PHYSIOLOGICAL STUDIES OF THE GROWING PROCESS OF BROAD BEAN PLANTS

X Effects of Plant Density on Carbon Dioxide Exchange of Leaves and Pods

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蚕豆の生育過程に関する生理学的研究

X 栽植密度を異にした場合における葉および莢の光合成・呼吸作用について

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The effects of plant density on carbon dioxide exchange of leaves and pods were studied to obtain further assessment on the nature of the competition of broad bean plants, using the cultivar "Sanuki-nagasaya" as material. The experiment was conducted with three densities of low (3.8/m^2), high (15.2/m^2), and very high (30.4/m^2).

The competition began after the start of flowering. Stems elongated and leaves resulted in much mutual shading and defoliated, the higher plant density, the more early and severely. With increasing plant density, however, the reproductive organ/vegetative organ ratio became low and finally this fact resulted in less seed yield and poor seed development.

The photosynthetic rate was accelerated in the upper section and retarded in the lower section with increasing plant density. The respiratory rate of leaves in the nighttime was heightened in the lower section especially in high density. The respiration of pods became high in the nighttime and in very high density with the growth advanced.

The daily stationary carbon dioxide per square meter was abundant with increasing plant density, but the respiration/photosynthesis ratio was simultaneously heightened. Moreover, the closely source-sink relationship was recognized between leaves of the 2nd plus 3rd section and reproductive organs in low density. The relationship of this kind, however, was not necessarily valid between leaves of the upper 4th section which occupied the major part of photosynthetic system and pods including inner seeds in very high density, showing the reason of less seed yield and poor seed development.

Judging from the results, it may be reassessed that high density of this experiment is the optimum density for winter type broad bean plants in warm regions of Japan.

栽植密度を異にした蚕豆の群落内競合について，葉・莢による光合成・呼吸作用の面から検討するため，「讃岐長莢」を用い，育成条件を疎植（3.8個体/m^2），密植（15.2個体/m^2），極密植（30.4個体/m^2）として追究した．

作物体の競合は開花始期以降に始まり，栽植密度が大となるに伴い，茎・節間の伸長，葉の相互被陰が著しくなり，生殖器官の栄養器官に対する重量比が低く，子実の発育がよくなかった．

葉の光合成速度は栽植密度が大なるほど，上方部位では下方部位と反対に大きくなったのに対し，夜間における呼吸速度は密植した場合，下方部位で大となった．また，莢の呼吸作用はとくに極密植した場合の夜間に大きくなった．

単位土地面積あたりで固定された炭酸ガス量は栽植密度が大なるほど多くなったが，呼吸量の光合成量に対する比

は増大した．しかして疎植した場合，中位葉と莢・子実との間でみられたSource-Sinkの密接な関係は，極密植した場合，光合成系の大きな部分を構成する上位葉と莢・子実との間には必ずしも認められず，これが子実の発育に強く貢献しなくなったものと思われる．

以上の諸点から，蚕豆の栽植密度は本実験における密植の場合が光合成・呼吸作用の面からも適当であることが確かめられた．

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Introduction

As a first approach to explain the changing pattern of competition which follows from altering plant density of broad bean (*Vicia faba*), detailed analyses have been made in a previous paper[16]. It was proved that the competition of tops began after the start of flowering and the leaf area was decided at the green pod maturing by the defoliation in the lower and upper portions. And the results confirmed that the optimum density for winter type broad bean "Sanuki-nagasaya" in warm regions of Japan was the density of 15.2 plants per square meter (high density).

On the other hand, with regard to the physiological status of leaves and stems, there have been reported many experiments about the activity of photosynthesis and respiration[1,13,17] and the effect of leaf removal[4,8,15]. In a previous paper[17] it was proved that the activity of photosynthesis and respiration was distinguishable by four sections based on the flowering and pod bearing habit and transmitted from lower to upper section accompanying with the growth advanced. The authors also pointed out that vegetative organs of the 2nd section, which was adjacent to pod bearing nodes, were very important for the normal growing process[15].

The object of this investigation is supplemental to these researches about the nature of competition. The present study is concerned with the effects of plant density on the difference of carbon dioxide exchange of leaves and pods and the meanings for the production and distribution of dry matter.

Materials and Methods

Broad beans, cultivar "Sanuki-nagasaya", were sown in a field on November 6 and seedlings were grown as a plant per hill. The fertilizer application was made as basal dressing: 27 Kg ammonium sulfate, 45 Kg calcium superphosphate, and 18 Kg potassium chloride per 10 a were plowed down. The experimental design was the same as mentioned in the previous paper[16] exclusive of medium density (Table 1.).

