Varietal Difference in Nitrogen Redistribution from Leaves and Its Contribution to Seed Yield in Soybean

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Abstract: A large amount of nitrogen is redistributed from vegetative organs to the seeds during seed filling in soybean (\textit{Glycine max} [L.] Merrill). However, the effect of nitrogen redistributed from leaves on the seed yield production is not clear. We evaluated the varietal difference in nitrogen redistribution and its contribution to the seed yield. Ten soybean cultivars were cultivated under conventional conditions in the field in Saga, Japan. The plant samples were collected at various reproductive stages, and then the nitrogen contents in each part were determined. The redistributed nitrogen was estimated by the difference in the nitrogen contents of leaves between the plants at the R5 and R7 stages. The nitrogen content of leaves began decreasing after R5 stage in all cultivars, indicating the start of nitrogen redistribution. About 13.8\% to 37.9\% of the total nitrogen in the seeds was estimated to have been redistributed from the leaf tissues in the ten cultivars. The seed yield was correlated positively with the amount of redistributed nitrogen from leaves but neither with the nitrogen concentration in the leaves at R5 nor with the proportion of redistributed nitrogen in the seeds. However, in high seed yielding years, 2008 and 2009, the seed yield was not associated with nitrogen redistribution; and the lowest nitrogen redistribution was associated with a relatively high seed yield in Tamahomare. Our results indicated that redistribution of a large amount of nitrogen does not always contribute to high seed yielding, implying the direct nitrogen uptake during seed filling could be more important factor for high seed yielding depending on the cultivars.

Key words: Leaf tissue, Nitrogen accumulation, Nitrogen redistribution, Seed yield, Soybean.

Soybean (\textit{Glycine max} [L.] Merrill) plants require much nitrogen for seed production, because of the high protein content of seeds compared with in the seeds of other crops such as rice and maize (Osaki et al., 1991). This high nitrogen requirement could be supplied from three sources, nitrogen absorption by roots, nitrogen fixation by nodules, and nitrogen redistribution from other vegetative organs during the seed-filling period.

A large amount of nitrogen is redistributed from vegetative organs to the seeds during seed filling in soybean. Before the start of seed filling, a part of the absorbed nitrogen is stored in vegetative tissues, such as leaves, stems, and petioles, and then redistributed to the seeds during the seed-filling period. Hanway and Weber (1971) reported that approximately half of the nitrogen in the matured seeds is redistributed from other plant parts, and the rest is supplied from the roots and nodules during the seed-filling period.

The nitrogen concentration in the leaves at the start of the seed-filling stage is highly correlated with the seed yield (Shibles and Sundberg, 1998). Shiraiwa and Hashikawa (1995) also observed that new cultivars having a high seed yield showed a high nitrogen concentration in the leaves before seed filling. These findings suggest that the high seed yielding cultivars accumulate a lot of nitrogen in the vegetative parts before seed filling.

On the other hand, the redistribution of nitrogen from the vegetative to the reproductive parts of soybean plants is considered to compensate for the shortage of nitrogen supply from the root system during seed filling. This redistribution may reduce the photosynthetic functions and cause leaf senescence and thus shorten the seed-filling period (Sinclair and de Wit, 1976; Egli et al., 1978; Shibles and Sundberg, 1998). However, there remains some disagreement about the relationships among redistributed nitrogen, the seed-filling period, and seed yield in soybean. For example, Zeiher et al. (1982) failed to find any relationship between the contribution of redistributed nitrogen and the seed yield.
nitrogen and seed yield in some commercial cultivars. Hayati et al. (1995) reported that leaf senescence was not caused by the increased seed nitrogen demand, and Egli and Bruening (2007a) pointed out that there is no relationship between increase in total seed nitrogen at maturity and the amount of redistributed nitrogen or rapid leaf senescence. Furthermore, Kumudini et al. (2002) concluded that higher seed yielding was associated with increased nitrogen acquisition during seed filling rather than nitrogen redistribution. These results imply the complexity of the role of nitrogen redistribution in the seed yield.

