Improvement of Photosynthetic Capacity in Soybean Variety

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The demand for soybean as protein and oil resources is increasing rapidly annually and the development of higher yielding varieties has become necessary to boost the production of soybeans. Efforts have been recently made to breed the plant types having high efficiency for capturing the energy of sun and to augment the harvest index.

Although the photosynthetic capacity per unit of leaf area is one of the components constituting the photosynthesis of the plant population, no attempt has been made to improve the energy converting efficiency in soybean breeding, as breeding of other crops.

An approach to find the possibility of improving leaf photosynthesis in soybean varieties was carried out at the National Institute of Agricultural Sciences⁶⁻¹⁰.

Significance of photosynthetic capacity in photosynthesis of plant population

Photosynthetic rates and leaf area of plant population and isolated plant of three new and old varieties were measured. As shown in Fig. 1, varietal differences in net photosynthesis under isolated conditions were due to the result of differences in total leaf area per plant rather than differences in photosynthetic rate per unit leaf area. That is, net photosynthesis of the Manshu variety with lower photosynthetic capacity and a large amount of leaf area per plant was higher than that of the Harosoy variety having higher photosynthetic capacity and a small amount of leaf area per plant. The net photosynthetic rate of the Norin 2 variety with medium capacity of photosynthesis and a large amount of leaf area was about equal to the Manshu.

Net photosynthesis of the plant population was mainly affected by the photosynthetic capacity and light-receiving coefficient (f). The variety with low photosynthetic capacity and low f required larger LAI than the variety having high photosynthetic capacity and high f to get the same level of population photosynthesis. For example, Fig. 2 showed that the LAI assimilated $5 \text{ gCO}_2 \text{ per m}^2$ of land area per hour was about 5.5 to 5.8 in Manshu, 4.7 to 5.2 in Norin 2 and 3.2 to 3.3 in Harosoy. In most cases, a maximum LAI of soybean plant population in Japan is about 7.

Therefore, the possibility of an increase in the population photosynthesis with more increased LAI is less in the variety having low photosynthetic capacity and low f as compared with the variety with high photosynthetic capacity and high f.

Importance of improvement photosynthetic capacity was also recognized from the relation between assimilation and exhaust of carbon dioxide. A great amount of respiration in the soybean plant population during the ripening period was attributed to respiration of leaves and pods. The ratio of total respiration to gross photosynthesis based on a whole day during the ripening period was higher in Manshu than in Harosoy, and net production of Manshu decreased.



The contribution of photosynthetic capacity to population photosynthesis changes with the development of soybean management. Photosynthesis of plant population in wide spacing and light fertilizer application having been old cultivation is dominated by the enlargement of LAI, and is little affected by photosynthetic rate per unit leaf area.

On the other hand, plant population in dense planting and heavy fertilizer application with modern management produces a large amount of leaves so the importance of photosynthetic capacity increases. It is not too much to say that the photosynthetic capacity should be improved with the improvement of plant type.



Fig. 1. Net photosynthesis, leaf area and net photosynthetic rate per unit leaf area in isolated plant (A-C) and plant population (D, E)

○: Harosoy, ●: Norin 2, ×: Manshu Photosynthesis at 70 Klux





○: Harosoy, □: Norin 2, △: Manshu. 1: June
24. 2: July 2. 3: July 15. 4: July 28. 5: Aug.
10. 6: Aug. 19. 7: Aug. 25. 8: Sept. 3 or 8

Varietal differences in photosynthetic capacity and stability among varieties under different cultivated conditions

Fifty-five varieties in total were tested for three years to find out whether there were varietal differences in photosynthetic rates.

Photosynthetic rates at saturated light intensity varied significantly with the varieties. Variation in photosynthetic rates among varieties was in 80 to 120% of the average rate of all the varieties.

