PHYSIOLOGICAL STUDIES OF THE GROWING PROCESS OF BROAD BEAN PLANTS

VII Effects of Plant Density on the Growth and the Seed Production

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As with cereals, the yield of pulse crops is a product of reproductive growth and in general is a rather complex character. In broad beans (*Vicia faba*), it can be resolved into next four components; the number of pod bearing stems, the number of pods per stem, the number of seeds per pod, and the seed size. Many investigators have reported that the growth of broad bean plants showed a high degree of plasticity and these yield components were all variable under various conditions of soil moisture(3,5,22), soil fertility(1,23), shading(2,8,24), and defoliation(10,12,19,25). In practice, according to the increase of plant density, it will be sure these conditions interact with each other and subsequently have complicated effects on the yield components.

Although the number of reports(6,7,15,16,17) with respect to the plant density is increasing, there have been few experimental works on the nature of competition in broad bean plants. The object of this investigation is to describe the effects of plant density on the growth and the seed production concerning with the nature of competition and its meaning for the production and distribution of dry matter. In this experiment, the plant number was varied by the change of spacing both between and within rows.

Materials and Methods

Broad beans, cultivar "Sanuki-nagasaya", were sown in the field on November 10 and the seedlings were grown as a plant per hill. Though the trials were set with four densities designed as Table 1, three densities, namely high, medium, and low, were compared concerning with the detailed analysis of the growth. Fertilizer application was made as basal dressing: 27 kg ammonium sulfate, 45 kg calcium superphosphate, and 18 kg potassium sulfate per 10 a were plowed down.

Table 1. Experimental design

Density	Row width cm	Hill distance cm	Plant number per sq. meter	Biological space per plant cm^2
Low	72	36	3.8	2592
Medium	36	36	7.6	1296
High	36	18	15.2	648
Very high	36	9	30.4	324

Plants were sampled five times. At the appropriate sampling time, the tops were clipped at every 10 cm height above the ground(9,13) and the roots were washed out. Then the tops were segregated into leaf blade, stem plus petiole, pod, and seed, and dried in an oven. At the same time, leaf area was estimated by means of blue print method for the leaves of all layers. The chlorophyll was extracted with 85% acetone and determined by the photoelectric colorimetric method for total chlorophyll[25]. With regard to the light transmission in the field, the relative light intensity was calculated from the readings taken with Toshiba Lux-meter (No. 5).

Results

Growing Status

The growing status of plants in three densities are shown in Fig. 1, Tables 2 and 3. In winter, the growth of tops in three densities were not remarkable except for the branching. But the significant differences among three densities occurred to the stem or internode elongation after the start of flowering when the stem length was 20 cm above the ground. The growth of branches decreased with decreasing the space both between and within rows; the total stem number, the pod bearing stem number, and the percentage of pod bearing stem were declined. Moreover, the flowering of plants in the high density began a few days later than other densities and this fact showed that the node order of 1st inflorescence raised in the high density; it was 7th node in contrast with 6th node of the low and middle densities. Consequently, the significant increase was noted in the height of 1st and final inflorescence, and of immature pod in the high density. It followed, however, the reduction in the number of pod bearing nodes in the high density owing to the pod shedding of immature pod at the upper nodes, the nodal position of mature pod was unaffected by the change of plant density.

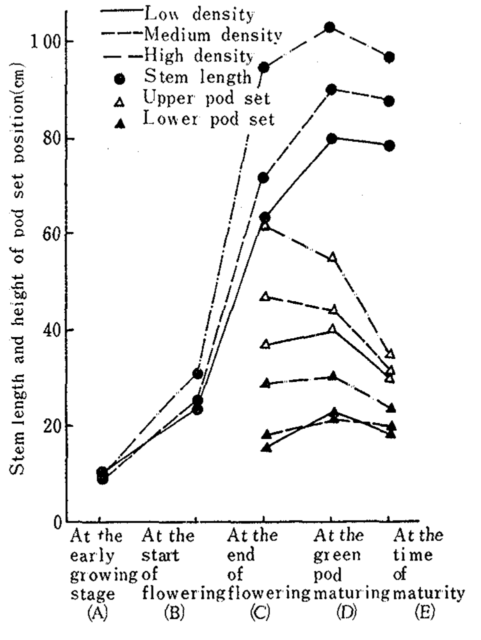

Fig. 1. Changes in stem length and height of pod set position.

