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Productivity of a Dwarf Type Soybean Induced by Mechanical Stimulation Applied during Vegetative Stage

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Abstract : As an attempt for better understanding the relationship between canopy architecture and seed production, the upper portions of the canopy, cv. Kitahomare, were mechanically stimulated during the period from the fifth trifoliolate leaf stage to the young pod stage, and its effect and after effect on morphology, canopy structure, light penetration, growth and yield was investigated. Mechanical stimulation inhibited growth of the main stem, but promoted that of the lateral branches ; the main stem-branch ratio of dry matter in each part was 1:1 in unstimulated control plants, but 1:2 or more in stimulated plants at the end of the treatment. Morphologically, stimulated plants had 1) shorter, thicker and sturdier stems, 2) smaller and thicker leaves with shorter petioles, and 3) greater a number of branches when compared with the controls ; thus modified to a typical dwarf type form. After the treatment has finished, stimulated plants showed a typical table type canopy throughout the pod filling period, but their light extinction coefficients were smaller than those of controls. The pod development was retarded by the treatment during the flowering stage. Stimulated plants, however, showed higher net assimilation rates and pod filling rates, and produced more pods than controls, resulted in 38% greater seed production at maturity, because of a greater increase in branch quantity. A plant form such as dwarf type with smaller sized leaves may be advantageous for high yielding under high population densities that cause a severe mutual shading and risks of lodging.
Key words : Canopy structure, Dwarf type, Growth, Mechanical stimulation, Morphology, Soybean, Yield.

栄養生長期における機械的刺激によって誘発された矮性型ダイズの生産性：中世古公男(北海道大学農学部)

要　旨：植物は一般に機械的刺激によって矮性化することが知られている．そこで本研究では，ダイズの草型と受光体制ならびに生育・収量との相互関係を解明する一環として，30 cm の正方形植えに栽植した有限型品種キタホマレについて，第5本葉展開期 (7月10日) から幼莢期 (栄養生長完了期，8月6日) まで4週間，群落上層に機械的刺激を与え，形態的変化を明らかにするとともに，その群落構造，乾物生産および子実収量に及ぼす影響を調査した．機械的刺激によって主茎の生長が抑制されたが，分枝の生長は促進され，処理後の各器官における主茎一分枝比(乾物ベース)は,無処理区1対1に対して処理区では1対2〜3となった．刺激を受けた植物体は，形態的には，茎が太く，短縮し，短い葉柄をもつ小型の厚い葉を着生し，分枝数の多い典型的な矮性型の草型を示した．また，葉は小型化したが，総節数が増加したため，葉面積指数は無処理区と大差なく推移した．処理後の葉群構造は，典型的な天井型構造を示したが，吸光係数は無処理区に比べ小さかった．莢の発育は，開花期間中は機械的刺激により遅れる傾向が認められた．しかし，処理終了後の登熟期間中では，処理区は純同化率および莢実乾物増加速度が大きく，分枝の着莢数が増加して成熟期の子実収量は無処理区に比べ38% 大きかった．このような矮性型の草型は，相互遮蔽が大きく，倒伏の危険性がある密植条件下では有利なものと推察された．
キーワード：機械的刺激，群落構造，形態，収量，生育，ダイズ，矮性型．

The light distribution within the canopy is an important factor influencing crop productivity throughout the photosynthetic rate. Field-grown soybeans often develop a typical table type canopy of which leaf area is concentrated near upper portions[2,14]. Therefore, it has been pointed out in regard to this crop that a large proportion of incident light is absorbed in the uppermost part of the canopy so that the lack of light within the canopy is one of the limiting factors for canopy photosynthesis[6].

The canopy structure of soybeans consists of more complicated elements than that of gramineous crops ; the length and inclination of petioles on each node and the stem structure including number and length of branches play an important part in the determination of spatial distribution of leaves[9]. Theoretically, the plants with erect, narrow and small sized leaves have been well known to penetrate light

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deeper in the canopy[8], but fundamental information is hardly available on the interrelationships between canopy architecture, light distribution and seed production in soybean canopies.

