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PHYSIOLOGICAL STUDIES OF THE GROWING PROCESS OF BROAD BEAN PLANTS

IX On the characteristics and the variations of 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

IX 開花期以後の葉および莢における光合成・呼吸特性とその推移

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The present investigation was undertaken to obtain some informations concerning the relation between the variations of carbon dioxide exchange of leaves and pods in four sections based on the flowering and pod-bearing habit and its meanings for the production and distribution of dry matter of broad bean plant.

The photosynthesis of leaves was adaptable in the wide range of 15 to 30°C, especially high in the later growing period. In this range of temperature, the light compensation and saturation point were 0.01 and 0.20 to 0.30 g cal, cm^{-2}, min^{-1} of photosynthetically active radiation. The maximum photosynthetic rate was recognized about 20 CO_2 mg, dm^{-2}, hr^{-1}, and the photosynthesis of leaves showed a mid-day depression.

Although the photosynthesis of leaves seemed to retain for a considerable long time after reaching high value, it behaved closely with the physiological age of leaves and with the presense of pods or not. The photosynthetic capacity was high at the flowering and the early stage of seed maturing. The respiration of leaves in the night time was generally low with the exception in the 2nd section of pods bearing. The respiratory capacity was relatively high in the 2nd and 3rd section.

The respiration of pod was vigorous throughout the all day and development. The diurnal course of the respiratory rate was unique; the high value of the night time declined with sunrise, which was found as the fastest but shortest phenomenon. Accordingly, though the green pod has somewhat photosynthetic activity, the high respiration, substantiating the translocation and distribution of the photosynthate, seems to overcome.

Judging from the results it may be pointed out that the shortage of the substances by the photosynthesis is an important factor for the growth and seed yield, and that the role of leaves in the 1st section participates to the following developing organs and that of middle 2nd and 3rd and upper 4th section moves up stepwise participating for the pod and seed development, especially that of 2nd section is the most important.

開花・結実習性に基づき４層位に分けた葉と莢の光合成・呼吸特性とそれが乾物の生産および分配に対する意義を検討した。実験は鉢植えした讃岐長莢の第１分枝に着生する３節分の葉または莢を同化箱に入れ，温度および自然光の光量を制限する室内実験と室外で生育に伴う変化を追究する実験を行なった。

葉の光合成は15～30℃の範囲で，とくに生育の後期には高温にも適応し，光補償点と同飽和点は0.01と0.2～0.3 g cal/cm²/min であり，20 CO_2mg/dm²/hr 前後の光合成速度が認められた。しかして光合成速度は葉の展開後かなり長期間高い値を持続したが，これには葉の生理的令と莢・子実の存否が大きく影響した。このため光合成能は開花期と子実充実初期に高くなった。これに対し呼吸速度は莢が着生する第２層位を除いて概して低く，呼吸能としては第２・３層位葉で高かった。

莢の呼吸は夜間・日中および発育の全期間にわたり著しかった。しかして緑熟期においては，日出後短時間に CO_2

排出速度が顕著に低下したことからみて，本来は光合成作用としては高いが，強い呼吸作用が光合成物質の転流・分配に深く関与しているものと思われた。

以上の結果，蚕豆の生育・子実収量は葉の光合成作用に深く影響し，第1層位葉はその後の生育に，中・上層位葉は順次莢・子実の発達に関与するが，とくに第2層位のそれが重要であることが確かめられた。

Introduction

Broad beans produce generally much waste reproductive organs with less mature pods or seeds in contrast with developing huge vegetative organs. SOPER[20] has suggested in review that the lack of specific growth substances and the shortage of carbonaceous and mineral substances accounted for this phenomenon. Authors have been examined this fact by means of treatments of varing the soil moisture[23], soil fertility[24], light intensity[25], light duration[28], leaf area[26], and plant density[27], and assured the shortage of carbonaceous substances was an important factor for this phenomenon.