As the growth progressed, leaves resulted in much mutual shading within the field, especially recognized earlier in the high density and dense leaves were defoliated. The flower number per plant was approximate in three densities. The pod number per plant and the podding percentage were considerably lowered with increasing plant density, but there were little differences among three densities for the pod length, the seed number per pod, and 100 seeds weight.

Table 2. Effects of density on the flower, pod, and seed

	Low density	Medium density	High density
Stem number* 1)	10.4	8.2	7.4
Pod bearing stem number* 2)	7.8	5.6	4.6
Percentage of pod bearing stem 2)/1) %	75.0	68.3	62.2
Flower number* 3)	156.6	160.5	150.0
Pod number at the time of maturity* 4)	26.8	18.8	13.8
Podding percentage 4)/3) %	17.1	11.7	9.2
Pod length cm	10.6	9.8	10.7
Seed number per pod	3.6	3.7	3.8
100 seeds wt. g	85.2	85.3	85.7

* Per plant

Table 3. Effects of density on the internodal length

Height above the ground cm	Low density cm	Medium density cm	High density cm
80–100	—	4.5	5.2
60–80	4.9	6.1	7.0
40–60	5.8	6.4	7.0
20–40	6.2	7.3	7.3
0–20	3.2	3.3	4.0

Dry Matter Production

The variations of dry weight in each organ per plant and per unit area (m^2) are shown in Figs. 2 and 3. With regard to the vegetative organ, the dry weight of leaf blade and stem became maximum at the end of flowering and at the green pod maturing, respectively, but that of root was recognized consistently during the flowering to the pod developing period. As for the reproductive organ, though the dry weight of pod was high at the green pod maturing, the dry matter accumulation in seed became high towards the maturity.

Within the range of three densities covering this experiment, the dry weight per plant fell consistently as the density increased after the flowering period at which much mutual shading occurred. Contrary to the above results, on the basis of the dry matter productivity per sq. meter, it was seen that the variations behaved consistently high with increasing density.

The dry weight of whole plant and seed including very high density trial at the time of maturity is shown in Fig. 4. Two items per plant were lowered with increasing density, especially in the very high density. But the dry weight per sq. meter became high in regular order of low, medium, and high density, but was again pressed severely when the density was beyond the range of this experimental "high".

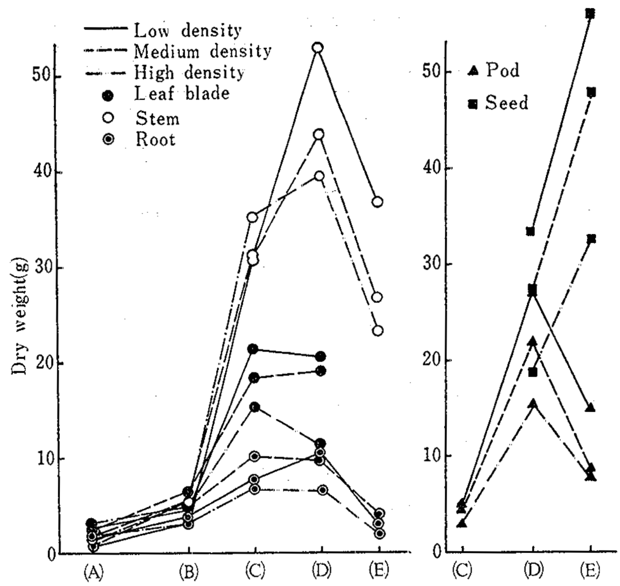

Fig. 2. Changes in dry weight of each organ per plant.

