The Relationship between Dry Matter Increase of Seed and Shoot during the Seed-Filling Period in Three Kinds of Soybeans with Different Growth Habits Subjected to Shading and Thinning

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Abstract: The ratio of dry-matter increase in seed (S) to that in shoot (W), referred to as $R_{S/W}$, during the seed-filling period may reflect the balance between the assimilate supply and the sink capacity of harvest organs. In the determinate soybean, cv. Tamahomare, $R_{S/W}$ during the seed-filling period was nearly the same under various growing conditions including shading and thinning of plants. Therefore, the S in the determinate soybean seems to correlate with the W under various conditions. However, the correlation of the S with the W in indeterminate soybeans in which shoot growth continues during the seed-filling period is unknown. In this study, three soybean cultivars [*Glycine max* (L.) Merr.], Tamahomare (determinate), Tozan69 (indeterminate) and Peking (semi-indeterminate), were grown under shading and thinning conditions during the seed-filling period. The $R_{S/W}$ approximated a positive linear regression in the three cultivars. $R_{S/W}$ was approximately 0.5 in each cultivar. Positive correlations were observed between W and S, pod number or total node number in all cultivars. However, the seed number per pod and individual seed weight were not significantly influenced either by shading or thinning in any cultivar. Hence the rate of partition of assimilate to seeds seems to be determined by pod number. Harvest index was stable except when W was extremely low as when plants were heavily shaded. Our results suggested that the $R_{S/W}$, harvest index and the yield-determining processes of the determinate and the indeterminate soybeans are fundamentally the same.

Key words: Determinate, Dry matter, Harvest Index, Indeterminate, Soybean.

Dry matter production during the seed-filling period had a significant effect on seed dry-matter increase and seed yield in determinate soybeans (Kakiuchi and Kobata, 2004) as well as in many other crops (Evans, 1996). The ratio of dry matter increase in the seed (S) to that in the shoot (W), referred to as $R_{S/W}$ hereafter, during the seed-filling period can reflect the balance between the assimilate supply and the sink capacity. In the determinate soybean, cv. Tamahomare, the ratio was almost fixed under various growing conditions including shading and thinning of plants and different years (Kakiuchi and Kobata, 2004). The $R_{S/W}$ was around 0.41–0.54, which suggests that approximately half of W was accumulated in vegetative organs. There is a positive correlation between the total pod number and S or W, and between the total pod number and the number of branch nodes, and hence W increased S via the increase in the number of branch-node bearing pods (Kakiuchi and Kobata, 2004).

In rice (*Oryza sativa* L.) (Takami et al., 1990; Kobata and Moriwaki, 1990) and wheat (*Triticum aestivum* L.) (Kobata et al., 1992) $R_{S/W}$ differed from that in soybean, S was higher than W, and S had a ceiling value. In rice and wheat the growth phase clearly changes from vegetative to reproductive stages and S is determined mainly by flower number, which barely changes during the seed-filling period (Evans, 1996). However, in soybean, the stem and leaf continue growing after the onset of seed-filling period (Ojima and Fukui, 1966), and the development of flower organs should vary the potential S during the seed-filling period. In the indeterminate soybean, the main stem growth (Bernard, 1972) and flowering (Yoshida et al., 1983) continue for a longer period than in the determinate soybeans. Additionally, the percentage of stem dry weight at the initial flowering stage to the final dry weight in the indeterminate cultivar was lower than that in the determinate cultivar (Egli and Leggett, 1973). Therefore, $R_{S/W}$ and the yield-determining process may differ between determinate and indeterminate soybeans.

Harvest index (HI) is an important factor that determines soybean yield (Morrison et al., 1999; Kumudini et al., 2001). HI in soybean has been considered to be invariable irrespective of growth habit (Spaeth et al., 1984). However, when plants suffer from water (Schapaugh and Wilcox, 1980) or shading (Kakiuchi and Kobata, 2004) stress during the...
seed-filling period, the percentage of the dry weight before the flowering stage to that of the final plant dry weight becomes higher reducing HI. Reduction of HI by low radiation after the flowering stage has also been observed in the Pacific side of the Tohoku district in Japan (Arihara, 2000). Furthermore, Board and Tan (1995) showed that defoliation treatment during reproductive stages decrease HI. Spaeth et al. (1984) showed that HI in the indeterminate soybean was more stable than in the determinate soybean, although Schapaugh and Wilcox (1980) suggested that HI was variable. Therefore, it is unclear whether the stability and response in HI to growth conditions during the seed-filling period in determinate and indeterminate soybean cultivars differ.

