Accumulation and Partitioning of Nitrogen During Seed Filling in Old and Modern Soybean Cultivars in Relation to Seed Production*

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Abstract : Seed productivity of old and modern soybean cultivars was analyzed in relation to accumulation and partitioning of nitrogen during seed filling. Four soybean cultivars were grown on a drained paddy field (silty caly loam). Dry weight and nitrogen content were determined for above ground parts weekly from the beginning of seed filling to maturity. The modern cultivars Enrei and Tachinagaha exhibited greater dry matter and nitrogen accumulations during seed filling and greater seed yield in comparison with the old cultivars Akazaya and Mizukuguri. Seed nitrogen per top nitrogen ($N_{\text{seed}}/N_{\text{top}}$) increased linearly against days after the beginning of seed filling, while leaf nitrogen per top nitrogen ($N_{\text{leaf}}/N_{\text{top}}$) decreased linearly. Cultivar differences in nitrogen partitioning were quite small. Thus N_{leaf} was mainly dependent on N_{top} . Nitrogen harvest index ($N_{\text{seed}}/N_{\text{top}}$ at maturity) was not very restrictive to either nitrogen yield or seed yield. It is concluded that the observed difference in seed productivity among old and modern cultivars was associated more with nitrogen accumulation during seed filling than with its partitioning pattern.

Key words : Cultivar difference, Dry matter production, Nitrogen accumulation, Nitrogen partitioning, Seed yield, Soybean.

新旧ダイズ品種における子実肥大期間中の窒素蓄積および分配と子実生産との関係 : 白岩立彦・橋川 潮 (滋賀県立短期大学農業部)

要 旨 : 水田転換畑(細粒グライ土)において, 新旧ダイズ4品種を栽培し, 子実肥大開始期から成熟期にかけて地上部の器官別乾物重と窒素含量の推移を1週間毎に調査した。子実肥大期間中の地上部乾物重と全窒素含量(N_{top})の増加量および子実収量は, いずれも新品種の‘エンレイ’および‘タチナガハ’が旧品種の‘赤荻’および‘みずくぐり’よりも優れていた。子実の窒素含量が地上部窒素含量に占める割合($N_{\text{seed}}/N_{\text{top}}$)は, 子実肥大開始後の日数経過とともに直線的に増加し, 一方葉身窒素含量の地上部窒素含量に占める割合($N_{\text{leaf}}/N_{\text{top}}$)は直線的に減少した。これらの面での品種間差異は小さかった。子実肥大期間中の葉身保有窒素量は主に個体の全窒素蓄積量に依存しており, 成熟期における $N_{\text{seed}}/N_{\text{top}}$ が窒素収量や子実収量におよぼす影響も小さかった。以上のように, 本実験でまとめられた子実生産力の新旧品種間差異には, 子実肥大期間における窒素蓄積活性がその分配様式よりも強く関与していた。

キーワード : 乾物生産, 子実収量, ダイズ, 窒素蓄積, 蓄積分配, 品種間差異。

In previous studies, we have evaluated soybean cultivars for dry matter productivity in terms of crop radiation conversion efficiency⁷⁾ and nitrogen fixation activity⁹⁾ and found that the modern cultivars were superior to the old cultivars in dry matter production and nitrogen accumulation. However the relationship between those activities and yielding ability have not been examined.

In general, soybean yield correlates closely to total nitrogen in plant because of the large amount of nitrogen accumulation in the seed³⁾. A number of studies^{1,2,4,5,12)} indicated that there were genotypic variations in nitrogen accumulation and its partitioning to seeds.

Significant correlations between total nitrogen or nitrogen harvest index and seed yield were also observed^{1,2,4)}.

Nitrogen accumulation and partitioning in plant can also affect dry matter production. Nitrogen supply to the leaf canopy would become a limiting step in crop photosynthesis, especially when it is limited¹¹⁾. Since the great demand for nitrogen by soybean seeds causes a rapid decline in nitrogen content of vegetative parts, nitrogen partitioning during seed filling may affect dry matter production and seed yield, as well as nitrogen accumulation^{6,10)}.

The objective of this study was to analyze the capacity of seed production in old and modern soybean cultivars in relation to accumulation and partitioning of nitrogen during seed filling.

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Materials and Methods

Four soybean cultivars listed in Tabel 1 were grown in 1991 on a drained paddy field with silty clay loam converted from successive rice production at the Shiga Agricultural Experiment Station at Azuchi. Enrei and Tachinagaha are modern cultivars that have been improved in yielding ability and were released in 1971 and 1986, respectively. The other two were chosen from old cultivars formerly grown commercially in the Shiga region in Japan. Cv. Akazaya was released in 1926 and Cv. Mizukuguri is one of the native lines in the region.