Broad beans cultivated in warm region of Japan, generally have four pod-bearing branched stems and in addition have few stems of flowering but pod-shedding. The former reproductive stems are developed during the early growing period in winter and have generally 20 to 24 nodes and compound leaves in following the flowering to maturing period of spring. And flowers begin to bloom from the seventh or its adjacent node order toward tip of stem. Consequently, it is clearly that the vegetative growth progresses together with the development of reproductive organs and that the physiological role of vegetative organs changes with the growing process[21,22].

It is well known that plant leaves of different age show differences in their physiological status, i.e. the dry matter production, photosynthesis, and respiration. As for broad beans, a physiological function of leaves and stems of different section based on the flowering and pod bearing habits had been examined by partial leaf removal[13,14,26] or leaf shading[7] trials. Author et al.[26] pointed out that the role of the vegetative organ transmitted from lower to upper section and the existence of that in the 2nd section were very important for the normal growing process.

The object of this investigation was to obtain some informations of the characteristics of carbon dioxide exchange of leaves and pods and its meanings for the production and distribution of dry matter throughout the growing period.

Materials and Methods

Broad beans (*Vicia faba*), cultivar "Sanuki-nagasaya" were sown in nursery bed on November 8 to 10, and seedlings were transplanted two plants per pot on December 13 to 18. Each pot received 1.9 g ammonium sulfate, 3.1 g superphosphate, and 1.7 g potassium sulfate. Soil moisture was maintained about 70 % of the field capacity.

Although the main stem die generally in winter, there have primary four branched stems at first and second node order of the main axis in the early growing period and these stems grow similarly following three to four months in spring (Fig. 1). With regard to the flowering and pod bearing habits of these stems above mentioned, 20 to 24 nodes are possible to be distinguished into the following four sections[26]; (1) no flowering, 1st to 6th node order (1st section), (2) first flowering and pod bearing, 7th to 11th node order (2nd section), (3) flowering but generally pod shedding, 12th to 16th node order (3rd section), and (4) no flowering, upward node order (4th section).

In this experiment, out of these primary stems, 1a, the first branched one was used, and middle three compound leaves in every sections and pods in the 2nd section were pursued measuring the activity of photosynthesis and respiration. The apparatus is shown in Fig. 1 ; measurement of carbon dioxide exchange was made by enclosing organs with a acrylic resin chamber, which was connected to an infra-red CO_2 gas analysis system. At the same time the photosynthetically active radiation was measured with the photosynthetically active radiometer.

Experiment I; In order to obtain some informations concerning the characteristics of photosynthesis and respiration of leaves, experiments were conducted with leaves on 4th section at the flowering and green pod maturing. Measurements were made in the air-conditioned growth chamber regulated the air and underground temperature

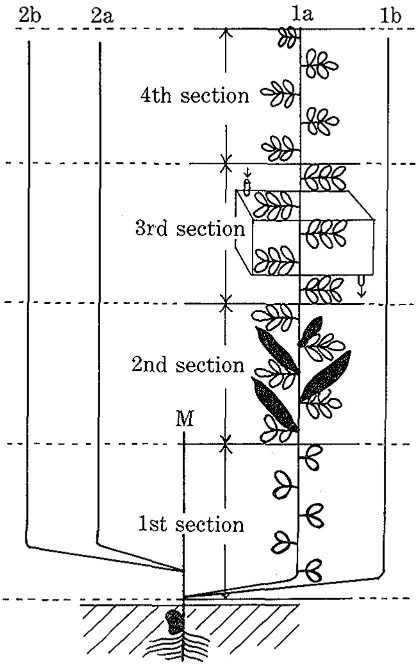

Fig. 1. Flowering and pod-bearing habit of broad bean plant and four section of stem and attached CO_2 measuring apparatus.