It has been recently discovered that mechanical stimulations such as rubbing, shaking, stroking and flexing, may cause morphological changes such as shorter stem and less leaf area in several plants[1,3,4,5,7,11,12,13,15]. Though mechanical stimulations are also known to retard plant growth, if the changes in leaf and stem morphology can be artificially induced during the vegetative stage in field-grown soybeans, it may be expected as an available means for investigating what kind of canopy structure is desirable for seed production during the pod filling stage when severe mutual shading takes place. This study was designed to examine the effects of mechanical stimulation applied during the vegetative stage on morphology, structure, light penetration, growth and yield of a soybean canopy.

Materials and Methods

Kitahomare, one of the determinate cultivars of soybean (*Glycine max* Merr.), was grown in the field of Experimental Farm of Hokkaido University in 1985. A 30 cm equidistant square pattern was used to induce, as much as possible, uniform leaf distribution in all directions. Seeds were sown by hand on May 15 at the rate of 2-3 seeds per hill and thinned to a single plant per hill when the first trifoliolate leaf expanded (11.1 plants/m^2). A combination of $N : P_2O_5 : K_2O$ as a fertilizer was applied at the ratio of 32, 100 and 80 kg/ha, respectively, just before seeding. A plot was comprised 4.2 m in width (east-west direction) and 12 m in length (north-south direction) and replicated two times. Plots of the same size were also devoted to unstimulated control. The mechanical stimulation was given by the following method.

The apparatus used for the mechanical stimulation treatment was shown in Fig. 1. An aluminum pipe frame was fixed on a steel wire stretched horizontally at a height of 1.5 m over the center line of the plot by using two fixed pulleys propped on the north and south sides of the plot. Two other wires were also stretched 50 cm apart to either side of the pulley wire through small rings on the frame to prevent itself from rolling. Seven aluminum pipes of a smaller diameter, 10 mm in diameter and 3 m in length, were suspended parallel (east-west direction) and 30 cm apart from each other by vinyl strings from the frame. The height of the pipes was adjusted within 10 cm of the upper portion of the canopy to move in tandem with plant growth during the treatment period. This frame was moved gently by hands from side to side 30 and 15 times in the morning (10:00—11:00) during the periods from the fifth trifoliolate leaf (July 10) to the flowering stage (July 24) and from the flowering to the young pod stage (Aug. 6), for 2 weeks respectively. After that the stimulated plants were grown without treatment until maturity (Oct. 11).

Leaf and stem morphology, leaf area and dry weight of the stimulated and unstimulated control plants were measured at the start (July 10), middle (July 24) and end (Aug. 6) of the treatment period, and on 2 days (Aug. 21 and Sept. 12) during the pod filling stage after the treatment. Five uniform plants were selected on a fresh weight basis from 10 plants taken at random from each plot, and the stem length, diameter (only of the main stem) and number of nodes of main stem and branches were recorded. After determining the morphology, dry weights of leaf, stem plus petioles, pod including seed and root were weighed after oven drying for 48 hours at 80°C. The leaf area of a representative plant was measured by an automatic leaf area meter (Hayashiden-

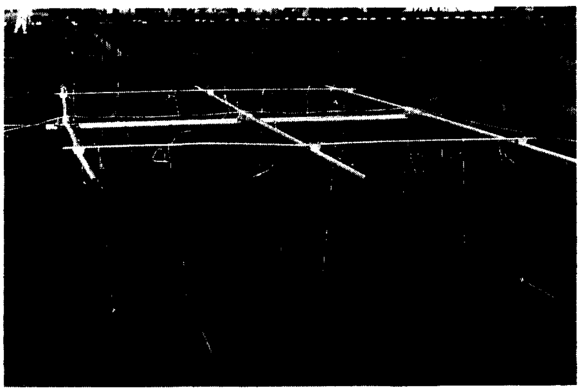

Fig. 1. The apparatus used for mechanical stimulation.