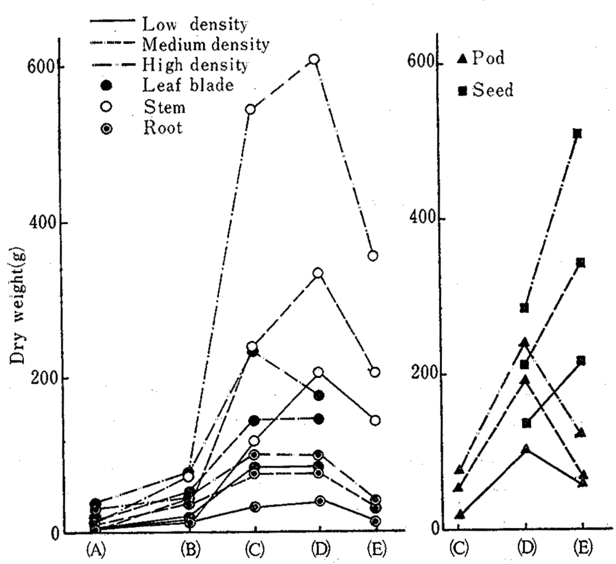

Fig. 3. Changes in dry weight of each organ per sq. meter.

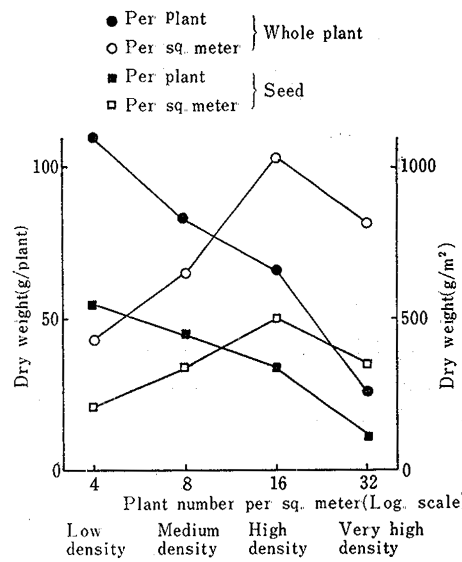

Fig. 4. Dry weight at the time of maturity.

Figures 5 and 6 are the variations of the productive structure obtained with the stratifying every 10 cm clip method. In general, the vertical distributions of the photosynthetic and non-photosynthetic system show the type of broad leaf plants(9,13). The leaves distributed vertically almost all layers in three densities till the end of flowering. Thenceforth, the lower portion began to defoliate and the green leaves became to a state of restricting upper portion. This fact was revealed earlier and clearer with increasing density. The distributions of pod and seed were recognized in wide range of layers due to the increase of internodal length. Two figures on the basis of dry weight per plant and per sq. meter show analytically the order of the structure among three densities.

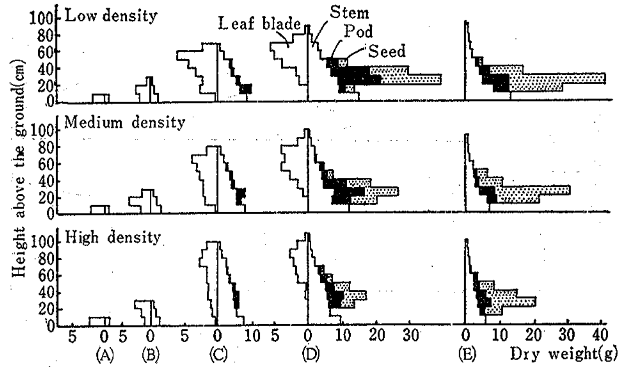

Fig. 5. Variations of the productive structure per plant.