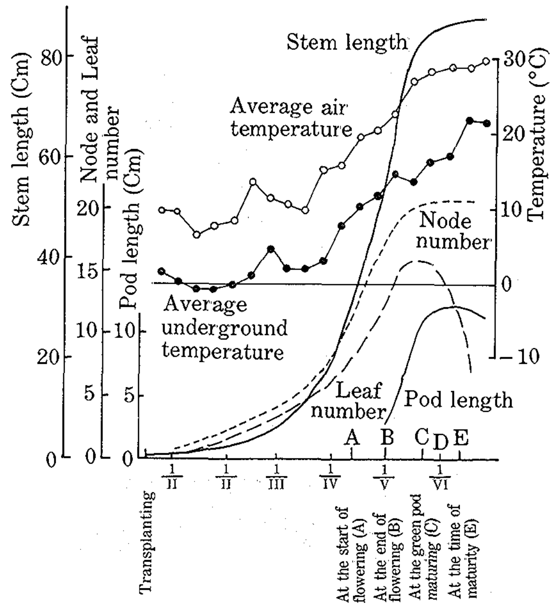

Fig. 2. Growing status and variation of temperature.

at 15 to 30°C so as to be under the range from 100 to 2 % of natural daylight intensity.

Experiment II; The variations of carbon dioxde exchange of leaves in every four sections and pods in 2nd section were pursued. Experiments were carried out five times; at the zero day(A), 20 days(B), the green pod maturing stage of 40 days(C), and the seed maturing stage of 50(D) and 60 days(E) after the start of flowering. Measurements were made on the outdoor under the natural condition. In this case, a temperature which was measured by the thermojunction was about 5°C higher in the chamber than that of open air in the day time, though the air inlet pipe was cooled by cooling system.

At the appropriate sampling time, tops were divided into the measured part and other, then segregated into leaf-blade, stem plus petiole, root, pod, and seed. These organs were dried in an oven and weighed. At the same time, the leaf area and pod surface area were estimated, and the chlorophyll of leaves and pods was extracted with 85 % acetone and determined by the photoelectric colorimetric method as total chlorophyll.

Results

Growing Status

The growing status of plant and the variations of air and underground temperature are shown in Fig. 2. The length of stem and number of leaves per stem increased rapidly in April and the flowering which began in late March to April continued about one month in the 2nd and 3rd sections. The flowers of 2nd section matured finally pods: it required about 40 days for green pod maturing and another 30 days for the seed maturing. Consequently, the growth of vegetative and reproductive organs were progressed together competitively for considerable long days.

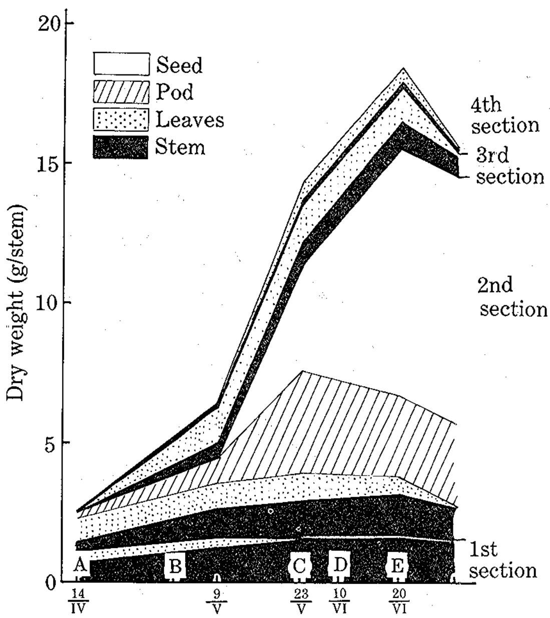

Fig. 3. Changes in dry weight of each organ per stem.

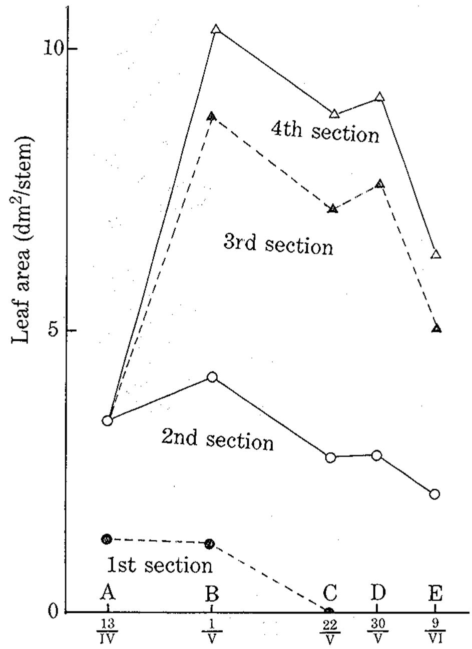

Fig. 4-1. Changes in leaf area.