Note. The frame suspending 7 aluminum pipes of smaller diameter was fixed on a steel wire stretched through two fixed pulleies, and moved gently from side to side.

ko Corp. AAM-7). The leaves were then dried and weighed for the calculation of specific leaf area (SLA, cm^2/g). At the end of the treatment, leaf size, thickness and petiole length of the upper three leaves on the main stem were measured.

During the pod filling stage, distribution of leaf area, stem and pod dry weight with canopy height were examined three times (on August 7, 31 and September 12). The measurements were taken at 10 cm height intervals with 4 plants within a land area 0.6 m $\times$ 0.6 m. At the same time, relative light intensities at the horizontal level of each height were recorded (20 points) noon time using a relative light intensity photometer sensitive in the range of 450nm to 700nm (Sanshinkogyo Corp. NS-II). On October 11, yield and yield components were recorded of the 10 uniform plants of each plot.

In this experiment, leaf area indices (LAI) were determined as the mean leaf dry weight per unit land area (g/m^2) $\times$ SLA. Net assimilation rates (NAR) were calculated using the equation proposed by Watson[16].

Results

1. *Stem and leaf morphology*

Mechanical stimulation was continuously given to the plant canopy until the young pod stage, because the vegetative growth of soybeans usually continues after flowering and is completed at about the young pod stage. Table 1 shows some morphological characteristics obserbed two weeks (on July 24, flowering stage) and four weeks (on Aug. 6, young pod stage) after the start of treatment. Continuous stimulation during the vegetative growth reduced the main stem length and total stem length of branches, but increased the number of branches. The number of nodes on stimulated plants was not different from that on the maim stem, but the number on all of the branches was greater than that of the controls. This increase was mainly due to an increase in the number of branches, because the node number per branch was not different between stimulated and control plants. Stem diameter measured at the middle of the internode between the cotyledon and primary leaf

Table 1. Effect of mechanical stimulation on some morphological characteristics.

Date	Treatment	Main stem: Stem length (cm)	Main stem: No. of nodes (/pl.)	Main stem: Stem diameter (mm)	Branch: No. of branches (/pl.)	Branch: Total node number (/pl.)	Branch: Total stem length (cm/pl.)
July 24	Control	45.7	11.5	8.1	4.3	20.8	101
	Stimulated	35.5	11.5	9.2	5.2	24.3	99
	Significance	**	ns	**	*	ns	ns
Aug. 6	Control	46.5	11.6	10.2	4.7	17.7	169
	Stimulated	34.4	11.5	10.2	6.7	23.7	128
	Significance	**	ns	ns	**	**	*

Note. July 24 : flowering stage, Aug. 6 : young pod stage. * : 5%, ** : 1% level of significance. ns : not significant. Stem diameter was measured at the middle of the internode between the cotyledon and the primary leaf.

Table 2. Effect of mechanical stimulation on leaf morphology (Aug.6).

Leaf position	Leaf area (cm^2/3 leaflets) 1	2	3	Leaf thickness (mm) 1	2	3	Length of petiole (cm) 1	2	3
Control	332	331	261	0.32	0.32	0.28	24	22	22
Stimulated	212	236	214	0.48	0.46	0.36	14	11	9
Significance	**	**	*	**	**	**	**	**	**

Note. Leaf position 1 is the top-most leaf (the 10 th trifoliolate leaf from the base) on the main stem. * : 5%, ** : 1% level of significance.

