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Effects of Leaf and Pod Removal on Photosynthesis and Assimilate Partition in Soybean

Woong Tae Kim*, Rak Chun Seong*, and Harry C. Minor**

摘葉·除莢처리가 콩의 光合成과 同化物質 配分에 미치는 影響

金雄泰*, 成樂春*, 해리 씨 마이너**

ABSTRACT : To clarify the effects of sink demand for assimilate on leaf photosynthetic rate, tissue composition, and leaf senescence of soybean [*Glycine max* (L.) Merr.] plants, pod and leaf tissues were removed at growth stage R_3. Plant responses were measured every 10days from 2 through 42days following treatment. Leaves of depodded plants exhibited increased starch and chlorophyll contents and specific leaf weight. Stomatal resistance was also increased and leaf photosynthetic rate was reduced. Dry weight of vegetative tissues except leaves was increased by pod removal. Leaf removal resulted in a decreased starch content of leaves from 22 to 42days after treatment and that of roots at all sampling times. Specific leaf weight was decreased while leaf photosynthetic rate was increased. Stomatal resistance and chlorophyll content were little affected. Weight per seed was decreased 3.0% by leaf removal. Except for the seed, tissue protein contents were increased by pod removal but decreased by leaf removal, however, seed protein content was not affected by either. Apparent senescence was delayed by depodding. Both apparent and functional senescence were accelerated by leaf removal.

Introduction

Seed yield of soybeans is accomplished by photosynthesis of source and transport of the assimilates. The seeds of the reproductive stages of soybean plants are dominant sink which restricts the partitioning of photosynthates for the vegetative sinks. During the seed developmental period, the most amount of producing and storing photosynthates are used to increasing the seed weight.

Gifford and Evans[8] reported that sink demand for assimilates was a control factor in photosynthetic rate of leaves as well as environmental conditions. The less accumulation of starch in leaf chloroplast was increased the photosynthetic rate and the more sink demand for the assimilates was also increased the net photosynthetic rate with decreasing starch accumulation of the leaf[9]. The variations of chemical compositions and dry matter accumulations in plant parts were found with the leaf or pod removal treatments of soybeans[12]. Sinclair and Dewit[16] suggested that the senescence of vegetative parts was created by increasing nitrogen demand of seeds which needed the remobilization of nitrogen from the vegetative tissues. When seed devel-

* 高麗大學校 (Dept. of Agronomy, Korea University, Seoul 136-701 Korea)
** 미조리 주립대학교 (Dept. of Agronomy, University of Missouri-Columbia, Missouri 65211 U. S. A.) 〈1993. 2. 27. 接受〉

opment was delayed, the period of total dry weight and nitrogen accumulation was extended[7]. Schweitzer and Haper[15] indicated that pod removal treatments of soybean plants showed decreasing more in photosynthetic rate than delaying the decrement of leaf chlorophyll content.

This study was conducted to examine the effects of sink demand for assimilate on leaf photosynthetic rate, tissue composition, and leaf senescence of soybean plants.

Materials and Methods

This experiment was conducted at the research farm of college of natural resources, Korea University, Seoul, Korea. Three seeds of soybean [*Glycine max* (L.) Merr.] determinate cultivar 'Paldalkong' was planted in sand soil inoculated with *Rhizobium japonicum* using 15kg rubber pots on June 1, 1990. One−half concentration of Hoagland No. 2 nutrient solution was supplied with 300mℓ per pot daily for 2 weeks, and full concentration with 400mℓ for next 2 weeks, then double concentration with 400mℓ until harvest. Water was added properly to prevent water stress. The first flowering was occurred at 37 days after emergence on July 15. Soybean plants were treated at the stage of beginning pod(R_3) on 57 days after emergence. A) Control, B) Approximately 50% pod removal, and C) Approximately 50% leaf removal alternatively. A completely randomized design was used with four replications. Newly produced pods and leaves were removed at the interval of several days.

Samples for the data collections were taken from 2DAT(days after treatments) to 42DAT(R_7 stage) with 10 days intervals and separated to leaves, stems+petioles, roots, and pods (the pods of last samples were separated to seeds and pod walls). The samples were dried at 70℃ oven for 48 hours and grinded with Udy cyclon miller (0.5mm screen). Starch content of leaves and roots was determined by Dale Smith method[17] treated with amino−glucosidase(SIGMA) at 55℃ for 34 hours. Nitrogen content was measured by boric acid modification micro−Kjeldahl method[1] and multiplied factor 6.25 to obtain protein content. Photosynthetic rate and stomatal resistance of complete terminal leaf were measured at 10A. M. on sampling day using LI−6250 CO_2 Analyzer and LI−6200 Portable Photosynthesis System (LI−COR,Inc.). Chlorophyll content of the terminal leaf was determined by Arnon method[2] using DMSO (Dimethylsulfoxide) extraction method[10] and O. D. value obtained using Spectronic 1201 (MILTON ROY). Specific leaf weight of the terminal leaf was measured using LI−3000A Portable Area Meter and LI−3050A Transparent Belt Conveyer. IBM−SAS package was used for the analyses of the collected data.