The differences in absolute value between the highest variety and the lowest one were 10 to 15 mgCO₂ dm⁻² hr⁻¹. Dornhoff and Shibles (1970) found that twenty varieties differed significantly in net photosynthetic rates at 100, 200, 300, 400 ppmCO₂ and ranged from 29 to 43 mgCO₂ dm⁻² hr⁻¹ at 300 ppmCO₂. Curtis et al. (1969) reported varietal rates varying from 12 to 24 mgCO₂ dm⁻² hr⁻¹ among 36 varieties. Dreger et al. (1969), and Watanabe (1973) have reported varietal differences.

Although absolute value of leaf photosynthesis varied with environmental conditions, the varieties having high photosynthetic capacity such as Harosoy and Mandarin (Ottawa)



Fig. 3. Variations in photosynthesis of each of different varieties for 2 or 3 years

•: 1964. True P of 1st and 4th leaves. \triangle : 1966. True P of 4th leaves, low level of fertilization. \blacktriangle : 1966. True P of 4th leaves, high level of fertilization. \times : 1967. Mean app. P of 4th and 6th leaves were always higher in photosynthetic rates than other varieties as shown in Fig. 3. Dornhoff and Shibles (1970) also reported that Harosoy and Mandarin had higher rates of photosynthesis, and that Lincoln had a lower rate.

Coefficient of variation in photosynthetic rates within the varieties varied from 5 to 25%. These values are larger than those of the length of main stem (5 to 20%), smaller than of number of branches (20 to 45%), grain weight per plant (10 to 50%) and top weight (15 to 45%), which are the characteristics for selection. It may be concluded that photosynthetic capacity can be taken as a target characteristic of breedings.

Relationship between photosynthetic capacities of improved varieties and their parents

Net photosynthetic rates of twenty-two varieties bred from Tokachinagaha, Ani and Mandarin (Ottawa) were determined to clarify whether the photosynthetic capacities of the improved varieties were increased with breeding. Tokachinagaha and Harosoy have a high photosynthetic capacity, while Ani has a low capacity. Table 1 shows the frequency of

Table 1.	Frequency of oc	currence	of	high
	photosynthesis v	ariety		

Photosynthesis of parents	Photosyn improve	nthesis of d variety
	L	н
$H \times H$	2	7
$H \times L$	1	6
$M \times L$	1	1
$L \times L$	3	1

 H, M, L indicate high P group, medium P group and low P group, respectively

2) Numerals indicate number of varieties

occurrence of improved varieties with high photosynthetic capacity.

Frequency was higher in the hybrid with the parent having high photosynthetic capacity. Relation between photosynthetic rates of the improved varieties and those of their parents is shown in Fig. 4. Straight line AB shows that photosynthetic rate of the improved variety is similar to that of the high photosynthesis parent, and straight line BC indi-



Fig. 4. Relation between photosynthetic rates of improved varieties and those of their parents

*: Relative value to the low photosynthesis parents in each case of hybrids cates that photosynthetic rate of the improved variety is similar to that of the low photosynthesis parent.

If we consider a range of $AB\pm5\%$ and $BC\pm5\%$, then two varieties of the improved 22 varieties are above AB+5% line, and 15 varieties are in $AB\pm5\%$ range. Only one variety is below the line of BC-5%

Therefore, 77% of the improved varieties are equal to or better than the high photosynthesis parent. This apparently indicates that there is a close relationship between photosynthetic capacity of the improved varieties and that of high photosynthesis parent, and there is a trend toward higher photosynthetic capacities in higher yielding varieties.

Genetic mechanism of photosynthetic capacity and possibility of increase in photosynthetic capacity

Two crosses of Norin 1 and Harosoy, Manshu and Harosoy were used to investigate the inheritance of photosynthetic capacity.