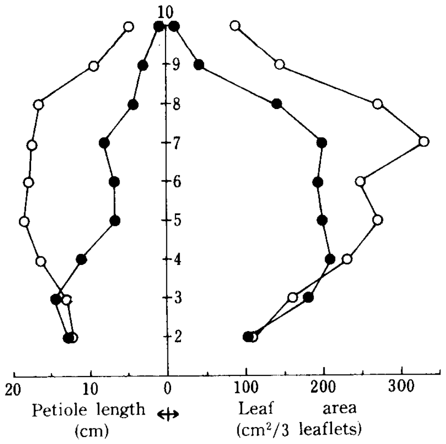

Fig. 2. Effect of mechanical stimulation on the length of the petiole and size of leaf of each node on the main stem (July 24).
Note. ○ : control, ● : stimulated. number: position of the node of trifoliolate leaves on the main stem.

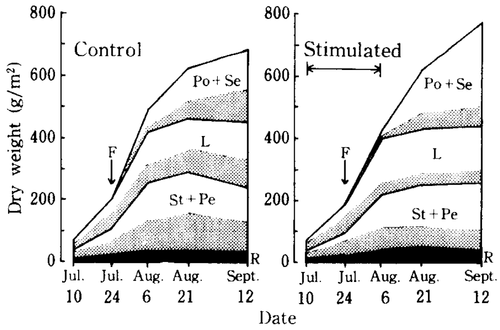

Fig. 3. Effects of mechanical stimulation on dry matter accumulation pattern.
Note. Po+Se: pod+seed, L: leaf, St+Pe: stem+petiole, R: root, F: flowering, dotted part: main stem, open part: branch.

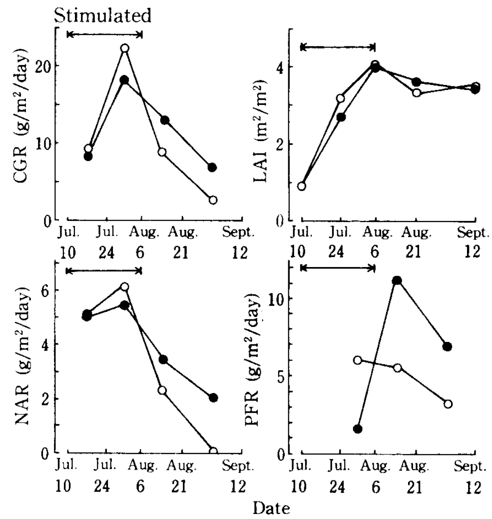

Fig. 4. Effects of mechanical stimulation on crop growth rate (CGR), leaf area index (LAI), net assimilation rate (NAR) and pod filling rate (PFR).
Note. ○ : control, ● : stimulated (July 10-Aug. 6).

was not different between stimulated and control plants on Aug. 6, though significantly greater in stimulated plants on July 24. After the treatment, however, stimulated plants had thicker and sturdier stems as a whole than controls (see Fig. 6).

Leaf morphology was also influenced by mechanical stimulation (Table 2). At the end of the treatment, leaf size and petiole length of the upper three leaves on the main stem of stimulated plants were reduced, on average, to 72% and 50% of those of controls, respectively. On the contrary, the leaf thickness was increased by 40% on average after mechanical stimulation. As shown in Fig. 2, the similar effects were already found on the lower leaves subjected to stimulation in the middle of the treatment period.

2. *Dry matter production and growth parameters*

Fig. 3 shows dry matter accumulation patterns by season. During the treatment, stimulated plants produced less biomass than controls, resulted in 14% greater in leaf, 17% less in stem (including petiole) and 73% less in pod dry weight at the end of treatment. In particular, the lower pod growth rate in stimulated plants during the period from the flowering to the young pod stage suggests that the pod development was fairly retarded by mechanical stimulation. At the end of the treatment, the number of pods exceeded 1.5 cm in length was 38.9 and 52.3/pl. in stimulated and control plants, respectively.

The most interesting difference in the growth of stimulated and control plants was in the change in the main stem to branch ratio. The main stem-branch ratio of dry matter in each part was 1:1 in controls, but 1:2 or more in stimulated plants at the end of the treatment, indicating that mechanical stimulation during the vegetative growth has inhibited growth of the main stem and promoted that of lateral branches.