Results and Discussion

Total dry weight accumulation by pod and leaf removal treatment of soybean plants was increased until 32DAT and decreased at 42DAT due to fallen leaves of lower parts(Fig. 1). Differences between pod removal treatment and control were not significant, but leaf removal treatment showed lower total dry weight compared to the other treatments. Dry weight of vegetative tissues (stems+petioles +roots) except leaves was decreased rapidly after 32DAT (Fig. 2). Dry weight of the vegetative tissues except leaves was increased significantly by pod removal treatment. Because reproductive sink demand for assimilates was decreased, translocation of assimilates in pod removal treatment was transferred to the vegetative sink. As a result, total dry weight of depodded soybean plants was compensated by increasing the dry weight of vegetative tissues except leaves as shown in Fig. 1. This trend was similar to the result of Schonbeck *et al.*[14] Number of seeds per soybean plant was decreased 43.6% by pod removal and 3.6% by leaf removal treatments compared to the control(Table 1). Seed weig-

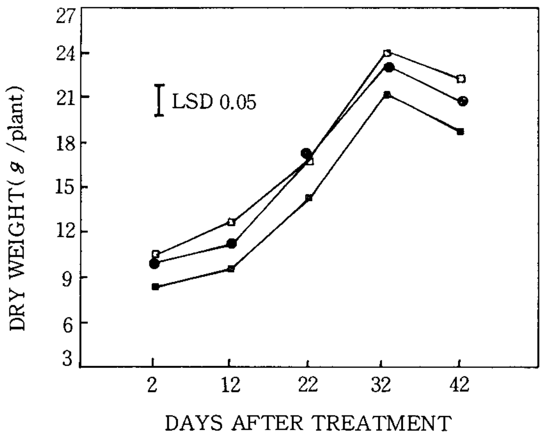

Fig. 1. Total dry weight accumulations of control (—□—), depoded(—●—) and defoliated (—■—) soybean plants on days after treatment.

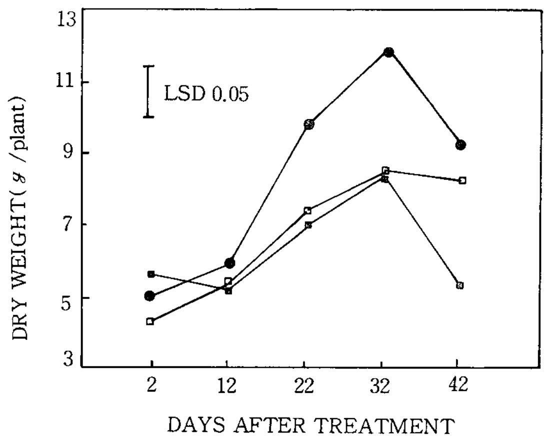

Fig. 2. Stem+petiole+root dry weight accumulations of control (—□—), depoded(—●—) and defoliated (—■—) soybean plants on days after treatment.

Table 1. Seeds weights, no. of seeds and 100 seed weight of control(A), depoded (B), and defoliated(C) soybean plants at physiological maturity(R7)

Treatment	no. seeds /plant	seeds wt. /plant	100 seed wt.
		-g-	-g-
A	55	8.49	15.42
B	31	5.01	16.41
C	33	7.89	14.96
$LSD_{0.05}$	5.35	0.89	0.41

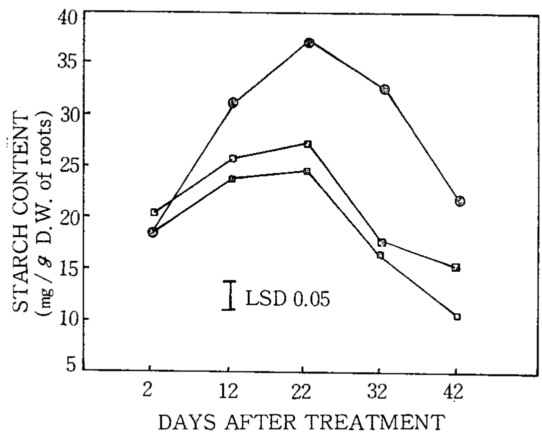

Fig. 3. Starch contents in leaves of control (—□—), depoded(—●—) and defoliated(—■—) soybean plants on days after treatment.

ht per soybean plant was decreased 41% by pod removal and 7.1% by leaf removal treatments. However, one hundred seed weight was increased 6.4% by pod removal and decreased 3.0% by leaf removal treatments. This result indicated that depodded soybean plants were decreased the competition among pods with decreasing sink demand for assimilates.