Table 1. Experimental design

Density	Row width cm	Hill distance cm	Plant number per sq. meter
Low	72	36	3.8
High	36	18	15.2
Very high	36	9	30.4

As for a portion measured, of primary four branches as shown in Fig. 1, la, the first branched one, was used. Three compound leaves in each section based on the flowering and pod bearing habit[15] or pods in the 2nd section were pursued measuring the activity of photosynthesis

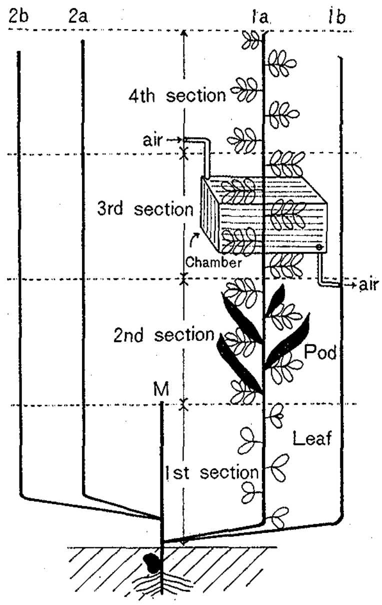

Fig. 1. Explanation of branches and four sections of stem
M: Main stem, 1a, 1b, 2a, 2b: Primary branched stem

and respiration. The apparatus was the same as mentioned in the previous paper(17); the measurement of carbon dioxide exchange was made by enclosing each organ with an acrylic resin chamber, which was connected to an infrared gas-analysis system, under the condition of natural daylight and air flow rate of 120 l/hr.

Experiments were carried out three times; at the start of flowering, at the end of flowering (20 to 30 days after the start of flowering), and at the seed maturing (50 to 60 days after the start of flowering). At the appropriate sampling time, tops were divided into the measured part and other sections, then segregated into leaf-blade, stem plus petiole, root, pod, and seed, respectively, these organs were dried in an oven and weighed. At the same time, the leaf area and pod surface area were estimated by means of the blue print method.

Results

Growing Status

The growing status of plants in three densities are shown in Figs 2 to 4. The results were essentially the same with the results of the previous paper(16). The branching was approximate among the three densities in winter. While, the effects of density, the competition of tops, began after the start of flowering. A high density promoted the elongation of stem- or internodal length, but retarded the increase of stem, pod, and seed number, especially pod bearing stem number per plant.

As the growth progressed, leaves resulted in much mutual shading within the field and this phenomenon was recognized earlier in high and very high densities. Thus, dense leaves began to defoliate in the upper mutual contacted section and in the lower shaded one(16). In very high density, however, in contrast with high density, vigorous growth of stems and leaves in the upper 4th section was accelerated secondarily, and these organs prevailed against the lower

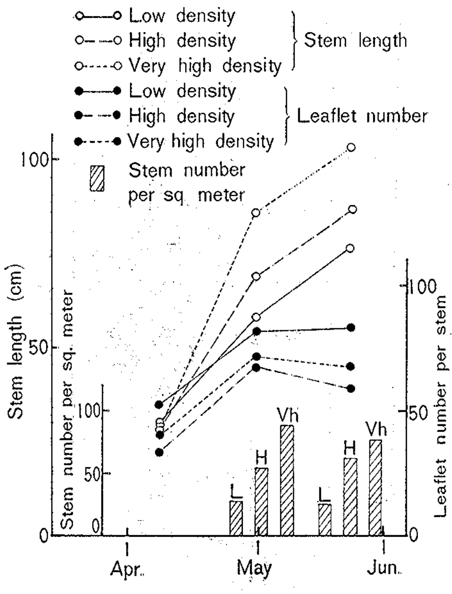

Fig. 2. Changes in growing status
L: Low density, H: High density, Vh: Very high density

section still more.