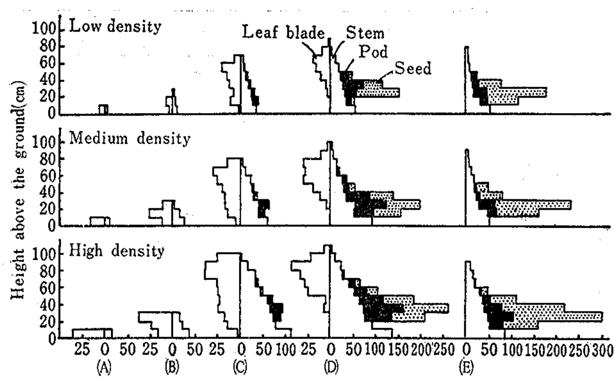

Fig. 6. Variations of the productive structure per sq. meter.

Profile of Photosynthetic System

The variations of the vertical distribution in leaf area per plant and per sq. meter are shown in Figs. 7 and 8. As for the leaf distribution pattern of individual plant, the leaf area, which was recognized mainly in the middle layers at the early growing stage, was found in the upper portion with the growth progressed. In the high density, the maximum area per 10 cm layer became about 1,000 cm^2 at the end of flowering, thenceforth declined rapidly. But this fact did not found in the low and the medium density. With regard to the leaf area per sq. meter distributed vertically, at the end of flowering, it was high in the order, high, medium, low density and especially in the upper layer. In the high density, however, the leaf area of the layers fell about 10,000 cm^2 same as the value in the medium density at the green pod maturing.

The variations of the leaf area index as shown in Fig. 9 increased with the growth progressed in the low and the medium density but not in the high density. The maximum value was 1.7, 5.0, and 9.1 in the low, medium, and high density, respectively, but in the high density the value was recognized about 5.0 at the green pod maturing.

In connection with the vertical distribution of leaves, the relative light intensities at three stages are shown in Fig. 10. The relative light intensity of the ground level which was above 20 per cent at the start of flowering fell along with the vigorous growth of vegetative organs. It became almost zero in the high and the medium density at the end of flowering. At this time the layer receiving under 10 per cent of natural daylight intensity was the first 10 cm above the ground

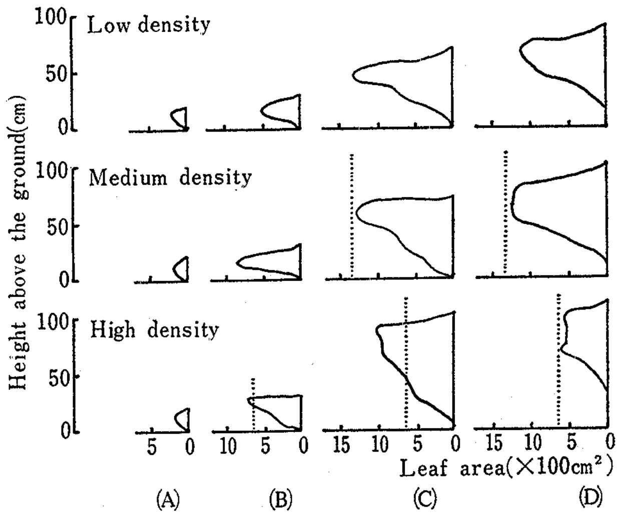

Fig. 7. Variations of the vertical distribution in leaf area per plant (Dotted lines show the biological space.)

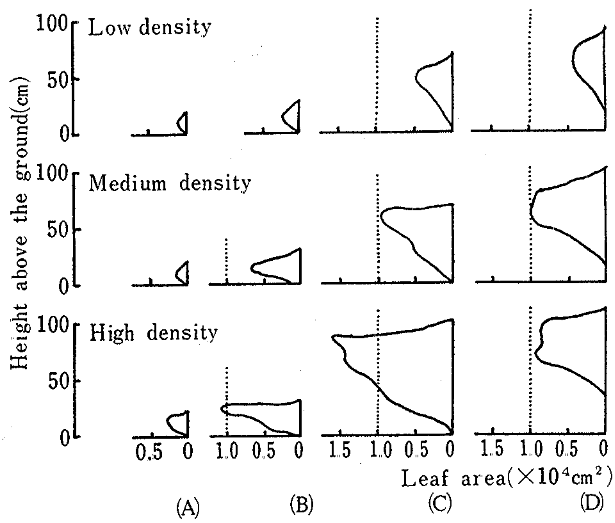

Fig. 8. Variations of the vertical distribution in leaf area per sq. meter (Dotted lines show the biological space.)

