsuzu | 10.47 | 2.74 | 11.63 | 0.229 | 0.563 | 0.435 |
| | | Enrei | 10.59 | 3.25 | 10.57 | 0.140 | 0.539 | 0.398 |
| | | Otsuru | 8.21 | 6.90 | 12.27 | 0.157 | 0.497 | 0.389 |
| | | Tachinagaha | 11.74 | 1.50 | 10.31 | 0.308 | 0.436 | 0.346 |
| | | Sachiyutaka | 12.24 | 8.77 | 11.90 | 0.219 | 0.552 | 0.419 |
| | US cvs. | Athow | 14.65 | 4.90 | 13.55 | 0.260 | 0.561 | 0.469 |
| | | LD00-3309 | 15.93 | 2.06 | 13.97 | 0.377 | 0.533 | 0.457 |
| | | Omaha | 12.36 | 4.81 | 12.38 | 0.373 | 0.510 | 0.432 |
| | | UA 4805 | 11.56 | 2.95 | 12.95 | 0.317 | 0.540 | 0.440 |
| | | 5002T | 10.92 | 9.02 | 13.39 | 0.332 | 0.546 | 0.452 |
| | | Osage | 11.74 | 1.91 | 11.19 | 0.346 | 0.542 | 0.451 |
| | | Ozark | 11.63 | 6.14 | 8.30 | 0.286 | 0.541 | 0.446 |
| | | 5601T | 19.07 | 2.88 | 15.50 | 0.236 | 0.536 | 0.451 |
| | Japanese cvs.mean | | 10.65 | 4.63 | 11.34 | 0.211 | 0.517 | 0.397 |
| | US cvs. mean | | 13.48 | 4.33 | 12.65 | 0.316 | 0.539 | 0.450 |
| | Whole mean | | 12.39 | 4.45 | 12.15 | 0.275 | 0.530 | 0.430 |
| 2013 | Japanese cvs | Ohsuzu | 13.43 | 2.28 | 9.93 | 0.177 | 0.472 | 0.356 |
| | | Enrei | 7.70 | 8.75 | 9.51 | 0.156 | 0.386 | 0.280 |
| | | Otsuru | 10.46 | 7.19 | 8.86 | −0.141 | 0.389 | 0.254 |
| | | Tachinagaha | 13.26 | 0.23 | 7.43 | 0.132 | 0.363 | 0.263 |
| | | Tamahomare | 8.14 | 6.41 | 9.44 | 0.031 | 0.486 | 0.316 |
| | | Sachiyutaka | 9.05 | 3.26 | 10.13 | 0.303 | 0.523 | 0.377 |
| | US cvs. | Athow | 12.52 | 2.60 | 10.38 | 0.329 | 0.458 | 0.377 |
| | | Omaha | 11.32 | 6.74 | 9.93 | 0.275 | 0.435 | 0.346 |
| | | LD00-3309 | 14.32 | 8.02 | 11.84 | 0.196 | 0.486 | 0.397 |
| | | UA 4805 | 9.25 | 3.73 | 10.98 | 0.277 | 0.506 | 0.379 |
| | | 5002T | 10.62 | 4.47 | 12.32 | 0.288 | 0.488 | 0.374 |
| | | Osage | 7.18 | 5.68 | 11.19 | 0.224 | 0.508 | 0.382 |
| | | Ozark | 10.69 | 4.03 | 11.34 | 0.317 | 0.516 | 0.403 |
| | | 5601T | 12.13 | 4.40 | 13.41 | 0.217 | 0.548 | 0.417 |
| | Japanese cvs. mean | | 10.34 | 4.69 | 9.22 | 0.110 | 0.437 | 0.308 |
| | US cvs. mean | | 11.00 | 4.96 | 11.42 | 0.265 | 0.493 | 0.384 |
| | Whole mean | | 10.72 | 4.84 | 10.48 | 0.199 | 0.469 | 0.352 |
| ANOVA[2] | | | | | | | | |
| | Year | | 2.22NS | 0.11NS | 8.60** | 5.15* | 14.11** | 41.70*** |
| | Cultivar group | | 3.50† | 0.00NS | 9.52** | 15.28*** | 5.35* | 28.87*** |
| | Year × Cultivar group | | 1.34NS | 0.08NS | 0.61NS | 0.57NS | 1.11NS | 1.02NS |