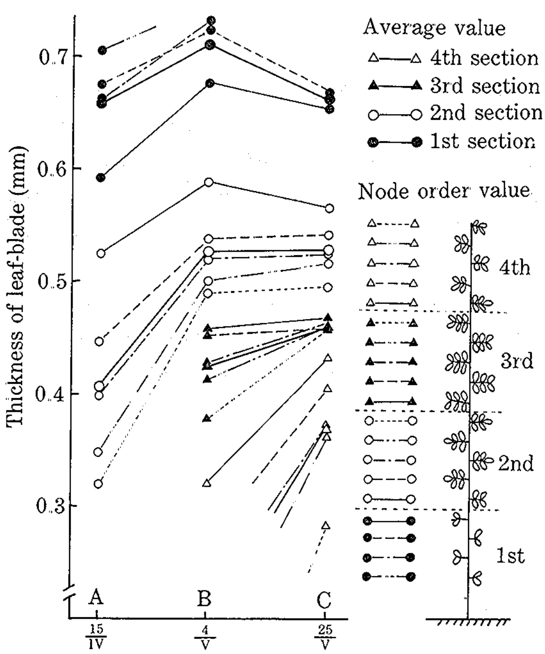

Fig. 4-2. Changes in thickness of leaf-blade.

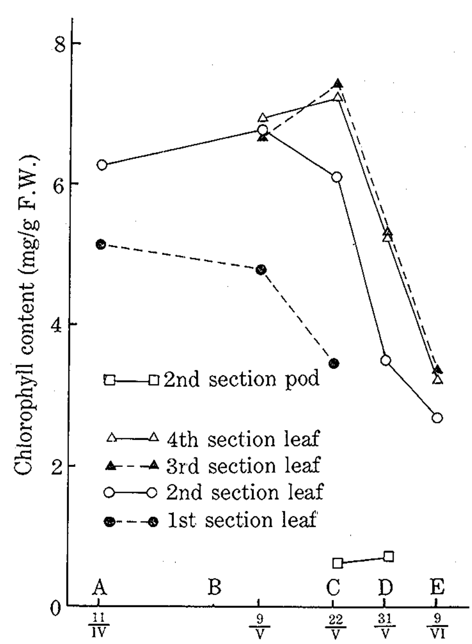

Fig. 4-3. Variations of chlorophyll content.

The dry weight of each organ per stem and its distribution in four sections at sampling times are shown in Fig. 3. The weight of total leaf blades was maximum at green pod maturing and especially those of 2nd and 3rd sections occupied about 70 to 60 % of total leaf-blades throughout the pod and seed developing period. On the contrary, the maximum value of stem weight was recognized lately and the dry weight of each section declined from lower section to upper one. And dry weight of root did not vary during the flowering to pod maturing stage. On the other hand, the dry weight of pods in the 2nd section was maximum at the green pod maturing and decreased forward. The seed weight increased up to the time of maturity.

Figure 4-1 to -3 show the status of leaves of four sections. The leaf area was high in the 3rd and 2nd section and the total leaf area was recognized high value at 20 and 50 days after the start of flowering. The thickness of the leaf-blade, however, was cleary superior with the lower section to the upper one. The chlorophyll content of leaves was generally high in upper section and decreased accompanying with the age preceeded, but the delay of this declination in the 2nd section was noteworthy.

Photosynthesis and Respiration

In the first experiment, Fig. 5 shows the relation between the temperature and the apparent photosynthesis and respiration of leaves. With regard to the apparent photosynthesis for temperature, an adaptability of broad bean plants recognized considerable high degree in wide range. The optimum temperature, however, was found out a comparatively low and narrow range at the flowering, then transfered high and wide range toward the green pod and seed maturing stage. The respiration of leaves which was showed an exponential increase in the whole temperature range at the flowering and seemed to unlike of exponential but parabolical to the increase of temperature at the green pod maturing.