The profile of photosynthetic system, the distribution of leaves in the four sections was clearly different among the three densities. And the leaf area index (LAI) was 2.29, 3.75, and 5.45 in low, high, and very high density, respectively, at the seed maturing. The dry weight of whole plant also increased with increasing plant number per unit area. The abnormal attitude of plants grown in very high density with the high ratio of non-photosynthetic organ/ photosynthetic organ (C/F), however, finally resulted in less seed yield and poor seed development in

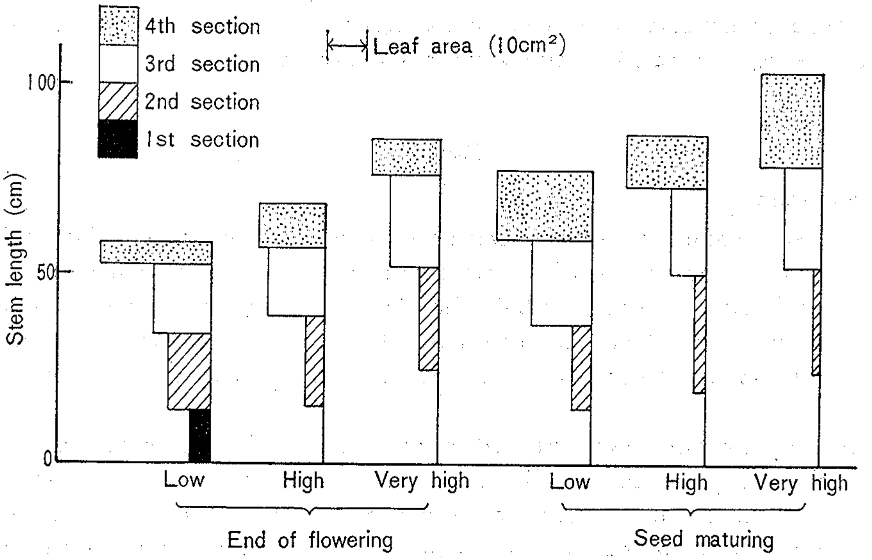

Fig. 3. Changes in leaf area per stem of four sections

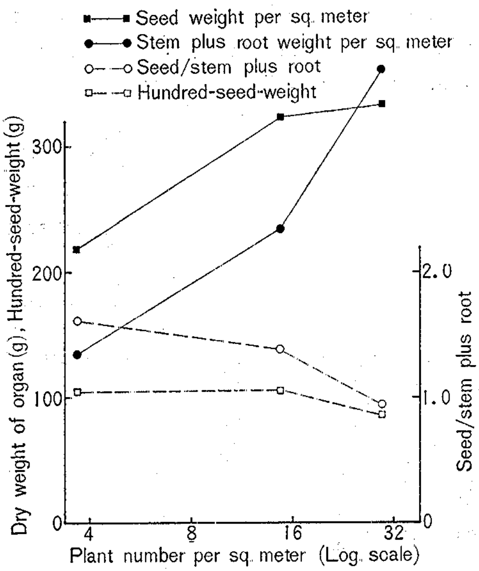

Fig. 4. Status of vegetative and reproductive organs at the time of harvesting

contrast with the development of huge vegetative organs.

Photosynthesis and Respiration

Diurnal changes in carbon dioxide exchange of leaves and pods at the seed maturing are shown in Fig. 5. The diurnal course in the three densities, which was approximate to another measuring time, conformed broadly with those which measured as the subject of isolated plant(17). Durations of the apparent photosynthesis of leaves in four sections, however, were different among the three densities. Those of the lower sections in low, high, and very high densities

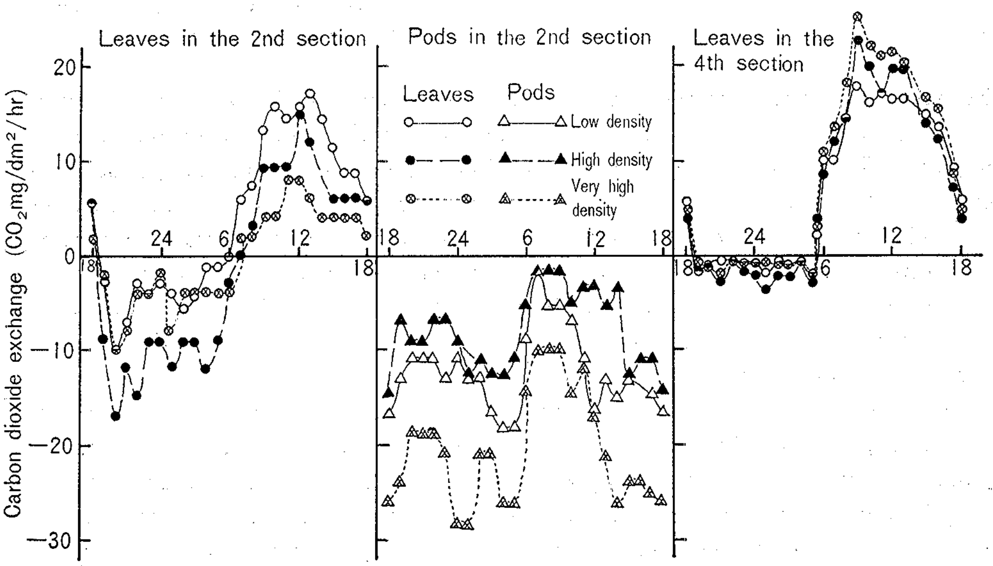

Fig. 5. Diurnal changes in carbon dioxide exchange of leaves and pods at the seed maturing

were the same at the start of flowering. It became short in high and very high densities about one hour at both times of sunrise and sundown at the seed maturing. It was also emphasized for the expansion of shading sphere in very high density.