Starch contents of soybean leaves were increased until 22DAT and decreased thereafter in all treatments(Fig. 3). Pod removal treatment increased highly starch content in leaves but leaf removal treatment decreased that compared to the control. Starch content in roots was decreased continuously after treatment (Fig. 4). Root starch content of depodded plants was higher and that of defoliated plants was lower than the content of the control plants. This resulted in relative increase of assimilate supply to the roots by decreasing sink demand in deppoded plants. Specific leaf weight of depodded plants was significantly higher than that of defoliated plants for all sampling times(Fig. 5). The increase of specific leaf weight is resulted from

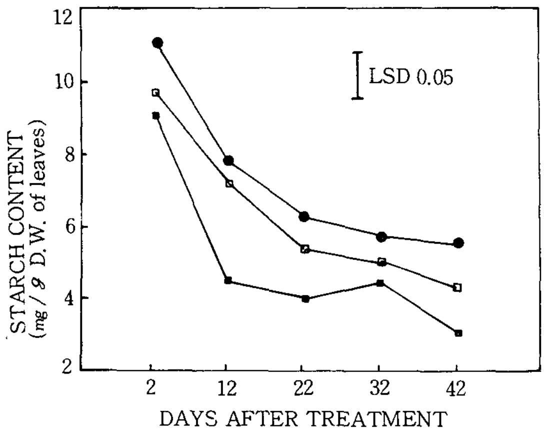

Fig. 4. Starch contents in roots of control (−□−), depoded(−●−) and defoliated(−■−) soybean plants on days after treatment.

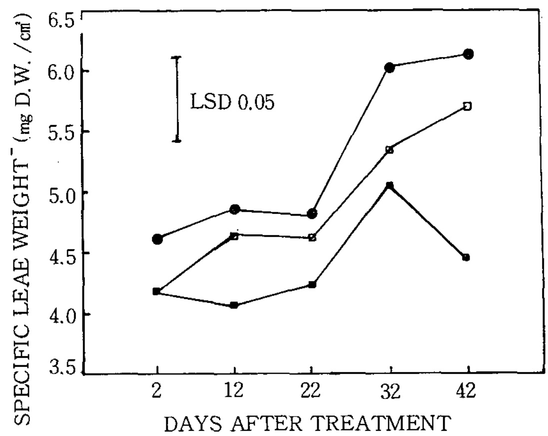

Fig. 5. Specific leaf weights of control(−□−), depoded(−●−) and defoliated (−■−) soybean plants on days after treatment.

starch accumulation in leaves as reported by Chatterton[3], Chatterton *et al*[4]., and Upmeyer and Koller[19].

Leaf photosynthetic rate of the treated plants was decreased continuously with the passage of time (Fig. 6). Pod removal treatment did not significantly affect the change of leaf photosynthetic rate compared to the control. On the contrary, leaf removal treatment increased the leaf photosynthetic rate significantly from 22 to 32DAT, then decreased rapidly at last sampling time. Leaf stomatal resistance for CO_2 diffusion, deducing factor of photosynthesis, showed the reverse pattern of leaf photosynthetic rate (Fig. 6 and 7). Leaf stomatal resistance by pod removal treatment was highly increased from 32 to 42DAT compared to the other treatments.

Pod removal and leaf removal treatments for the purpose of change the sink demand to assimilate partitioning increased and decreased the starch content of leaves respectively (Fig. 3). Thorne and Koller[18] reported that physical resistance for CO_2 diffusion took place in leaves because of starch accumulation occurred in chloroplast of mesophyll cells[21]. In this experiment, pod removal treatment increased starch content in leaves (Fig. 3) and also increased significantly leaf stomatal resistance (Fig. 7), but leaf photosynthetic rate of the treatment was no different from the control (Fig. 6). In addition, leaf removal treatment did not influence on the leaf stomatal resistance (Fig. 7) and increased significantly the leaf photo- synthetic rate compared to the control (Fig. 6). These results are not agreed to the view that the factor decreasing leaf photosynthetic rate by starch accumulation is increase of leaf stomatal resistance[19]. No significant difference of total dry weights between pod removal treatment and the control supports no difference of the leaf photosynthetic rates by this 50% depodded soybean plants (Fig. 1 and 6).