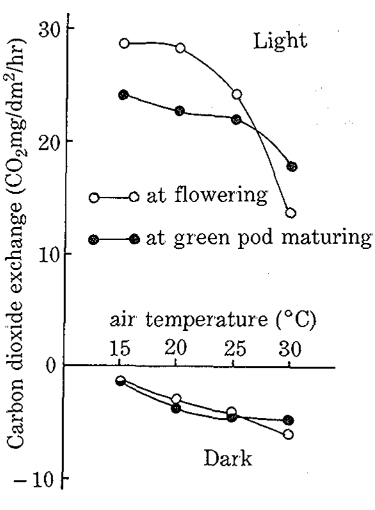

Fig. 5. Relationship between temperature and photosynthetic rate. (underground temperature, 15°C)

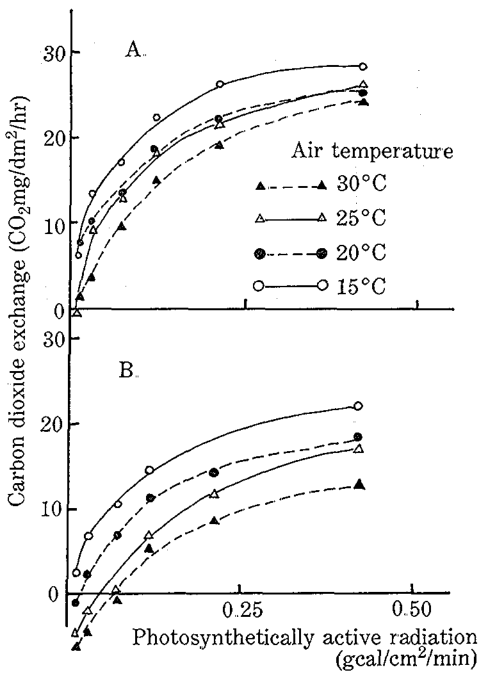

Fig. 6. Relationship between light intensity and photosynthetic rate.
A: underground temperature, 25°C
B: underground temperature, 15°C

The relation between the light intensity and the apparent photosynthesis at the green pod maturing are shown in Fig. 6. Regardless of air and underground temperature, it showed with a hyperbola. The light compensation point was recognized 0.010 to 0.012 g cal, cm^{-2}, min^{-1} of photosynthetically active radiation and the light saturation point was varied 0.20 to 0.30.

In the second experiment, diurnal changes in carbon dioxide exchange of leaves in four sections and pods in the 2nd section are shown in Fig. 7. The apparent photosynthesis of leaves began at the time of sunrise and reached about 100 % of the daily maximum within two to four hours. Throughout the following nine to seven hours the photosynthesis remained relatively constant, subsequently declined during the last two to three hours of the day time. Though the photosynthetic rate of leaves was different among four sections throughout the growing process, it was similarly recognized that the light compensation point was above 0.010 g cal, cm^{-2}, min^{-1} of photosynthetically active radiation and the light saturation point was 0.20. Respiration, however, was got immediately after entering the night time and there found high value at two times, but less variable rate.