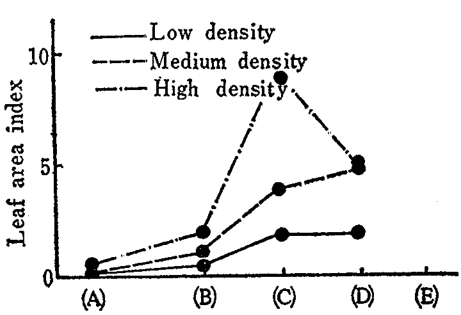

Fig. 9. Variations of the leaf area index.

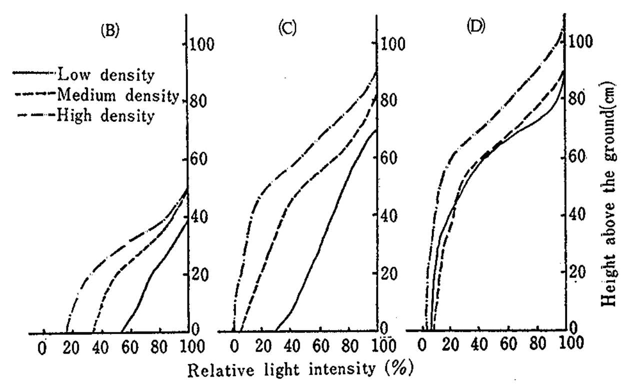

Fig. 10. Variations of the relative light intensity.

in the medium density, and 30 cm height in the high density. These phenomena were recognized more severely at the green pod maturing: the range under 10 per cent of light was 20 cm height in the low and the medium density, and 40 cm in the high density.

Discussion

In a plant density trial any final analysis on the nature of the competition must take a serious view of the biological space of individual plant. From this point of view, the authors considered the interrelationships between the growth and the plant number per unit area, i.e. the planting rate, and the plant arrangement, i.e. the distribution of plants was uniform or not. In broad beans (*Vicia faba*), it has been revealed that the characters in connection with the seed production have close relation with the planting rate, but not with the planting arrangement, especially row width(6,16,17). In this experiment, though the row width in the low density was unlike other densities, the results could be persuaded as the identical effects of the planting rate or the plant density.

The results obtained in this experiment were in agreement with the results of other reports on broad bean plants(6,7,15,16,17,) and on soybean plants(11); the high density promoted the elongation of stem or internodal length, but retarded the increase of the stem or node number, decreased the development of the reproductive organs, and had little efficiency on the seed size or the seed number per pod.

As for the elongation of stem or internodal length, similar effects of high density were recognized by Nagase et al.(14) with soybean plants. They pointed out that though soybean plants had usually short internode in the upper and the lower layers and long one in the middle layer, the long internode moved to the lower layer with increasing density. Such a phytosociological phenomena as the elongation of internodal length were also recognized on broad bean plants by the increasing density (Table 3). Thus, the height of flowering and of pod setting node was generally high in the high density at first, and the height of pod bearing node declined by the immature pod shedding at the upper layer during the pod maturing.

With regard to the characters of leaves, broad bean plants have usually 20 to 24 compound leaves per stem and the compound leaf consists of two single leaves at the lower 6 or 7 nodes and 3 to 7 single leaves upside node order. In this experiment, the leaf area per single leaf and chlorophyll content per unit leaf area at every 10 cm leaf layer are shown in Fig. 11. The single leaf area was approximate among three densities; rather small leaf on the upper and lower layers, large or spreaded leaf on the middle layer, especially on the uppermost flowering node. The chlorophyll content was also similar among three densities. Therefore, it seems that the new leaves differentiate and develop similarly in three densities, because those new leaves, which are always present on uppermost layer, are developed under the abundant light, regardless of the different plant densities.