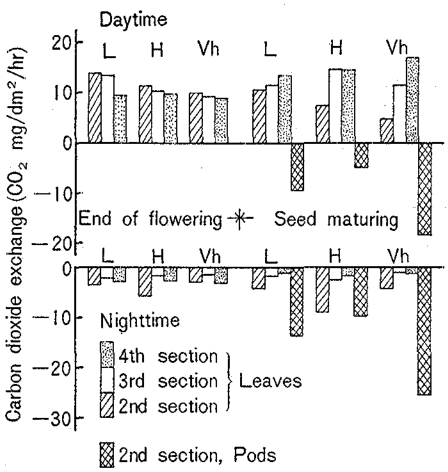

Fig. 6. Variations of photosynthetic and respiratory rate
L: Low density, H: High density, Vh: Very high density

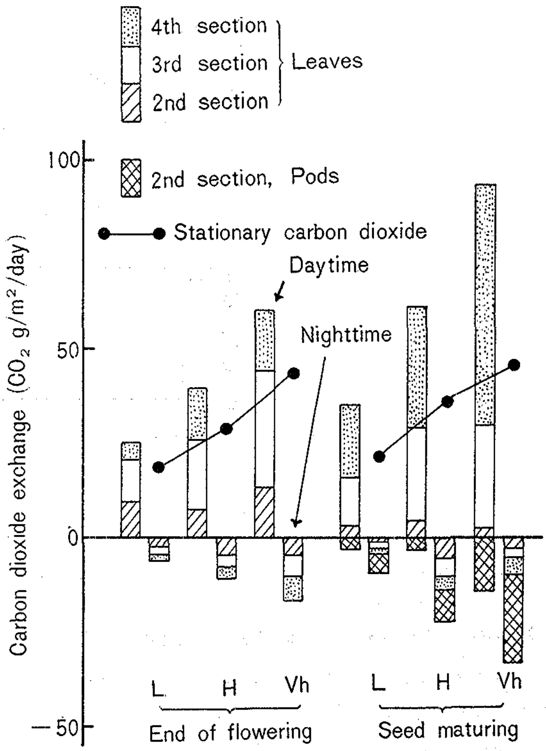

Fig. 7. Variations of photosynthetic and respiratory capacity and the amount of stationary carbon dioxide
L: Low density, H: High density, Vh: Very high density

The variations of apparent photosynthetic and respiratory rate (CO_2 mg, dm^{-2}, hr^{-1}) of leaves and pods are shown in Fig. 6. As for leaves, the photosynthetic rate at the end of flowering was generally superior in the lower section to those of the upper section and also superior in low density to others. But, it became low in the lower shaded section and those of the upper sections became contrastively high with increasing plant density. On the contrary, the respiratory rate of leaves in the nighttime, which was generally low, was accelerated in the lower section accompanying with the growth advanced, especially in high density. On the other hand, the average value of respiratory rate of pods was high throughout the daytime and nighttime, especially in the nighttime and in very high densities.

Figure 7 shows the status of photosynthetic and respiratory capacity (CO_2 g, m^{-2}, day^{-1}) of leaves plus pods. At the end of flowering, when leaves began to defoliate in the lower section, though the photosynthetic capacity was but yet considerably high in the 2nd section as shown typically in low density, it became rather high in the 3rd section with increasing plant density. Moreover, after this measured time, an important role of photosynthesis succesively transmitted to the upper most 4th section, especially in very high density. On the contrary, the respiratory capacity became high with leaves in high density and pods in very high density. Therefore, although the amount of daily stationary carbon dioxide per square meter increased accompanying with increasing plant density at the end of flowering, the increase was still held, but with relatively less amount in very high density at the seed maturing.

Discussion

In plant density trials, such photosociological phenomena as the elongation of stem- or internodal length have been recognized with pulse crops(3,4,7,10,16). The results obtained in this experiment were in agreement with the results of other reports; the long internode which was usually located in the middle portion or section moved to the lower one with incresing density. Moreover, the long internode was also recognized in the upper 4th section of very high density. Thus, mutual shadings within the vegetative organs began, when the development of flower bud and the flowering were found.