To clarify the difference in $R_{S/W}$ and HI between determinate and indeterminate soybean cultivars, we investigated the effect of light conditions changed by shading and thinning treatments during the seed-filling period on the S and W in three kinds of soybean cultivars with different growth habits.

Materials and Methods

1. Plant Materials

The field experiment was conducted in 2002 in Mihama, Wakayama, Japan. The experimental site was a 20 m by 15 m plot of silty clay loam in a well-drained paddy field. Three soybean cultivars, Tamahomare, Tozan69 and Peking were used. Tamahomare is a determinate cultivar and Tozan69 is an indeterminate cultivar bred in Japan. Peking was an ancestral line of US cultivars and selected as a semi-intermediate cultivar. Peking is considered as a determinate cultivar, but Peking has some characteristics typical for both determinate and semi-indeterminate types, and has been called a tall-determinate type (personal communication from Dr. R. Nelson). Seeds of Tamahomare and Tozan69 were sown on 8 June 2002 in rows 0.60 m apart, with 0.20 and 0.10 m plant spacing, respectively; 8.3 and 16.7 plants m$^{-2}$ of both cultivars were thinned to one-half (8.3 plants m$^{-2}$), and that of Tozan69 to one-quarter (4.2 plants m$^{-2}$) on 21 July. In Peking, thinning treatment to one-quarter was omitted because the number of plants was limited. Shading treatment was applied to the 1.6 m × 2.4 m areas in the control plots of both varieties on 27 July. The shading frames and covering were the same as those used on the Tamahomare plot. The experimental plots were laid out in a randomized block design with three replications for each treatment (control, thinning, and shading treatments).

2. Shading and Thinning Treatment

The plants of each cultivar were shaded or thinned from the R2 growth stage (flowering stage) to R8 stage (maturing) (Fehr and Caviness, 1977) to change W during the seed-filling period.

(1) Tamahomare

On 27 July, at the R2 stage, either every other plant or every three plants per four plants were thinned, reducing the plant density to one-half (4.2 plants m$^{-2}$) or one-quarter (2.1 plants m$^{-2}$). Shading treatment was applied to the 2.0 m by 2.4 m areas in the plots without thinning on 3 August. Shading frames were constructed with steel posts and plastic rope. These frames were 1.1 m high and were placed over the plants. The frames were covered with one layer of black cheesecloth (moderate-shading treatment) or two layers of black cheesecloth (heavy-shading treatment). Short-wave radiation inside the shading frame was measured with a solar meter (SOLAR130, HAENI, Jegenstorf, Switzerland). Heavy-shading and moderate-shading treatment reduced full-sun radiation by 78 and 47 $\%$, respectively. The control plots were neither thinned nor shaded, and the plants in these plots were grown under natural conditions throughout the growing season (control). The experimental plots were laid out in a randomized block design with three replications for each treatment (control, thinning, and shading treatments).

(2) Tozan69 and Peking

The date at stage R2 was 20 July and 27 July in Tozan69 and Peking, respectively. The control plants of both cultivars were thinned to one-half (8.3 plants m$^{-2}$) and that of Tozan69 to one-quarter (4.2 plants m$^{-2}$) on 21 July. In Peking, thinning treatment to one-quarter was omitted because the number of plants was limited. Shading treatment was applied to the 1.6 m × 2.4 m areas in the control plots of both varieties on 28 July. The shading frames and covering were the same as those used on the Tamahomare plot. The experimental plots were laid out in a randomized block design with three replications for each treatment (control, thinning, and shading treatments) in each cultivar plot.

3. Measurements

Four plants were harvested from each plot at the R2 stage (21 July in Tozan69, 27 July in Tamahomare and Peking) and at the R8 stage (5 October in Peking, 12 October in Tozan69, 9 November in Tamahomare). The numbers of nodes, total pods, filled pods, and seeds in each plant were counted. Then, the sampled plants were dried in an oven at 80°C for 48 h and weighed. At the R2 stage, the plants were tagged, and organs immediately before abscission were carefully gathered two or three times each week. These organs were dried at 80°C for 48 h and then weighed as abscissing organs. These weights were added to the appropriate dry sample weights. The flower vestige number was counted at R8, and it was included as the...
total flower number. The podding rate was calculated from the ratio of the number of total pods to the total number of flower vestiges.

Results and Discussion

1. Yield, Yield Components, and Plant Dry Weight

Seed yield of control plants in Tamahomare, Tozan69, and Peking were 417, 542, and 291 g m⁻² at 14 % water content, respectively (Table 1). When seed dry weight was compared among the plants at the same plant density (8.3 plant m⁻²), the seed yield per plant in Tamahomare (43.1 g) was similar to that in Tozan69 (43.1 g) and that in Peking (22.2 g) was the lowest.