Seeds were hand-sown on June 29 in rows of 0.65 m width after fertilizing the soil with 100 kg per ha of P_2O_5 and K_2O . The inter-plant spacing was 0.15 m (10.3 pl m^{-2}). To avoid lodging, flower nets were set up at mid canopy level at about flowering stage for the less lodging resistant cultivars Akazaya and Mizukuguri.

From the begining of seed filling to maturity, the above ground plant parts were harvested weekly from about 1 m^2 of land area. The date of the begining of seed filling was recorded when the seed grew three mm in diameter in the most developed pods at the top several nodes on the main stem of the representative plants. The abscised leaves and petioles were not collected. Dry weights were determined for leaf, stem+petiole and pod. For the samples later than about 20 days after begining of seed filling, seeds were segregated from pods. Nitrogen concentration was analyzed for leaf, petiole+stem+pod (pod wall)

and seed using the Kjeldahl method.

The experimental plots were placed randomly in each of three replication blocks. The land area of each subplot was about 50 m^2 .

Results

1. Seed yield and accumulations of dry matter and nitrogen

As shown in Table 1, seed dry weight was significantly differnt among cultivars studied. It ranged from 237 g m^{-2} of cv. Mizukuguri to 323 g m^{-2} of cv. Enrei. These values are equivalent to 279 and 380 g m^{-2} , with 15% moisture content, respectively.

Total top dry weight at the beginning of seed filling was considerably greater in the two old cultivars than in the other modern cultivars. This may be attributable to the longer duration of vegetative growth in the old cultivars by eight to 10 days. On the other hand, dry matter accumulation from the beginning of seed filling to maturity was remarkably greater in the modern cultivars regardless of the length of growth duration. The maximum top dry weight of cv. Tachinagaha was significantly greater than the old cultivars, though the difference in top dry weight at maturity was not detected among cultivars. Harvest index at maturity (seed dry weight per top dry weight) was higher for the modern cultivars than the older ones.

The comparison of nitrogen accumulation among cultivars proved to have similar tendencies to those of dry matter accumulation (Table 2). The modern cultivars were considerably superior to old cultivars in nitrogen accumulation after the beginning of seed fill-

Table 1. Growth period, dry matter accumulation and its distribution at maturity.

Cultiver	Growth period		Total top dry weight				Dry matter distribution at maturity		
	Emergence ~BSF*	BSF~ Maturity	at BSF	Maxi- mum value	at Maturity	Increase from BSF to Maturity	Seed	Stem+ Pod wall	Seed DW per top DW
	day		g m^{-2}						g g^{-1}
Enrei	51	53	300	694	507	207	323	183	0.64
Tachinagaha	51	63	264	754	502	238	320	182	0.64
Akazaya	59	51	376	661	476	100	284	192	0.60
Mizukuguri	61	55	404	663	444	40	237	207	0.53
LSD. 0.05			54	63	n.s.	81	26	n.s.	0.04

* BSF= Beginning of seed filling.

Table 2. Nitrogen accumulation and distribution at maturity.

Cultiver	Total top nitrogen content (N_{top})				Nitrogen concentration at maturity		Nitrogen distribution at maturity		
	at BSF*	Maximum value	at Maturity	Increase from BSF to Maturity	Seed	Stem + pod wall	Seed (N_{seed})	Stem + pod wall	N_{seed} per N_{top}
	$g\ m^{-2}$				%		$g\ m^{-2}$		$g\ g^{-1}$
Enrei	9.6	24.8	21.8	12.2	6.43	0.52	20.8	1.0	0.95
Tachinagaha	8.5	25.0	19.8	11.3	5.89	0.55	18.8	1.0	0.95
Akazaya	12.0	22.1	19.0	7.0	6.10	0.86	17.3	1.7	0.91
Mizukuguri	13.0	20.8	16.4	3.4	6.34	0.69	15.0	1.4	0.91
LSD 0.05	1.4	2.2	2.6	2.5	0.20	0.11	2.5	0.3	0.02

*BSF = Beginning of seed filling

ing. In this case, both the maximum value of total top nitrogen content ($N_{top}\ g\ m^{-2}$) and N_{top} at maturity differed significantly among the cultivars. Cv. Mizukuguri showed the lowest value. In view of the seasonal change of N_{top} (Fig. 1), the cultivar difference in the maximum N_{top} and N_{top} at maturity resulted from the greater nitrogen accumulation rate of modern cultivars during early seed filling. The mean nitrogen accumulation rates for 25 days after the beginning of seed filling were 0.55 and $0.31\ mg\ m^{-2}\ day^{-1}$ on the averages of modern and old cultivars, respectively.