To understand clearly the function of nitrogen redistribution from leaves in the seed production, we evaluated the varietal difference in nitrogen redistribution and its contribution to the seed yield using various cultivars which are grown widely in Japan and other countries.

Materials and Methods

1. Plant cultivation

Four soybean cultivars, Fukuyutaka, Akiyoshi, Sachiyutaka, and Tamahomare, all of which are widely cultivated in western Japan, were used to evaluate the nitrogen accumulation and redistribution in 2008 and 2009. Sachiyutaka and Tamahomare were the comparative cultivars with high and low protein contents, respectively, and slightly earlier maturing than the other two cultivars. Fukuyutaka is the most commercialized cultivar and is grown widely in western Japan, and Akiyoshi was a leading cultivar before Fukuyutaka was bred. The seeds were sown on 10 July in 2008 and 9 July in 2009 in a loam field of the Coastal Bioenvironment Center, Saga University (33°27’N and 129°58’E). Four seeds were sown in each hole, with holes arranged at 15-cm intervals and 70 cm rows spacing. The plot for each cultivar consisted of six rows with 12 m long in each row. Plants were thinned to allow only one plant per hole to grow (9.5 plants m-2) at the stage when the first trifoliate leaf fully extended. Chemical fertilizer was applied at a rate of 3 : 10 : 10 g m-2 of N : P2O5 : K2O before sowing, and 100 g m-2 of lime was also applied at the same time. The weeds were controlled by plowing or by hand and pesticides were sprayed as necessary. The growth stages were determined according to Fehr et al. (1971).

We further analyzed the relationship between redistributed nitrogen and seed yield in a sandy field in 2010 and 2011. The cultivars used in 2010 were Fukuyutaka, Akiyoshi, Sachiyutaka, Tamahomare, Akisengoku and Enrei from Japan, Caviness and Stressland from USA, and Parana and IAS-5 from Brazil. The cultivars used in 2011 were Fukuyutaka, Sachiyutaka, Tamahomare, Akisengoku, Caviness and IAS-5. The plots were arranged in a random completely blocked design with three replications in each experiment. The seeds were sown on 20 July in 2010, and 15 July in 2011. Each plot design consisted of four rows with 70 cm spacing and ten hills with 20 cm intervals (2.8 m × 2 m). The other cultivation methods were the same as in 2008 and 2009.

2. Sampling and measurements

In 2008 and 2009, five plants of each cultivar were collected mainly at R1 (beginning of flowering), R5 (beginning of seed filling), R6 (full seed size) and R7 (beginning of maturity) and at other stages when needed (Fehr et al., 1971). The sample plants were separated into stems, leaves, petioles and pods, and weighed after drying at 80°C for 48 hours. Each part of the plant sample was ground into powder for the determination of total nitrogen content by the Kjeldahl method. The leaf SPAD value was measured one or two times per week on the second or third fully expanded leaf from the top during the period from R1 to R7. At maturity stage (R8), eight medium-size plants of each cultivar were taken for the determination of the seed yield, yield components, and nitrogen content of the seeds. However, in 2010 and 2011, the plant samples were taken only at R5 and R7, and the seed yield determination was conducted for 10 plants per plot with three replications.

The redistributed nitrogen was estimated as the difference in the nitrogen content of vegetative parts between R5 and R7. The nitrogen contents at R5 and R7 were calculated as multiplying the dry weight at R5 by the nitrogen concentration in each part at R5 and R7, respectively. This estimation method was in accord with Egli and Bruening (2007a). It was assumed that nitrogen lost from the vegetative parts was redistributed to the seeds. The same estimation of nitrogen redistribution from vegetative parts was described also by Zeiher et al. (1982) and Kumudini et al. (2002).

3. Statistical analysis

The significance of parameters related to the redistributed nitrogen among cultivars in Table 1 was analyzed using the Tukey-Kramer test. The relationship between yield and nitrogen redistribution was estimated using Pearson’s correlation coefficient test. Statcel 3 was used as software for the multiple comparison analysis.