Shoot dry weight at final harvest and total pod number, filled-pod number, seed number, and one seed weight were not significantly influenced by shading or thinning (Table 1). However, seed number per pod and one seed weight were significantly influenced by shading or thinning (Table 1).

2. Relationship between S and W

The relationship between S and W was regressed to a line in each cultivar. Slopes of the positive linear regressions (RS/W) in Tamahomare, Tozan69, and Peking were 0.50 (r² = 0.998), 0.49 (r² = 0.998) and 0.48 (r² = 0.975), respectively (Fig. 1). There was no significant difference between the slopes for the three cultivars when the significance of differences between regression lines (P<0.05) was tested by covariance analysis. This means that in all cultivars with different growth habits, approximately half of the assimilate was accumulated in vegetative organs. Similar results were obtained in our experiments performed in 1999 and 2000 with determinate soybean, cv. Tamahomare, under various degrees of population and shading treatments at another experimental site (Kakiuchi and Kobata, 2004).

The coefficient of correlation between seed yield and crop growth rate (CGR) during 20 days after the R5 stage was higher than that in other stages in all 16 soybean cultivars including different growth habits (Shiraiwa et al., 2004). The 20th day after R5 approximately corresponds to the 10th day before R6, and most of seed-filling was completed before the R6 stage (Kakiuchi and Kobata, 2004). These results suggest that the assimilates during the seed-filling period highly contributes to seed production in diverse soybean cultivars.

3. Yield-Component Determining Factor

Total pod number per plant was greatly influenced

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Table 1. Shoot dry weight at final harvest, yield and yield components of soybean cultivars Tamahomare, Tozan69, and Peking in thinning and shading treatments during seed-filling period. Tamahomare is the determinate cultivar, Tozan69 is the indeterminate cultivar and Peking is the semi-indeterminate cultivar.

| Treatment          | Planting density (m⁻²) | Shoot dry* weight per plant (g plant⁻¹) | Total pod no. (plant⁻¹) | Filled pod no. (plant⁻¹) | Seed no. per pod (pod⁻¹) | One seed weight (g) | Seed dry weight (g m⁻²) | Seed yield (g m⁻²) |
|--------------------|------------------------|----------------------------------------|-------------------------|--------------------------|--------------------------|---------------------|------------------------|---------------------|
| Tamahomare         |                        |                                        |                         |                          |                          |                     |                        |                     |
| Control            | (8.3)                  | 113.2**                              | 161.1                  | 106.1                    | 199.9                    | 1.88                | 21.5                   | 43.1***              |
| Heavy shading      | (8.3)                  | 55.7                                 | 62.9                   | 38.4                    | 73.3                    | 1.91                | 20.3                   | 15.2**               |
| Moderate shading   | (8.3)                  | 71.1                                 | 94.7                   | 57.1                    | 105.8                   | 1.85                | 24.1                   | 25.4ab               |
| One-half thinning  | (4.2)                  | 194.3                                | 310.4                  | 206.3                    | 376.8                   | 1.83                | 22.9                   | 86.4***              |
| One-fourth thinning| (2.1)                  | 276.5c                               | 441.8c                 | 302.7c                   | 532.6c                   | 1.76                | 22.6                   | 120.7d               |
| Tozan69            |                        |                                        |                         |                          |                          |                     |                        |                     |
| Control            | (16.7)                 | 70.6                                 | 78.2                   | 74.8                    | 153.4                   | 2.05                | 18.2                   | 27.9ab               |
| Heavy shading      | (16.7)                 | 32.6                                 | 31.8                   | 26.1                    | 54.5                    | 2.09                | 16.4                   | 9.0ab                |
| Moderate shading   | (16.7)                 | 45.2ab                               | 48.2                   | 44.0                    | 94.3                    | 2.15                | 18.0                   | 17.1ab               |
| One-half thinning  | (8.3)                  | 106.9                                 | 126.0                  | 115.1                    | 224.4                   | 1.95                | 18.8                   | 42.4***              |
| One-fourth thinning| (4.2)                  | 153.1ab                              | 186.4ab                | 172.5ab                  | 341.4ab                  | 1.98                | 18.7                   | 63.6b***             |
| Peking             |                        |                                        |                         |                          |                          |                     |                        |                     |
| Control            | (16.7)                 | 44.8ab                               | 76.7ab                 | 74.1                    | 159.8                   | 2.16                | 9.7                    | 15.0b                |
| Heavy shading      | (16.7)                 | 21.0                                 | 13.5                   | 9.0                     | 17.8                    | 2.01                | 9.1                    | 1.6ab                |
| Moderate shading   | (16.7)                 | 37.3ab                               | 36.4ab                 | 34.3b                    | 71.2b                    | 2.05                | 10.1                   | 7.0b                 |
| One-half thinning  | (8.3)                  | 58.4                                 | 105.8b                 | 104.3b                   | 228.1b                   | 2.19                | 9.7                    | 22.2                 |