During the pod filling stage after the treatment, the total dry weight of stimulated plants exceeded that of controls, mainly due to the higher pod growth rates in branches. For 2 weeks after the end of the treatment, stimulated plants produced more pods than controls, especially in branches, so that on Aug. 21 the pod number was 82.2 and 73.5/pl. in stimulated and control plants respectively, and always greater in stimulated plants than in controls after that. Root dry weight was not different between stimulated and control plants during the treatment, but significantly greater in stimulated plants after the treatment.

The seasonal patterns of growth parameters were shown in Fig. 4. In spite of smaller sized leaves, after the treatment stimulated plants had the same values of leaf area index as controls, because of the greater number of leaves in branches, though a slightly lower value during the middle of the treatment. The crop growth rates (CGR) of stimulated plants were lower during the treatment, but higher during the pod filling stage than those of controls. This was much the same as in net assimilation rates, of which time trend was almost parallel to those of CGRs. The pod filling rates of stimulated plants were about twice of those of controls during the pod filling stage, though much lower during the period from the flowering to the young pod stage.

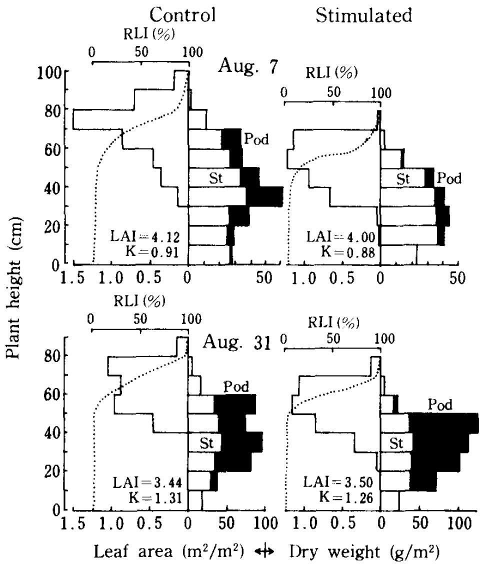

Fig. 5. Effect of mechanical stimulation on canopy structure.

Note. RLI : relative light intensity (%), K : light extinction coefficient, St : stem including petiole, pod : pod including seed.

3. *Canopy structure and light penetration*

Canopy structures during the pod filling stage are illustrated in Fig. 5. On Aug. 7, just after the treatment ended, the vertical distribution of leaf area of controls was an oval type, but changed to a table type on Aug. 31, of which canopy height was 10 cm lower than on Aug. 7. Although the mode of leaf area distribution on Sept. 12 (not shown) was almost similar to that on Aug. 31, its canopy height was continuously reduced 20 cm. On the other hand, stimulated plants had a typical table type with the same canopy height on each sampling date, indicating a very stable canopy structure throughout the pod filling stage.

In table type canopies, either stimulated or control plants, more than 90% of incoming light was intercepted by the upper three layers only, but the light extinction coefficients (k) were always lower in stimulated plants than in controls (the k on Sept. 12 is 0.88 and 0.99 in stimulated and control plants, respectively). In these layers stimulated plants distributed more leaf area of branches (90%) than controls (69%); in particular, there were no main stem leaves within the upper 20 cm of canopy. Stimulated plants tended to produce larger stem dry weight in the lower strata when compared with controls. The distribution of pod dry weight of controls was relatively uniform over all layers on each sampling date, but that of stimulated plants became larger towards the top after Aug. 31.

4. *Yield and yield components*

Table 3. Effect of mechanical stimulation on yield and yield components.

	Dry seed yield (g/m^2)			No. of pods (/pl.)			No. of seed per pod	100 seeds weight (g)
	M	B	Total	M	B	Total		
Control	89.5 (40.0)	134.3 (60.0)	223.9 (100)	21.1 (41.5)	29.8 (58.5)	50.9 (100)	1.92	20.3
Stimulated	75.7 (24.5)	233.8 (75.5)	309.5 (100)	15.8 (24.3)	49.3 (75.7)	65.1 (100)	1.88	22.8

Note. M : main stem, B : branches, ( ) : percentage.