Frequency distribution of photosynthetic rate of Norin 1 and Harosoy, their reciprocal F_1 populations, a backcross to Norin 1, and the F_2 generation is shown in Table 2. Net

Table 2. Frequency distribution (number of plants) for photosynthetic rates of parents, F_1 , F_2 , and backcross F_1 progenies

(1) Hybrid of Norin 1 and Harosoy

Ca									1	Net 1	phot	osyn	thes	is							-	
Generation		16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	Mean	CV %	
1968	Mean of	f 3rd ar	nd (5th 1	leave	es																
	Norin 1					1	2	1	3	1	4		2	1							23.4	10.1
	Harosoy												2	3	3		2	2	2		29.1	7.7
	F1, (N	o. 1×H	ar.)						4		5	2	2								24.4	6.1
	F2, (N	o. 1×H	ar.)					6	5	10	7	8	12	5	6	3	4	4			25.9	11.0
1970	Mean of	f 5th ar	nd 8	8th 1	leave	s																
	Norin 1		1		1	4	6	2	2	2											20.5	8.2
	Harosoy											1	2	1	2	6	3	2		1	29.3	6.6
	(N1	\times Har.						3	4	1	4	2		1	1	1	1				24.6	12.1
	F, Ha	r.×N1				1		4	2	6	3	1		1							23.2	8.1
	(N1 H,	$\times (N1 \times F_i)$	1		2	1	2	7	7	7	6	5	4	1	1		1				23.4	11.3

	Photosynthesis of F ₃ generation								
Photosynthesis of F. generation	Norin $1 \times$	Harosoy	Manshu×Harosoy						
	High	Low	High	Medium	Low				
High	5	2	1	5	0				
Low	1	5	0	3	3				

Table 3. Frequency of occurrence of high photosynthesis line

1) Numerals indicate number of lines

2) F3 pedigrees were classified according to the Duncan's multiple range test (5% level)

photosynthetic rate of Norin 1 was lower than that of Harosoy. Photosynthetic rate of F_1 progeny was lower than the mid-parent, and significantly lower than of Harosoy, but showed no significant difference between F_1 and Norin 1.

In the hybrid of Manshu and Harosoy, similar results were obtained. There was also no heterosis of net photosynthesis in a cross of Wasekogane and Harosoy. Therefore, low capacity of photosynthesis of Norin 1 and Manshu was noticed as a dominant character. The reciprocal F_1 did not differ from each other. It is suggested that there is no cytoplasmic control.

Distribution of net photosynthetic rates of F_2 generations in two crosses, Norin 1×Harosoy and Manshu×Harosoy, were similar to the normal distribution. This suggests that the genetic mechanism controlling the capacity of photosynthesis is quantitative inheritance. Quantitative inheritance and no heterosis of soybean substantiate the result of bean (Phaseolus vulgaris L.) reported by Izhar and Wallace (1967).

 F_3 lines of two crosses were selected from F_2 individual plants having higher or lower photosynthetic capacity. Correlation coefficient of net photosynthetic rates in F_3 lines (mean value of respective lines) to F_2 individual plants was low as much as 0.45 (not significant) and 0.66 (significant at 5% level) for Norin 1×Harosoy and Manshu×Harosoy, respectively.

Although correlation between F_2 and F_3 generation was low, there was a tendency that a number of F_3 lines having higher photosynthetic capacity were derived from F_2 plants having higher photosynthetic capacity (Table 3). These results indicate the validity of selection for increasing the photosynthetic capacity. The differences in photosynthetic rate of F_3 lines were significant at saturating or near saturating light intensities as shown in Fig. 5.





Fig. 5. Light-potosynthesis curves of F_3 lines *, **: Significant at 5% and 1% level, respectively

Grain yield of F_4 progenies are shown in Table 4. The highest yielding F_4 lines in both early and medium maturity for Norin 1×Harosoy were obtained from high photosynthesis lines in F_4 generation. Similar result was secured from Manshu×Harosoy. This suggests that photosynthetic capacity improvement is very important for an increase in yielding ability and also supports the results attained from the relation between improved varieties and their parents.