The leaf canopy, thus, was accomplished primarily at the end of flowering in the manner described above. From this time toward the green pod maturing, however, the changes of the vertical distribution in leaf area became severely as shown in Figs. 7 and 8. Two decreased portions of the lower and the upper layers were recognized in leaf area.

With regard to the lower portion, the leaf area decreased at the green pod maturing within a range which received under 10 per cent light intensity at the end of flowering. In the present experiment, this range was under 10 cm height in the medium density and 30 cm height in the high density. One of the authors has recognized with unpublished data that the light com-

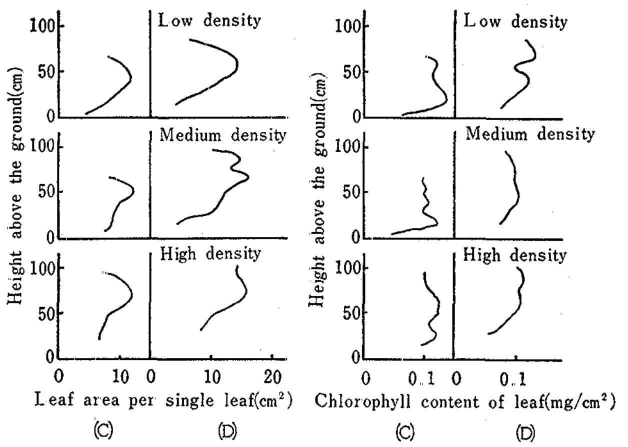

Fig. 11. Variations of the characters of single leaf.

pensation point of broad bean plant was 10 per cent of daylight and the plant died during ten or twenty days in this light condition. Similar results of light compensation point of broad bean plants were also reported by Blackman et al.(4) and Hodgson et al.(7). Nagase et al.(14) reported that the light compensation point of soybean plants and a range of yellowing leaf were under 20 per cent of daylight on the field, but irrigation moved them under 10 per cent of daylight.

As for the upper portion, the leaf area decreased at the green pod maturing in the high and the medium densities. Thus, the survived leaf area was equal in some upper portions of two densities. The land surface area available to the individual plant, was 2592, 1296, 648, and 324 cm^2 in the low, medium, high, and very high densities in this experiment, respectively. A dotted line in Fig. 7 shows the border of the space and at the same time indicates the limitation of the active leaf survivors. Figure 8 shows the variation of leaf profile and the position of 10,000 cm^2 leaf area as the dotted line, too. The process of thus typical decrease of leaf area was recognized in the range of the mutual shading(13), the leaves contact, and the intermittently or partially failure of receiving direct rays of the sun. It seems that these conditions induce the defoliation very mechanically on the broad bean plant community as mentioned above, and these phenomena depend severely on the biological space(18).

Therefore, though the leaves of all layers differentiated and developed similarly during the early growing to flowering period, thenceforth defoliated at two portions and decided final figure at the green pod maturing. The leaf area index in the medium and the high densities became 5.0 at that time, and this was minimum value of published data(9) on the broad leaf plant community. Concomitant with increasing density, thus, the ratio of the photosynthetic organ was limitted in contrast with the ratio of the non-photosynthetic organs. Subsequently, this fact restrained the development of the reproductive organs in the maturing period as reported with the shading or defoliating trials on broad bean plants(24,25).

On the other hand, the crop growth rate (CGR) increased with increasing the plant number per unit area from the early growing to the end of flowering, but it fell suddenly in the high density to the time of green pod maturing (Table 4). With regard to the net assimilation rate (NAR) during the end of flowering to the green pod maturing period, the values were 0.45, 0.19, 0.16 gram/100 cm^2/week on the low, medium, and high densities, respectively, if we calculated for the total leaf area at the end of flowering. However, the value was 0.45, 0.21, and 0.20 gram/100 cm^2/week, respectively, if it were not for the leaf area which should be defoliated

Table 4. Effects of density on the crop growth rate (CGR) $g/m^2/day$

	Low density	Medium density	High density
At the early growing stage			
↓	0.76	2.56	3.48
At the start of flowering			
↓	7.31	12.18	26.03
At the end of flowering			
↓	15.81	24.59	24.23
At the green pod maturing			

afterward, and accordingly, little differences were recognized between the medium and the high densities.