[1] Including abscised leaves and petioles.
[2] †, *,**,*** F values significance at 0.10, 0.05, 0.01 and 0.001 probability levels, respectively. NS means nonsignificant at $P = 0.10$ level.

year × cultivar group interaction on the CGR for the period from 30 d after R5 to R8 were not significant. The pod growth rates from R5 to 30 d 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. Pod growth rates from R5 to 30 d after R5 were significantly greater in 2012 than in 2013. The US cultivar group showed a higher pod growth rate. The effect of year × cultivar group interaction on the pod growth rate was not significant. The change in the ratio of DM in the leaves and petioles from R5 to R8 (ΔLDM) ranged from –0.141 $g\ g^{-1}$ (Otsuru) in 2013 to 0.377 $g\ g^{-1}$ (LD00-3309) and the change in the US cultivar group was significantly greater than that in the Japanese cultivar group. The apparent HI was significantly higher in 2012 than in 2013, with a range from 0.363 (Tachinagaha) in 2013 to 0.552 (Sachiyutaka) in 2012, and was higher in the US cultivar group than in the Japanese cultivar group. The effect of year × cultivar group interaction on the apparent HI was not significant. The actual HI ranged from 0.254 (Otsuru) to 0.457 (LD00-3309), and was significantly higher in 2012 than in 2013. The US cultivar group showed a higher actual HI than did the Japanese cultivar group. The difference between indeterminate cultivar group and determinate cultivar group in actual HI of US soybean cultivar group was not significant (data not shown). The effect of year × cultivar group interaction on the actual HI was not significant.

## 4. Discussion

In a previous report, the authors compared Japanese and the US soybean cultivars, and found that the US soybean cultivars tended to show higher seed yields than did Japanese cultivars (Kawasaki et al., 2016); the results of the present study confirmed the high yielding ability of US cultivars. The range in seed yield recorded in this experiment was similar to that in the previous report. Although the yield comparison was conducted between recent commercial cultivars in US and Japan, the US cultivars tested in this experiment were relatively new cultivars compared to those from Japan (Kawasaki et al., 2016). Rincker et al. (2015) reported that increases in yield accelerated in US cultivars after the 1970s and pointed the contribution of the increase in the number of soybean breeders in commercial company or public sector to the genetic gain in seed yield. On the other hand, Ministry of Agriculture, Forestry and Fisheries (2018) reported that major commercial cultivars in warm regions in Japan were Tachinagaha, Enrei, Sachiyutaka, and Fukuyutaka in 2015. Among these four cultivars, the latest release is 2001 (Sachiyutaka) and the oldest release was 1971 (Enrei). That mean Enrei was commercially cultivated more than 40 years in Japan. While recent US cultivars endured severe yield pressure and obtained high yielding abilities, the renewal of commercial cultivars has been slower in Japan than in the US; this could be a reason for the gap in yielding ability between US and Japanese soybean cultivars.

The aim of this experiment was to compare actual DM production between US and Japanese cultivars; without this information, it is difficult to identify the important factors that differentiate yield. For ease of measurement, and because of the strong correlation between apparent HI and actual HI, DM measurements usually do not contain abscised leaves and petioles (Kumudini, 2002). Only leaves and petioles attached to the stems at maturity are measured. However, this makes it difficult to detect the actual DM production during the seed-filling period.