The nitrogen remaining in the stem and pod wall at maturity was significantly greater in the two old cultivars due to their higher nitrogen concentrations (Table 2). Consequently, the apparent nitrogen harvest index defined by seed nitrogen content ($N_{seed}\ g\ m^{-2}$) per N_{top} at maturity was significantly higher in the two modern cultivars.

2. Nitrogen partitioning during seed filling

Nitrogen accumulation in and partitioning ratio to seeds during seed filling are represented in Fig. 2. N_{seed} of the two modern cultivars was greater than that of the old cultivars at later seed filling stage (Fig. 2A). The ratio of N_{seed} to N_{top} (N_{seed}/N_{top}) increased almost linearly with seed filling (Fig. 2B). The variance in N_{seed}/N_{top} among the cultivars was quite limited when it was compared at the same stage defined by the days after the beginning of seed filling. A regression line between the days after beginning of seed filling and N_{seed}/N_{top} combining all cultivars is drawn in the figure. It was calculated exclud-

Fig. 1. Change in top nitrogen content (N_{top}) during seed filling.

ing values at maturity because they swerved from the entire linearity. The slope of the line was $0.0199\ g\ g^{-1}\ day^{-1}$ ($r^2=0.94$).

Nitrogen content in leaves per unit land area ($N_{leaf}\ g\ m^{-2}$) and its ratio to N_{top} (N_{leaf}/N_{top}) are shown in Fig. 3. The two old cultivars showed greater N_{leaf} at the beginning of seed filling than the modern cultivars (Fig. 3A). However, in those cultivars, a rapid decline of N_{leaf} occurred shortly after beginning of seed filling, consequently N_{leaf} values of cultivars soon became quite close to each other. N_{leaf}/N_{top} decreased linearly during seed filling showing a clear contrast to increasing N_{seed}/N_{top} , and approached zero roughly 10 days before maturity or earlier (Fig. 3B). There were only small variances in N_{leaf}/N_{top}

Fig. 2. Changes in seed nitrogen content (N_{seed} , A) and ratio of seed nitrogen to top nitrogen ($N_{\text{seed}}/N_{\text{top}}$, B).

Fig. 3. Changes in leaf nitrogen content (N_{leaf} , A) and ratio of leaf nitrogen to top nitrogen ($N_{\text{leaf}}/N_{\text{top}}$, B).

at the same date after beginning of seed filling among the cultivars. Thus the greater N_{leaf} at the beginning of seed filling observed in the old cultivars resulted from the greater N_{top} at that time. The slope of the regression line between the days after beginning of seed filling and $N_{\text{leaf}}/N_{\text{top}}$ during the linear period was calculated $-0.0137 \text{ g g}^{-1} \text{ day}^{-1}$ ($r^2=0.95$).

The linear regressions of $N_{\text{seed}}/N_{\text{top}}$ and $N_{\text{leaf}}/N_{\text{top}}$ versus the days after beginning of seed filling were obtained for each cultivar (Table 3). The slopes ranged from 0.019 to 0.022 $\text{g g}^{-1} \text{ day}^{-1}$ for $N_{\text{seed}}/N_{\text{top}}$ and from -0.012 to $-0.015 \text{ g g}^{-1} \text{ day}^{-1}$ for $N_{\text{leaf}}/N_{\text{top}}$ among cultivars. Cultivar Tachinagaha exhibited the slowest daily decline in $N_{\text{leaf}}/N_{\text{top}}$ and the slowest increase in $N_{\text{seed}}/N_{\text{top}}$.

Discussion

In the present study, the modern cultivars were superior to the old cultivars in both N_{top} at maturity and seed yield. Seed yield was closely related to total nitrogen accumulation as suggested in the previous studies where diverse genotypes^{1,2)} were used. Those above variances were not related to the whole growth duration of the cultivars (104 days for Enrei, 114 days for Tachinagaha, 110 days for Akazaya and 116 days for Mizukuguri), indicating that a significant difference in productivity exists between modern and old cultivars.

Nitrogen harvest index was also significantly higher for the modern cultivars. But all the cultivars exhibited entirely high values of nitrogen harvest index and its range was narrow (from 0.91 to 0.95) compared to obser-

Table 3. Regression lines of $N_{\text{seed}}/N_{\text{top}}$ and $N_{\text{leaf}}/N_{\text{top}}$ versus days after beginning of seed filling.