Yield and yield components were given in Table 3. Stimulated plants produced 15% less yield on the main stem, but 74% greater yield in branches than controls, resulted in 38% greater seed production as total. Similarly, the pod number of stimulated plants was 25% less on the main stem, but 65% greater in branches and 28% greater as total when compared with those of controls. These differences between stimulated and control plants might be regarded as appropriate, though not significant at a 5% level, in view of the differences in changes of pod dry weight (Fig. 3) and pod filling rate (Fig. 4). The number of seed per pod was not different between them, but 100 seeds weight was larger (12%) in stimulated plants.

Discussion

The mechanical stimulation used in this experiment contains some kinds of stimulation, such as stroking, bending and rubbing. For about 3 days following the start of treatment, leaf damage (broken and torn off) was observed sparsely in the uppermost leaves of canopy, but this was not true later. As time progressed, the leaves subjected to stimulation became smaller and thicker when compared with unstimulated leaves. In addition, the petioles and branches tended to elongate away from the direction of stimulation, as if they averted it, resembling ribs of a fan as seen in the photograph (Fig. 6) and a more concentrated leaf arrangement to the unstimulated east-west direction (see Fig. 1) during the middle of treatment period. Such responses to mechanical stimulation are certainly effective to avoid the leaf damage.

Continuous mechanical stimulation on the upper portions of canopy for 4 weeks during the vegetative growth inhibited the growth of the main stem, but promoted that of branches, resulted in the alteration of main stem-branch balance from the ratio of 1 : 1 in unstimulated controls to 1 : 2 or more in stimulated plants on the dry weight basis. Morphologically,