Table 4. Distribution of grain yield (number of pedigrees) and maximum yield in each maturing time for \mathbf{F}_4 pedigrees

(1) Norin 1×Harosoy

0	Early ¹⁾ (106~	115)20	Medium (116~126)				
Grain yield	High ³⁾	Low	High	Low	08		
Above parents	0	. 0	1	0			
Intermediate	6	3	3	2			
Below parents	1	5	0	1			
Total	7	8	4	3			
Mean yield	313	269	386	333			
Maximum yield	383	323	439	361			

(2) Manshu×Harosoy

Grain yield	Extremely early (~ 105)	Early ()	106~115)	Medium	Late (140)	
	High	High	Low	High	Low	Low
Above parents	0	1	0	1	1	2
Intermediate	1	5	1	1	3	0
Below parents	1	0	0	0	0	0
Total	2	6	1	2	4	2
Mean yield	255	294	343	363	343	364
Maximum yield	284	395	343	393	384	375

1) Maturing time

2) Growth duration, days

3) Group of photosynthesis in F_3 generation

4) Yield: gm^{-2}

Relationship between photosynthetic capacity and some characteristics and simple technique for selecting higher photosynthesis plant

Success in improvement of photosynthetic capacity depends on finding superior genotypes and selection of desirable progenies.

Dornhoff and Shibles (1970) reported that the high photosynthesis varieties such as Corsoy, Amsoy, Hark and Harosoy had Mandarin and A.K. in their background.

Ojima et al. (1968) also reported that the high photosynthesis varieties, Wasekogane, Tokachishiro and Koganejiro had been derived from Tokachinagaha. No individual plants having C-4 dicarboxylic acid cycle for CO₂ fixation have been found in Glycine species (Cannel et al., 1969). We must search for genotypes with higher photosynthetic capacity from a number of varieties and mutants.

The measurement of photosynthesis for many varieties and progenies consumes much time. It is convenient to use the simplified method for preliminary selection of photosynthetic capacity. Ojima and Kawashima (1968), and Dornhoff and Shibles (1970) reported that specific leaf weight, nitrogen content per unit leaf area and leaf thickness were highly correlated with photosynthetic rate. Both correlation coefficients of leaf nitrogen content and specific leaf dry weight to net photosynthesis ranged from 0.6 to 0.8.

Leaf characteristic method, therefore, may be effective for preliminary selection of varieties. After plants have been selected for high value of these characteristics, photosynthetic rate then should be determined to identify superior genotypes. Determination of net assimilation rate may be useful as well as leaf characteristic method in case of variety.

Net photosynthesis of F_2 individual plants of two crosses was low positively correlated with leaf nitrogen content, specific leaf weight and leaf thickness (Ojima et al., 1969). In F_3 lines (mean value of respective lines), however, the relationship between net photosynthesis and leaf characteristics became more closely than F_2 (Ojima and Kawashima, 1970).

Correlation coefficients were from 0.82 to 0.87 in nitrogen content and 0.77 to 0.87 in specific leaf dry weight. Most of F_2 individual plants with high value of leaf characteristics had high photosynthetic rates in F_3 generation.

Distributions of nitrogen content per unit leaf area and specific leaf dry weight in F_1 and F_2 plants showed a similar distribution of photosynthetic rates. Low nitrogen content and low specific leaf weight were some dominant characters.

It can be considered that selection of photosynthetic capacity of progenies on the basis of leaf characteristics or measurement of net photosynthetic rate should begin at the F_3 or later because net photosynthesis in F_2 individuals is poorly correlated with leaf characteristics and heritability of photosynthesis between F_2 and F_3 is low.

Most of the high photosynthesis varieties were early maturing. A little negative or no correlationship was found between net photosynthetic rates and growth duration of F_2 individual plants. No relationships between net photosynthesis and growth habit, flower color, pubescence color of pod and leaf shape (ratio between length and width) were found in F_2 individual plants. It is possible to introduce the high photosynthetic capacity of a variety having indeterminate growth habit to a determinate variety.

Variation of photosynthetic capacity within Glycine species is not very large, about $15 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ so far as we know. But

among high yielding varieties, there are many varieties having low capacity. If the improvement of photosynthetic capacity is made in practical process of breeding, it is possible to reach to a higher yielding level than present.

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