Results

1. Nitrogen accumulation in vegetative organs and its redistribution

Fig. 1 shows the total nitrogen concentration in various vegetative organs of Fukuyutaka at R5 and R7 in 2009. The total nitrogen concentration in the leaf, pod wall, stem and petiole was 50.3, 28.3, 16.5 and 11.2 mg g⁻¹, respectively, at R5, whereas it decreased to 11.9, 8.5, 3.7 and 5.1 mg g⁻¹ at R7, respectively.

Based on the hypothesis that the decrement of nitrogen
content in the vegetative organs is caused by redistribution to the seeds, the redistributed nitrogen from the leaves, stems, pod walls, and petioles was 28%, 11%, 6% and 3% of total nitrogen in the matured seeds, respectively, showing that the leaves were the largest nitrogen source for the redistribution to the seed (Fig. 2). Approximately 48% of the nitrogen in the matured seeds was redistributed from vegetative organs, and others were considered to have been supplied from the roots and nodules during seed filling.
Data are expressed as mean values ± SD of five replications. Means followed by the same letter in the same column do not differ significantly at the 0.05 level by Tukey-Kramer test.

1) Nitrogen redistribution to seeds means the proportion of redistributed nitrogen in seed total nitrogen content.

Table 1. Characteristics of nitrogen accumulation, redistribution and seed yield in 4 cultivars.

|         | Nitrogen concentration in leaves | Leaves weight | Nitrogen redistributed from leaves | Seed yield | Nitrogen content in seeds | Nitrogen concentration in seeds | Nitrogen redistribution to seeds (%) |
|---------|----------------------------------|---------------|-----------------------------------|------------|--------------------------|-------------------------------|------------------------------------|
|         | R5 (mg g⁻¹)          | R7            | R5 from leaves (g m⁻²) | Seed yield (g m⁻²) | (g m⁻²) | (g m⁻²) | (g m⁻²) | |
| 2008    |                     |               |                      |              |                          |                               |                                    |
| Sachiyutaka | 47.5 ± 3.4 a | 10.3 ± 1.7 c | 19.6 ± 2.1 b | 6.9 ± 0.8 a | 377 ± 49 b | 26.9 ± 3.7 b | 71.3 ± 0.6 a | 25.8 ± 5.7 ab |
| Tamahomare | 41.6 ± 2.2 b | 14.2 ± 1.4 b | 17.8 ± 1.9 b | 4.6 ± 0.5 b | 416 ± 18 a | 26.7 ± 1.8 b | 64.3 ± 1.8 c | 17.3 ± 2.7 c |
| Akiyoshi  | 47.7 ± 3.9 a | 17.3 ± 1.1 a | 24.8 ± 1.7 a | 7.2 ± 0.9 a | 361 ± 26 b | 24.0 ± 1.9 b | 66.4 ± 0.5 b | 29.9 ± 3.6 a |
| Fukuyutaka | 48.5 ± 2.1 a | 12.2 ± 1.6 bc | 21.3 ± 2.2 ab | 7.3 ± 0.5 a | 452 ± 26 a | 30.5 ± 2.2 a | 67.5 ± 0.7 b | 24.1 ± 2.1 b |
| 2009    |                     |               |                      |              |                          |                               |                                    |
| Sachiyutaka | 46.9 ± 0.7 b | 9.8 ± 1.8 c | 21.1 ± 2.2 ab | 7.4 ± 0.3 a | 322 ± 23 b | 22.8 ± 1.7 b | 70.7 ± 1.5 a | 32.7 ± 3.3 a |
| Tamahomare | 42.3 ± 2.2 c | 13.9 ± 1.3 b | 18.5 ± 1.5 b | 5.0 ± 0.4 c | 334 ± 33 b | 20.1 ± 2.7 b | 60.1 ± 2.1 c | 24.9 ± 5.4 c |
| Akiyoshi  | 49.1 ± 1.5 a | 18.2 ± 1.2 a | 22.2 ± 1.8 a | 6.5 ± 0.3 b | 270 ± 31 c | 17.2 ± 2.1 b | 63.7 ± 2.3 bc | 37.9 ± 6.8 a |
| Fukuyutaka | 50.3 ± 1.8 a | 11.9 ± 1.2 c | 19.9 ± 2.1 ab | 7.3 ± 0.7 a | 382 ± 42 a | 25.7 ± 2.8 a | 67.2 ± 2.5 ab | 28.3 ± 4.0 b |