Cultiver	$N_{\text{seed}}/N_{\text{top}}$ versus days after BSF*		$N_{\text{leaf}}/N_{\text{top}}$ versus days after BSF		
	Slope**	r^2	Slope	Intercept	r^2
	$\text{g g}^{-1}\text{day}^{-1}$		$\text{g g}^{-1}\text{day}^{-1}$	g g^{-1}	
Enrei	0.0218	0.98	-0.0153	0.606	0.99
Tachinagaha	0.0190	0.98	-0.0119	0.545	0.99
Akazaya	0.0202	0.98	-0.0139	0.612	0.95
Mizukuguri	0.0188	0.99	-0.0131	0.608	0.97

* BSF=Beginning of seed filling.

** The intercept was assumed to be zero.

vations by Jeppson et al. (from 0.85 to 0.95)²⁾ and Leffel et al. (from 0.62 to 0.76, abscised leaves were included)⁴⁾. For its limited difference, nitrogen harvest index was not very restrictive to yield in present study. Since the old cultivars had been grown in Shiga region for a long period, they might be well adapted to the environment in the experimental site, resulting in fairly high nitrogen harvest indices.

The superior nitrogen accumulation in the modern cultivars was achieved by the higher rate at early seed filling period. Since nitrogen fixation rate in some old cultivars declined earlier after beginning of seed filling as compared to the modern cultivars⁹⁾, the above difference in nitrogen accumulation may be attributable to different nitrogen fixation activity.

Nitrogen partitioning pattern through seed filling was examined because it was speculated to have some association with dry matter productivity^{6,10)}. In the present study, dry matter production after the beginning of seed filling was evidently greater in the modern cultivars. However, nitrogen partitioning ratio to leaves was not very variable among cultivars during the period. When examined for the individual cultivars, some variances in daily changes in $N_{\text{seed}}/N_{\text{top}}$ and $N_{\text{leaf}}/N_{\text{top}}$ were detected (Table 3). The modest partitioning of nitrogen to seeds observed in cv. Tachinagaha coincided with its lowest seed nitrogen concentration and the longest seed filling duration (Table 1, 2). This result was consistent with the self destruction hypothesis advanced by Sinclair and deWit¹⁰⁾ and field observation by Salado-Navarro et al.⁶⁾. How-

ever, cv. Tachinagaha exhibited only slightly greater N_{leaf} than the other cultivars at late seed filling (Fig. 3A). As a whole, the nitrogen partitioning pattern during seed filling was fairly similar among the observed cultivars. N_{leaf} of each cultivar was primarily dependent on its N_{top} . For this fact, nitrogen accumulation through seed filling seemed to be important, because a rapid decline of N_{leaf} occurred in the old cultivars when nitrogen demand by seed growth became crucial.

Variability in nitrogen partitioning pattern with environmental factors is not fully known. Shiraiwa et al.⁸⁾ showed that before the beginning of seed filling nitrogen partitioning ratio to leaves was fairly stable among plants under different sowing dates and plant population densities, and among cultivars. In respect to the period of seed filling, further attempts would be needed for full understanding of the interactive effects of environmental and genetic factors on nitrogen partitioning.

The greater dry matter accumulation after the beginning of seed filling in the modern cultivars was not related to N_{leaf} difference among cultivars, because N_{leaf} was rather greater in the old cultivars at around the beginning of seed filling. Shiraiwa et al.⁹⁾ reported, observing the same cultivars, that nitrogen supplied to leaves of the modern cultivars was apportioned more to increase specific leaf nitrogen (nitrogen content per unit leaf area) than leaf area expansion, as compared to the old cultivars. The higher specific leaf nitrogen would result in greater crop dry matter productivity^{7,11)}. Thus the greater dry matter production during seed filling of modern cultivars may be attributable

to their high specific leaf nitrogen and other unknown factors. In this aspect, too, nitrogen accumulation and its supply to leaves would be important for dry matter production, because the high specific leaf nitrogen of the modern cultivars must have been achieved by well sustained N_{leaf} during seed filling in spite of relatively lower N_{leaf} at the beginning of seed filling.

In conclusion, the modern cultivars exhibited greater dry matter and nitrogen accumulation during seed filling and seed yield in comparison with the old cultivars. Nitrogen partitioning to the seed and the leaf was fairly similar among observed cultivars. Although the nitrogen amount in leaves did not correlate directly to dry matter production, the results in the present study emphasized the importance of nitrogen accumulation through seed filling as a limiting trait on soybean yield.

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