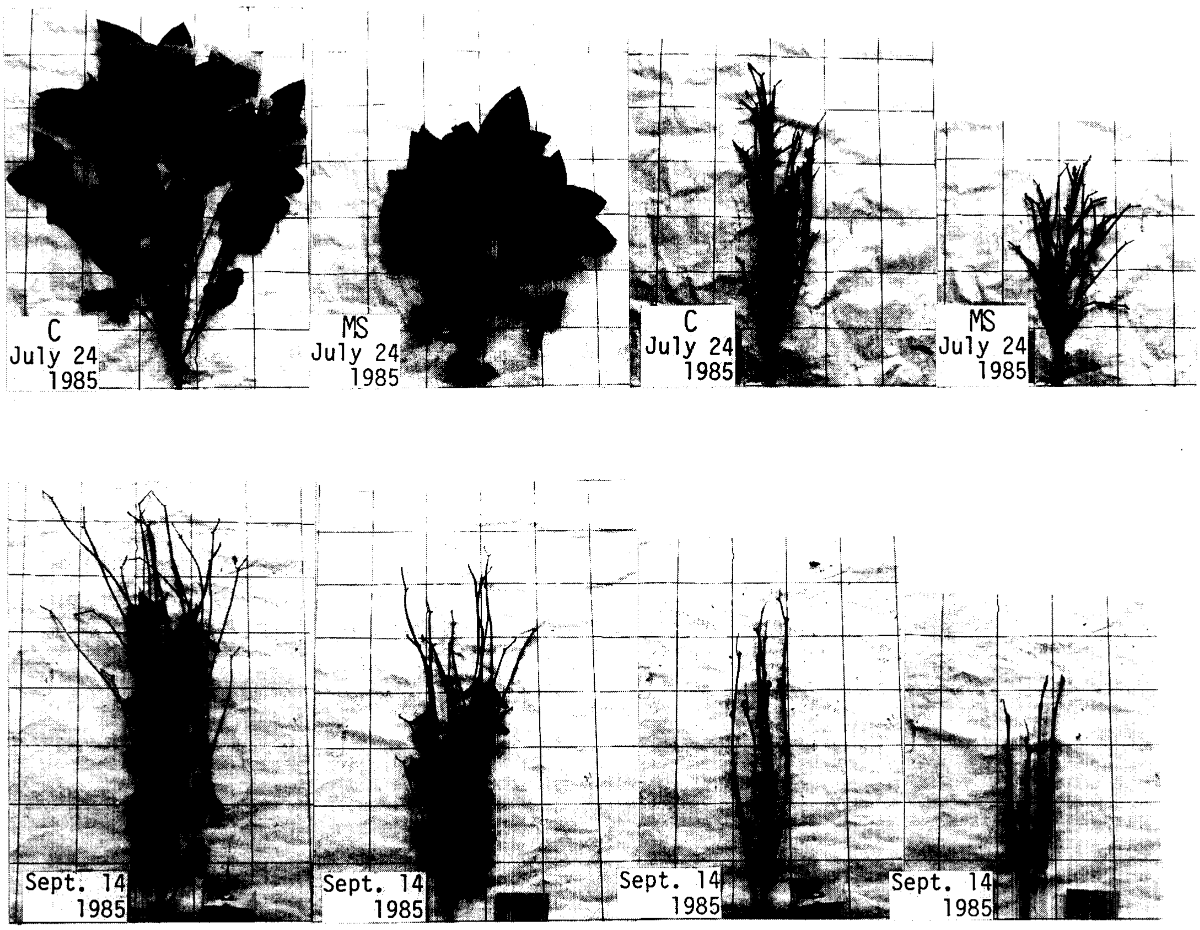

Fig. 6. The plant form of Kitahomare as affected by mechanical stimulation.
Note. C : control, MS : stimulated. Grid length was 10 cm.

stimulated plants were also dramatically modified; they had 1) shorter, thicker and sturdier stem, 2) smaller and thicker leaves with shorter petioles, 3) greater number of branches and as a whole, 4) a compact foliage with greater number of smaller leaves, that is, a typical dwarf type plant form, as shown in Fig. 6.

Although the pod development was retarded by mechanical stimulation during the period from the flowering to the young pod stage, stimulated plants produced more pods than controls during the pod filling stage after the treatment, resulted in 38% greater seed production at maturity, because of the greater increase in branches. These phenomena were also accompanied with higher net assimilation rates and pod filling rates in stimulated plants, though their leaf area index did not differ from those for controls, suggesting that the canopy photosynthesis was higher in stimulated plants and the photosynthate translocated more to pods, especially to those of branches, than those in controls.

As mentioned above, the canopy of the stimulated plants, the branch leaves occupied three fourth of the total leaf area as compared to one-half of those of controls, showed a typical table type, and more than 90% of incoming light was intercepted by the leaves distributed within the upper 30 cm of the canopy.

However, the stimulated plants had lower light extinction coefficients than controls throughout the pod filling stage, presumably due to smaller sized leaves. In addition, in the upper portions of the canopy, the stimulated plants distributed a greater number of smaller branch leaves, and the pod dry weight with canopy height was larger towards the top during the latter half of the pod filling stage. From these facts, it was interpreted that the higher net assimilation rates in stimulated plants might be attributable not to the increase in photosynthetic activity itself in the individual leaves, but to the changes in stem structure and leaf morphology and distribution, involved in the improvement of light conditions within the canopy.

Another interesting change observed in the stimulated plants is the increase of root dry weight after the treatment. It suggests that the root growth was also influenced by mechanical stimulation. However, lacking detailed measurements, what changes were induced in root morphology and its functions were not made clear in this experiment; thus requiring further detailed study.

In general, the grain yield of soybeans responds to population density in an asymptotic manner, mainly because the number and growth of branches decrease rapidly as population density increases[10]. A dwarf type plant having a greater number of vigorous branches with smaller sized leaves may produce a higher yield under high population densities that occur in an environment of severe mutual shading and risks of lodging.

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