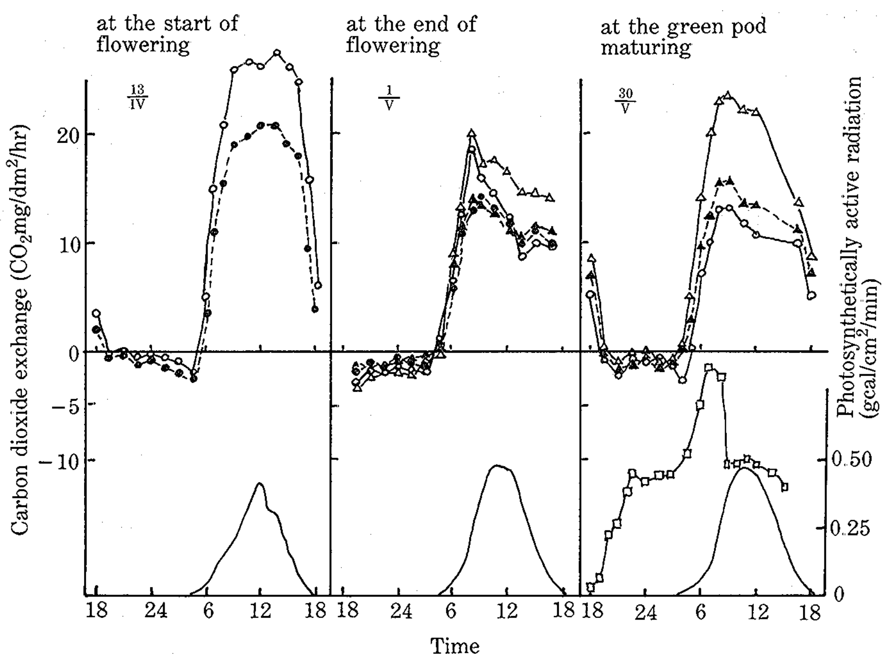

Fig. 7. Diurnal changes in carbon dioxide exchange of leaves and pods.
●---● leaves of 1st section, ○---○ leaves of 2nd section,
▲--▲ leaves of 3rd section, △--△ leaves of 4th section,
□---□ pods of 2nd section, ——— photosynthetically active radiation

As for pods, the apparent photosynthesis did not recognized in this experiment but the diurnal course was unique. At the green pod maturing, the high respiration in the night time suddenly decreased with receiving sunlight at the time of sunrise and soon reached minimum value. After maintaining this value for a few hours, the respiration again increased strongly for all the remaining day time. In the night time, it was temporarily very high after entering the night time and thereafter declined gradualy toward the following morning exclusive of the mid-night hightening.

The variations of daily average apparent photosynthetic rate of leaves in four sections are shown in Fig. 8. It was high at the flowering and the early stage of seed maturing. Throughout the whole stage it was always high with leaves in the upper section which was composed with younger leaves. The maximum value was measured 19,25,23

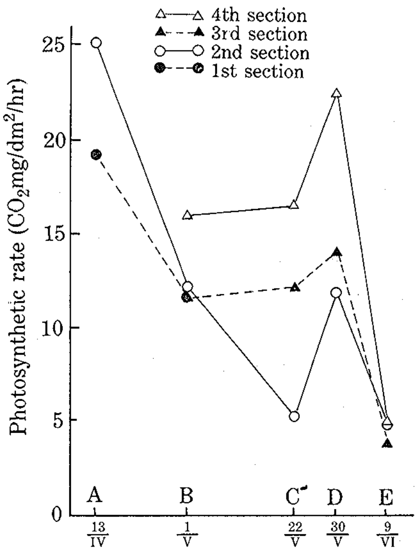

Fig. 8. Variations of photosynthetic rate.

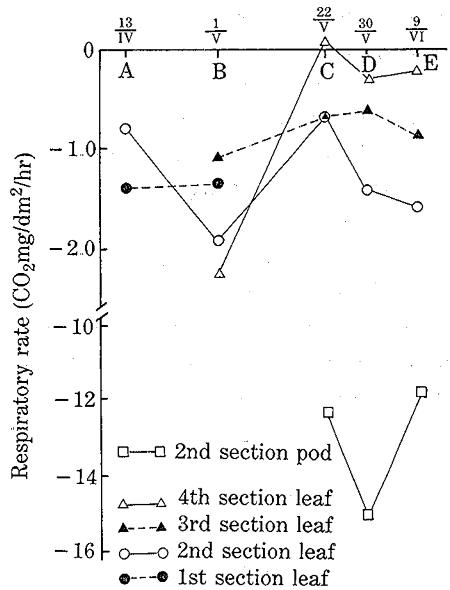

Fig. 9. Variations of respiratory rate.

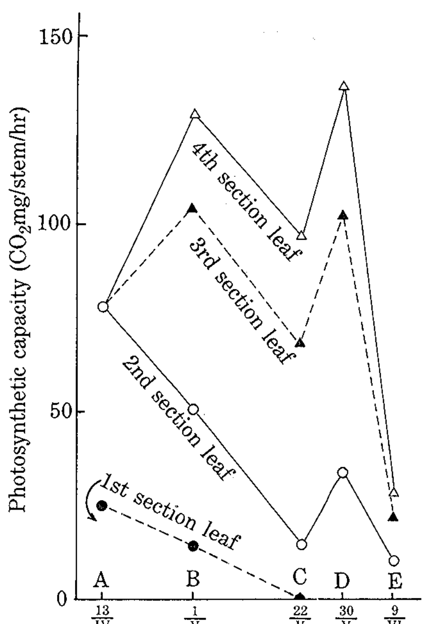

Fig. 10. Variations of photosynthetic capacity.