Consequently, the light intensity within leaf canopies declined more early and severely with increasing competition(16). What effects do these facts have on the physiological status of leaves in four sections? Here, various propositions will be described about the effects on (1) the status of defoliation, (2) the duration of photosynthesis, (3) the activity of photosynthesis and respiration, and (4) finally the relationship between these items and the production and distribution of dry matter.

Accompanying with the progress of competition, leaves decreased in two portions: the lower and upper in the same manner as in the previous paper(16). The defoliated lower portion coincided with the range receiving under 10 per cent of daylight previously and this range was different among three densities. Thus, leaves seemed to restrict and retain about 5 of LAI value even in very high density in the same manner for broad bean plants as in the previous paper(16).

In this connection, the duration of apparent photosynthesis of leaves in the lower shaded portion was clearly short. At the seed maturing, though the difference of this between the lower 2nd and the upper 4th section was only a half hour in low density, it was about one and a half hour in high and very high densities. Therefore, leaves of the lower portion in high and especially in very high densities grew under unfavourable conditions for photosynthesis.

In the previous paper(17), the authors pointed out that the photosynthetic rate was generally superior with the upper younger leaves to that with the lower older ones of isolated plant. In this density trial, however, the photosynthetic rate of leaves in the upper section was accelerated with increasing plant density. Moreover, when grew in dense population, leaves in the upper section might gain the sun-leaf character and function compensatory, as compared with leaves in the lower section possesing more shade-leaf character(2,9,14). Many reports have been published that the light saturation point was heightened for leaves located at higher position in the leaf canopy(2,5,6,12). With this experiment it was also recognized that though the light saturation point was 0.20 gcal, cm^{-2}, min^{-1} of photosynthetically active radiation in low density, it was 0.30 in very high density.

On the other hand, the authors realized that the relationship between the activity of photosynthesis of leaves and other factors was very important, with respiration(9,11,19) and source-sink relationship(15,17). In this experiment, the respiratory rate of leaves in the 2nd section and of pods including inner seeds setting in the 2nd section were very high. Thus, high photosynthesis seemed to be accompanied or supported by vigorous respiration especially in high and very high densities.

In the previous paper(15,17), it was clear that the source activity, the photosynthesis, was related with sink ability, translocation, and accumulation of photosynthate. Although the daily stationary carbon dioxide per square meter was clearly abundant in very high density, the total respiration/ total photosynthesis ratio became 37.6, 41.8, and 51.1% in low, high, and very high density, respectively, at the seed maturing. With regard to the redistribution of dry matter synthesized with leaves for reproductive organs especially in seeds, it fell in very high density as seen in Fig. 4. Moreover, the seed/ top plus root ratio and hundred-seed-weight also declined in very high density.

The authors[18] proved that by $^{14}CO_2$ feeding trials for broad bean plants, the closely source-sink relationship was generally found between leaves in the 2nd plus 3rd sections and reproductive organs of pods plus seeds. Other leaves, especially in the upper 4th section, however, played an important role in the physiological status; at the seed maturing, ^{14}C-photosynthate from this section distributed over all organs of the whole plant and played an auxiliary role via maintaining of root activity. In this experiment, the fact seemed to be true in low density. But, such a source-sink unit as mentioned above did not easily change toward the upper 4th section-reproductive organ relationship in very high density, and much stationary photosynthate by the upper leaves seemed to be consumed mainly for increase or preservation of huge vegetative organs and vigorous respiration of pods and seeds.

Consequently, the authors state that though a considerable high photosynthetic activity may be essentially retained for long time after reaching the completion of the leaf expansion, especially with leaves in the 2nd section, the function seems to be governed by the growing status and the seed development, i.e. the consumption of products when plants are encountered such an unfavourable condition as severe competition. And the existence of a proper quantity of leaves in the middle section, 2nd and 3rd, as shown in high density may be very important for the stability of seed yield.

From these facts described above, it may be concluded that the function of leaves transmits from lower to upper section accompanying with leaves assembled in the upper with increasing plant density, and that leaves of the upper section become more sun-leaf ones and have high photosynthetic activity, but at the same time plants consume much more photosynthate for useless building of vegetative organs and vigorous respiration. Accordingly, it seems that high density in this experiment is again recognized as the optimum density for winter type broad bean "Sanuki-nagasaya" in warm regions of Japan.

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