* Data indicate the mean of three replications.
** Different letters are significantly different according to the Rayan test at 5% level of probability.
*** Seed yield (g m⁻²) at 14 % of moisture content.
Relationship between Seed and Dry Matter Increase in Different Growth Habit Soybeans

by the shading and thinning treatments (Table 1). A positive linear relationship existed between S and total pod number in all cultivars (Fig. 2). Pod number is one of the important soybean-yield determining factors (Bernard and Harville, 1993; Board and Tan, 1995; Mathew et al., 2000; Kokubun, 2001; Kakiuchi and Kobata, 2004). The pod number per plant was highly correlated with W in all cultivars (Fig. 3). However, the numbers of seeds per pod and individual seed weights were not influenced by the treatments (Table 1). In the past experiment also, the number of seeds per pod and seed size were not affected but the number of pods per reproductive node and the pod number was decreased by restricting light interception during the period from the R1 to R7 stages (Egli and Yu, 1991; Board and Harville, 1993). In the present experiment, light interception might affect yield by reducing pod number.

The total flower number per plant and podding rate were correlated with W in all cultivars (Fig. 4). This result agrees with our previous data (Kakiuchi and Kobata).
Kobata, 2004), although the slope of the regression line of total flower number plotted against $W$ was steeper in this experiment than in previous results (Fig. 4). The podding rate in soybean increased with an increase in source strength when the ratio of sink to source was changed by defoliation or flower thinning treatments at the full-flowering stage (Saitoh et al., 2001). CO$_2$ enrichment also increased podding rate and stem dry weight (Nakamoto et al., 2004). Podding rate in our experiment could be increased more if source strength was increased more, because it seemed not to reach a ceiling under strong thinned conditions. Therefore, the $W$ might be a key factor determining the podding rate in soybean. These results indicate that $W$ determines $S$ via total pod number irrespective of the growth habit of the variety.

The node number increased during the seed-filling period was correlated with $W$ in all cultivars. In Tozan69 and Peking four to nine nodes were formed on the main-stem during the seed-filling period instead

Fig. 3. Relationships between $W$ during the seed-filling period and total pod number in each cultivar. See Figure 1 for symbols and treatments.

Fig. 4. Relationships between $W$ during the seed-filling period and total flower number (solid line) or podding rate (dotted line) in each cultivar. See Figure 1 for symbols and treatments.
of about two nodes on the main stem in Tamahomare. However the main-stem node number hardly increased with increasing W in all cultivars (Fig. 5). Thus, the seed yield was more influenced by the number of branch nodes than by that of the main-stem nodes.

4. Harvest Index (HI)

The HI, defined by the slope of the relationship between S and shoot dry matter at maturity, was stable in the plants with over 30 g W (Fig. 6). Therefore, HI may be stable except when the assimilate during the seed-filling period is strongly suppressed by low solar radiation in all cultivars used. Our results were supported by a result that HI is a conservative characteristic among soybean cultivar including determinate and indeterminate types (Spaeth et al., 1984). There was no difference in the response of HI to different light intercept conditions during the seed-filling period among soybeans with different growth habits, unless dry matter production during the seed-filling period is strongly suppressed.

Conclusion

There was no significant difference in $R_{S/W}$ among three soybean cultivars with different growth habits, when plants were grown under variable light intercept conditions during the seed-filling period. Almost half of the assimilate during the seed-filling period was stored in vegetative organs in three cultivars. The stable $R_{S/W}$ resulted in the stable HI under diverse W ranges except when W was heavily restricted. The main-stem node number in the indeterminate and semi-indeterminate soybeans increased during the seed-filling period more than that in the determinate soybean. However, seed yield was influenced more strongly by branch node number than by main-stem node number in both indeterminate and determinate soybeans. It is suggested that dry matter partition into seeds during the seed-filling period and yield-determining process are approximately the same in the determinate and indeterminate soybeans. The $R_{S/W}$ and the yield component-determining process under...
variable light conditions seem to be similar and stable among different locations and years (Kakiuchi and Kobata, 2004). However, whether the present results can be adopted to diverse cultivars remains to be examined. Furthermore, variability of Rs/W and other yield determining factors under various light intercept conditions should be investigated more to confirm these results for diverse cultivars.

Acknowledgements

We thank staffs in Nagano Chusin Agricultural Experimental Station for seed supply of Peking and valuable suggestions of cultivation characteristics.

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