Data are expressed as mean values ± SD of five replications. Means followed by the same letter in the same column do not differ significantly at p < 0.05 level by Tukey-Kramer test.

2. Varietal differences in nitrogen accumulation in leaves and its redistribution to seeds

Fig. 3 shows the changes in nitrogen concentration in the leaves in 4 commercial cultivars in 2008 and 2009. The nitrogen concentration in leaves remained at a high level for 40 to 60 days after sowing (DAS) in most of cultivars, and then it declined gradually from 60 to 80 DAS and very sharply after 80 DAS. The nitrogen concentration decreased quickly in Sachiyutaka and Tamahomare, which were two early maturing cultivars, whereas it decreased slowly in Akiyoshi in 2009, especially after 80 DAS. However, the nitrogen concentration was constantly lower in Tamahomare in both years compared with the other three cultivars. The leaf SPAD value increased even after flowering, reached the maximum at 80 DAS, and then decreased sharply, synchronized with the changes in the nitrogen concentration (Fig. 4).

Table 1 shows the nitrogen concentration in the leaves and the redistribution of nitrogen to the seeds in four cultivars in 2008 and 2009. The nitrogen concentration in leaves at R5 was the highest in Fukuyutaka and the lowest in Tamahomare. However, the concentrations decreased almost to the same level at R7 in all cultivars, except for Akiyoshi, in both 2008 and 2009.

The nitrogen redistributed from leaves to the seeds was 6.5 to 7.4 g m⁻² in Sachiyutaka, Fukuyutaka, and Akiyoshi, but significantly less in Tamahomare (4.6 to 5.0 g m⁻²) in both 2008 and 2009. Therefore, the two-year average proportion of redistributed nitrogen in the seeds was 33.9% in Akiyoshi, 29.3% in Sachiyutaka, and 26.2% in Fukuyutaka, while it was only 21.1% in Tamahomare. Even though the redistributed nitrogen did not vary much with the year, the proportion of redistributed nitrogen in the seeds was lower in 2008, which was a high seed yielding year, than in 2009. The proportion of nitrogen redistribution did not correlate with the seed yield. The nitrogen concentration in the seeds showed a significant difference among cultivars, that is, it was highest in Sachiyutaka (71.3 and 70.7 mg g⁻¹) and lowest in Tamahomare (64.3 and 60.1 mg g⁻¹) in both years.

3. Relationship between nitrogen redistribution from leaves and seed yield in different cultivars

Fig. 5 shows the correlation of the seed yield with leaf nitrogen concentration, the proportion of redistributed nitrogen in the seeds and the amount of nitrogen redistributed from leaves to seeds over four years. The seed yield did not correlate with the nitrogen concentration in leaves at R5 and the proportion of redistributed nitrogen in the seeds (Fig. 5-A, B), but significantly correlated with the amount of nitrogen redistributed from leaves to seeds (r = 0.6447, p < 0.01) (Fig. 5-C). Therefore, compared with the nitrogen concentration in leaves at R5 and the proportion of redistributed nitrogen in the seeds, the amount of nitrogen redistributed from leaves to seeds was more suitable as an indicator for forecasting the seed yield.