In the previous papers[20,21,22,23,24,25], the authors indicated that the stem, root, and pod play the role as a temporary storing organ for the components in seeds. As for the translocation of dry matter, in this experiment, there were little differences among three densities.

Therefore, it is clear that the competition of tops of broad bean plants in the high density begins at the start of flowering, and the leaf area is decided at the green pod maturing by the lower and upper defoliation, and that though the seed yield per plant decrease, the high yield per unit area can be obtained in the high density. Accordingly, it seems that an individual potential for capturing resources is decided by the biological space and the optimum density is the high density of this trial for the winter type broad bean "Sanuki-nagasaya" in warm region of japan.

Summary

In order to obtain some informations on the effects of the density on the growth, the seed production, and the nature of competitive pattern concerning with the variations of the productive structure of broad bean plants, using the cultivar "Sanuki-nagasaya" as material. The experiment was conducted under four densities; low ($3.8/m^2$), medium ($7.6/m^2$), high ($15.2/m^2$), and very high ($30.4/m^2$).

The results obtained may be summarized as follows:

(1) The effects of density, the competition of tops began in the flowering period. The high density induced the elongation of stem or internodal length and the retardation of stem number, pod number, podding percentage, and seed number per plant. As for the results per sq. meter, however, the growth of vegetative and reproductive organ increased with increasing density within a range of low, medium, and high.

(2) With regard to the productive structures obtained with the stratifying 10 cm clip method, the photosynthetic systems varied from a state of distributing all layers in the flowering period to a state of restricting upper layers in the maturing period. This fact was revealed earlier and clearer with increasing density.

(3) The defoliated lower portion coincided with the range receiving under 10 per cent of natural daylight previously. The leaf area was also restricted on the upper portion where occurred the mutual shading and contact of the leaves. The restricted area was almost the same as the land surface area available to the individual plant, the biological space.

(4) The role of the vegetative organ and pod as a temporary storing organ for the components in seeds was approximate among the low, medium, and high densities.

(5) Judging from the results obtained in this experiment, it may be pointed out that an individual potential for capturing resources is decided by the biological space and the optimum density for the winter type broad bean "Sanuki-nagasaya" in warm region of japan is the high density of this experiment.

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蚕豆の生育過程に関する生理学的研究
VII 栽植密度が生育ならびに子実生産に及ぼす影響について

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要　旨

栽植密度が生育ならびに子実生産に及ぼす影響を検するため，群落内における競合の様相を物質生産構造，とくに光合成系と群落内相対照度との関連から追究した。実験には「讃岐長莢」を用い，栽植密度を疎（3.8 個体/m^2），中（7.6 個体/m^2），密（15.2 個体/m^2），極密（30.4 個体/m^2）として育成した。

生育経過をみると，初期にはいずれも類似していたが，開花始以降はその様相が異なり競合が始まった。すなわち密植するほど茎長，とくに節間長を伸長させ，個体あたりの茎数・莢数・結莢率・子実数を減少させた。しかして単位土地面積あたりの生育は疎＜中＜密であったが，極密では劣っていた．

光合成系と非光合成系の 10 cm ごとの垂直分布をみると，いずれの密度でも生育の後期には明らかに広葉型の特徴を呈した．しかして密植するほど早くから地表面への光線の透過が悪くなり，相対照度10%以下の範囲も広くなった．

開花期間にすべての層位でみられた葉身は，その後の落葉により上層位に集まる状態となったが，これは密植するほど顕著であった．すなわち密植した場合の落葉は相対照度が10%以下の下層位と，上層位のうち互いに遮蔽しあい，触れあう部分において認められた．

以上の諸点より，蚕豆の栽植密度と生育・子実収量との関連において，物質生産構造の面から個体占有面積の意義が明らかとなった．

(Received May 31, 1973)