Protein contents of soybean plant parts after pod removal and leaf removal treatments are shown in Table 2. At the last sampling time, 42DAT, pods were separated to seeds and pod walls. Protein contents of vegetative tissues were decreased gradually because of the nitrogen requirement of seeds. Protein contents of leaves were appeared significant differences for all sampling times and were highest in depodded plants among the treatments except the first sampling time. The similar results were found in stems + petioles

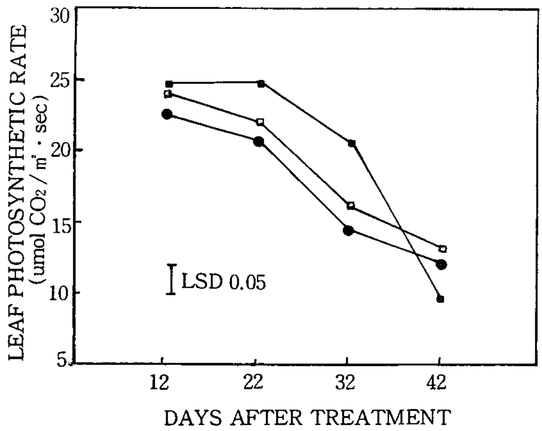

Fig. 6. Leaf photosynthetic rates of control (−□−), depoded(−●−) and defoliated(−■−) soybean plants on days after treatment.

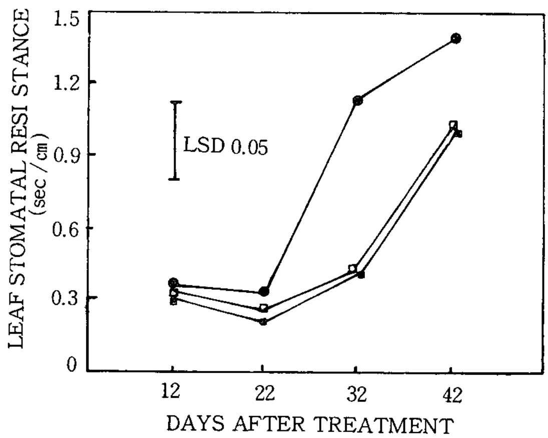

Fig. 7. Leaf stomatal resistances of control (−□−), depoded(−●−) and defoliated(−■−) soybean plants on days after treatment.

Table 2. Protein contents in leaves, stems+petioles, roots, pods, seeds, and pod-walls of control(A), depoded(B), and defoliated(C) soybean plants on days after treatment.

Item	Treat-ment	DAT* 2	12	22	32	42	$LSD_{0.05}$
leaf	A	33.78	29.70	27.28	23.13	19.85	
	B	33.95	31.05	28.50	24.45	20.74	
	C	32.73	30.00	25.86	22.64	19.14	
	$LSD_{0.05}$	1.00	0.80	0.84	0.64	0.96	1.93
stem+	A	20.47	14.60	12.59	9.30	8.39	
petiole	B	20.03	17.51	13.36	11.13	10.96	
	C	19.95	14.64	11.66	8.60	6.48	
	$LSD_{0.05}$	1.09	0.64	0.63	1.23	0.89	0.89
root	A	17.62	17.34	14.79	12.97	11.59	
	B	18.06	18.88	15.62	13.43	12.08	
	C	18.32	15.69	14.47	11.38	10.24	
	$LSD_{0.05}$	0.55	0.68	0.73	0.55	0.60	0.50
pod	A	28.97	24.63	24.93	24.95		
	B	28.17	25.91	25.79	25.10		
	C	28.23	25.31	24.29	24.66		
	$LSD_{0.05}$	1.08	0.81	0.57	0.61		0.74
podwall	A					6.63	
	B					6.76	
	C					6.24	
	$LSD_{0.05}$					0.77	
seed	A					39.62	
	B					40.16	
	C					38.95	
	$LSD_{0.05}$					0.97	

* Days after treatment

and roots on protein contents of the treatments. Protein contents of pods from 2 to 32DAT, and seeds and pod walls at 42DAT were not show significant differences among the treatments. However, protein contents of vegetative tissues were increased by pod removal and decreased by leaf removal treatments. Considering the positive correlation between root dry weight and total nodule activity[11], these results corresponded with Fig. 2. It is assumed that increased starch content of roots by pod removal treatment (Fig. 4) accelerated the assimilate supply to root nodule system and caused increase of nitrogen fixation as indicated by Schonbeck *et al.*[14].