The difference in actual TDM at maturity between US and Japanese soybean cultivars was not significant. US cultivars achieved a greater CGR or pod growth rate after R5 with smaller distribution to leaves at R5. The Japanese cultivars showed higher average CGR values from emergence to R5 ($P < 0.05$) and the US cultivars tended to show higher CGRs from R5 to 30 d after R5 ($P < 0.10$). Japanese cultivars also showed a significantly greater DM distribution to leaves at R5. On the other hand, US cultivars showed a higher dry matter distribution to pods instead of leaves at R5. Board and Harville (1993) reported the importance of CGR from R1 to R5 in terms of pod setting. The above finding further suggests that a difference in pod-setting efficiency may exist between US and Japanese cultivars. The pod growth rate from R5 to 30 d after R5 was significantly higher in US cultivars than in Japanese. The greater CGR before R5 in the Japanese cultivar group could be attributed to its larger LAI during its early growing stages (Kawasaki, Tanaka, Katsura, & Shiraiwa, 2013).

On the other hand, the greater CGR at 30 d after R5 in US cultivar group could be attributed to its higher photosynthetic activity. From a comparison between the Japanese cultivar Tachinagaha and the US cultivar Stressland, Tanaka et al. (2008) reported that Stressland exhibited a higher photosynthetic rate in its uppermost leaves during the seed-filling period, from R5 to around 30 d after R5. Though in this experiment, R7 ranged approximately 3wk in both US and Japanese cultivar groups, the clear trend in CGR from R5 to 30 d after R5 was not observed between early and late maturing cultivars in both cultivar groups. In this experiment, the difference in LAI between the US and Japanese cultivars was not significant. Thus, it is likely that the difference in DM productivity from R5 to 30 d after R5 is attributable to leaf photosynthetic activity. In the present study, the physiological factor determining high and sustained activity was not identified, but could include associations with stomatal conductance (Tanaka et al., 2010), sustained nitrogen (N) supply to plants by N fixation and consequent delay of leaf senescence (Imsande, 1989; Sinclair & De Wit, 1976), and/or the absence of inhibitive factors of carbon fixation due to starch accumulation associated with insufficient sink demand (Sinclair, 2004). Although the difference in leaf photosynthetic capacity between US and Japanese cultivars has been evidenced (Tanaka et al., 2010), the other possibilities demand further study. In addition, the stem growth habit type also might play an important role in yielding ability. However, the effects on seed yield, apparent TDM and actual TDM were not significant in this experiment. Further research is also needed to reveal the relationship between dry matter productivity and photosynthetic capacity.

Significant differences in actual HI were observed in the experiments conducted in both 2012 and 2013. Importantly, the difference between US and Japanese groups in actual HI was considerably larger than that in apparent HI. This suggests that the importance of DM distribution from the context of yielding ability was under estimated in the previous report; this means that the difference in DM distribution was emphasized by measuring the actual HI. Morisson et al. (1999) compared 14 old and new soybean cultivars, and reported that the TDM at maturity was not significantly related to the yield improvement, but related to a corrected HI value. In their study, the TDM at maturity used for the calculation of HI was the sum of biomass at maturity plus leaf dry weight at R6. Although it is possible that the estimation of actual DM at maturity using the leaf weight at R6 may overestimate the DM because it ignores remobilization (Kumudini, 2002), their finding of greater actual HI in higher yielding US cultivars was in accordance with the present study. Compared to Morisson et al. (1999), our results did not contain estimations due to the direct collection of abscised leaves and petioles after R5, and clarify the importance of actual HI. In addition, by measuring the change in the ratio of DM in the leaves and petioles from R5 to R8, it was observed that the Japanese cultivar group tended to lose a larger amount of DM than did the US cultivar group at R8. Further research is needed on canopy respiration and retranslocation, US cultivar group supposed to distribute or collect assimilate supply effectively. This was the first report that measuring actual DM production and its distribution in order to elucidate the genetic difference in yielding ability of soybeans.

## 5. Conclusions

US soybean cultivars showed higher yields than did Japanese cultivar group. The difference in actual TDM at maturity was not significant between the US and Japanese cultivars. On the other hand, the actual HI was significantly higher in US cultivars than in Japanese cultivars. US cultivars exhibited a higher pod distribution ratio before R5 and pod growth rate from R5 to 30 d after R5. CGR from R5 to 30 d after R5 were greater in US cultivars and related to pod growth rates. Therefore, the higher actual HI was associated with greater DM productivity during the seed-filling period and higher pod distribution before R5.

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No potential conflict of interest was reported by the authors.

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