Discussion

Most of the nitrogen assimilated in soybean plants is ultimately partitioned into the seeds. Before seed filling starts, except for the nitrogen used to support the development of vegetative tissues, most of the assimilated nitrogen is stored in the vegetative organs (Egli et al., 1985; Warembourgh and Fernandez, 1985; Hortensteiner and...
Many researchers have discussed the importance of the nutrient assimilation in vegetative organs to the seed yield. For example, Munier-Jolain et al. (1996) analyzed the relationship between seed growth speed and the seed-filling period, noting that the amount of available nitrogen in vegetative organs was a decisive factor for the length of the seed-filling period. Wittenbach (1983) described how depodding can increase leaf dry weight and delay the loss of leaf chlorophyll and protein, thus increasing the nutrient storage function of vegetative organs indirectly. Shibles and Sundberg (1998) reported a positive linear relationship between nitrogen concentration in leaves at R5 and seed yield. Our extensive investigation also showed a significant positive correlation between the seed yield and amount of redistributed nitrogen from leaves to seeds, but not with the nitrogen concentration in the leaves at R5 (Fig. 5-A, C), which is inconsistent with the results of Shibles and Sundberg (1998). Our results indicated that the amount of nitrogen redistributed from leaves was suitable as an indicator for forecasting seed yield.

In the high seed yielding year 2008, the highest yielding cultivar Fukuyutaka showed the largest amount of redistributed nitrogen, but a relatively lower proportion of redistributed nitrogen in the seeds (24.1%), while the highest proportion of redistributed nitrogen in the seeds (29.9%) was associated with the lowest seed yield in Akiyoshi (Table 1). In contrast, in Tamahomare, the lowest nitrogen redistribution was associated with a relatively high seed yield compared with Sachiyutaka, which belongs to the same maturity group with Tamahomare. Almost the same trend was observed in 2009. The results indicated that the high seed yield could be supported by not only a large amount of redistributed nitrogen but also more nitrogen uptake (include nitrogen fixation) during the seed-filling period (R5 – R7). Kumudini et al. (2002) pointed out that the new varieties with a high seed yield showed a high ability to take up nitrogen during seed filling. Even though we found a significant correlation between the redistributed nitrogen and seed yield in ten cultivars over four years, high seed yielding is considered to be supported by both nitrogen remobilization and nitrogen uptake during seed filling (e.g. Fukuyutaka), mostly by nitrogen uptake during seed filling (e.g. Tamahomare).

A large amount of nitrogen redistributed from leaves during seed filling could cause early leaf senescence (Sanetra et al., 1998; Guinaut et al., 2002; Domnison et al., 2006), and reduce photosynthesis (Boon-long et al., 1983; Buttery and Buzzell, 1988; Sinclair and Horie, 1989). Faster nitrogen partitioning and dry matter allocation into seeds are associated with shorter seed-filling duration, and lower seed yield in high seed protein genotypes (Salado-Navarro et al., 1985). In our experiment, although the nitrogen content of seeds in Sachiyutaka was higher than that in Feller, 2002). Therefore, the leaf nitrogen concentration and leaf SPAD value reached the maximum before seed filling started (Figs. 3, 4). However, the leaf nitrogen concentration decreased at around 70 DAS, after the seed filling started (R5), indicating that the nitrogen in the leaves was redistributed (Fig. 3). Hanway and Weber (1971) reported that almost half of the nitrogen, phosphorus, and potassium in the matured seeds were translocated from other plant parts in soybean. Our results are consistent with this conclusion (Fig. 2). Moreover, the leaf tissue was the biggest nitrogen exporter, supplying around 30% of the total nitrogen in the seeds.
Tamahomare, the yield was lower in Sachiyutaka (Table 1). However, there was little difference in seed filling period (Fatichin et al., 2013) and leaf chlorophyll deterioration (Fig. 4) between Sachiyutaka and Tamahomare. Although prolonging the seed-filling period could increase the seed yield, Egli and Bruening (2007a, b) found that a large nitrogen requirement of seeds was not associated with a short seed-filling period, and the use of the stay-green genotype with a delayed onset of leaf senescence could not increase the seed yield (Luquez and Guiamet, 2001). Therefore, the relationship between nitrogen assimilation and seed yield involves multiple physiological and environmental factors.

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