Leaf chlorophyll contents of the treatments were increased from 2 to 32DAT and decreased rapidly at 42DAT (Fig. 8). Leaf chlorophyll content of depodded plants was increased compared to the other treatments at all sampling times. The decreases of leaf chlorophyll contents of the treatments at 42DAT(R_7 stage) indicate the beginning of leaf senescence. As a result, pod removal treatment delayed the leaf senescence of the plants. Leaf senescence is separated into apparent senescence(leaf chlorophyll content) and functional senescence(leaf photosynthetic rate).

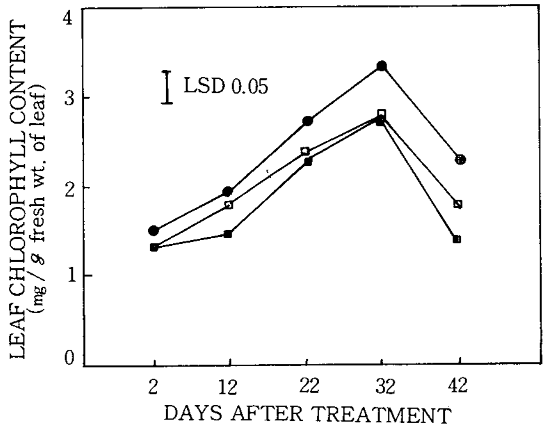

Fig. 8. Leaf chlorophyll contents of control (−□−), depoded(−●−) and defoliated(−■−) soybean plants on days after treatment.

Referring to Fig. 6, the leaf photosynthetic rate of depodded plants was lower than that of defoliated plants until 32DAT, and the defoliated plants showed lowest the leaf photosynthetic rate among the treatments at 42DAT. Therefore, pod removal treatment delayed apparent senescence by increasing the leaf chlorophyll content but did not influence to functional senescence by decreasing the leaf photosynthetic rate of the plants. Mondal *et al.*[13] reported the similar results as in the other researches[5,6,15,20]. In leaf removal treatment, the decreases of leaf chlorophyll content at all sampling times and leaf photosynthetic rate at 42DAT indicated the promotion of both apparent and functional senescences.

摘　　要

大豆에서 各各 50%의 莢除去와 葉除去 처리에 의해서 變化된 同化物質에 대한 sink demand가 葉의 光合成率과 各 部位別 蛋白質 含量 및 葉의 老化에 미치는 影響을 究明하기위하여, 1990년 高麗大學校 自然資源大學, 食糧資源學科 實驗圃場에서, pot에 팔달콩을 供試하여 總乾物重과 葉을 除外한 vegetative tissues의 乾物重, 잎과 뿌리의 澱粉含量, 葉의 光合成率과 氣孔抵抗性, 各 部位別 蛋白質含量, 葉의 chlorophyll content등을 調査한 結果를 要約하면 다음과 같다.

1. 葉을 除外한 vegetative tissues의 乾物重은 莢除去 처리에 의해서 增加되었고, 따라서 莢除去 처리에 의한 總乾物重의 減少는 有意性이 없었다.
2. 種實의 100립중은 대조구와 비교할 때, 50% 莢除去 처리에 의해 6.4% 增加하였으며, 50% 葉除去 처리에 의해서 3.0% 減少하였다.
3. 葉의 澱粉含量은 처리 후 22일부터 減少되었고 뿌리의 澱粉含量은 全 時期에 걸쳐 減少되었는데, 잎과 뿌리의 澱粉含量은 莢除去 처리에 의해 높아지고 葉除去 처리에 의해 낮아지는 傾向을 보였다.
4. Specific leaf weight는 莢除去 처리에 의해 增加되었고 葉除去에 의해 減少 되었다.
5. 葉의 光合成率은 全 時期를 통하여 低下되었으며, 葉除去 처리에 의해 增加 되었다.
6. 氣孔抵抗性은 全 時期에 걸쳐서 높아졌으며, 莢除去 처리에 의해 增加되었다.
7. 잎, 줄기＋엽병, 뿌리 등의 蛋白質含量은 점차로 減少되는 傾向이었으며, 莢除去 처리에 의해 높아졌고 葉除去에 의해 낮아지는 傾向을 보였다.
8. 成熟期(R_7)의 種實의 蛋白質含量은 莢除去와 葉除去 처리에 의해 有意性 있는 차이를 나타내지 않았다.
9. 葉의 chlorophyll content의 減少에 의한 葉의 外觀上 老化는 莢除去처리에 의해 遲延되었고 葉除去에 의해 促進되었다.
10. 光合成率의 減少에 의한 葉의 機能上 老化는 葉除去 처리에 의해 促進되었다.

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