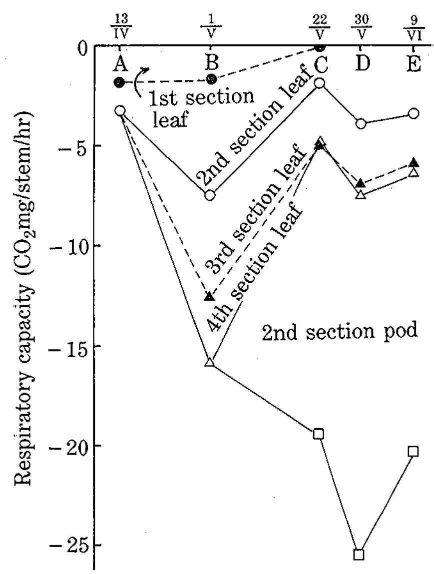

Fig. 11. Variations of respiratory capacity.

CO_2mg, dm^{-2}, hr^{-1} in the leaves of 1st, 2nd, and 4th section, respectively, but 14 in the 3rd section.

The variations of daily average respiratory rate of leaves in the night time and the pods in the day and night time are shown in Fig. 9. As for leaves, there was less variable value throughout the whole stage but it was generally high in the 2nd section, pod-bearing one. With regard to the respiration of pods, however, it was remarkably higher than that of leaves. Contrast with the average value in the night time, it was considerably low in the day time, throughout the pod maturing toward the early stage of seed maturing. This fact showed having somewhat high photosynthesis of the green pod surface for a few hours. Just before the time of maturity, however, it became high in the day time and low in the night time conversely.

The variations of the apparent photosynthetic and respiratory capacity of leaves and pods per stem are shown in Fig. 10 and 11. Total photosynthetic capacity was high in the growing stage of vegetative organs and the early stage of seed maturing. With regard to that of each section, very important meanings were recognized in the 2nd section at the former stage and in the 3rd section at the latter stage. And at the latter stage, leaves in the 3rd section carried about a half of total photosynthetic capacity and every one-fourth of them were recognized in the 2nd and 4th section. Throughout the experiment, the respiration of leaves was considerably high in the 2nd and 3rd section and became high again toward the scenescence. On the contrary, that of pods was remarkably high than leaves till the suddenly declination just before the time of maturity. Consequently, total respiration of leaves plus pods was maintained very high value after the green pod maturing stage.

Discussion

An optimum air temperature for the apparent photosynthesis of broad bean (*Vicia faba*) which showed relatively wide range in this experiment was different from that of other Vicia plants, common vetch (*Vicia sativa*)[15], especially at the green pod maturing stage. As for an influence of temperature and light intensity on the growth of fababean, SCHRÖDER[18] stated that there found not a few difference among varieties depending on an adaptability and dry matter productivity. MURATA et al.[15] stated there was a difference on the photosynthesis for temperature response between winter-grown and summer-grown northern type, C_3 plants; the former plant is more resistant to low temperature and less resistant to high temperature in their photosynthetic activity compared with the latter plant of the same species. So, broad bean plants seem to gain some high photosynthetic ability even at high temperature in the later growing period accompanying with the progress of growth. Similar results was reported by FUKUYAMA et al.[6] using the larger seed variety in warm region of Japan. On the other hand, the highness of the optimum temperature at the green pod maturing may be explainable also that the photosynthesis is complementary forced owing to continuous translocation of photosynthate from leaves to reproductive organs. Consequently, the results mentioned above are realizable by considering items of "thermo-adaptation phenomenon" and "source-sink relationship" together.

The diurnal cource of the carbon dioxide exchange of leaves in every sections conformed broadly with those observed in leaves of other crops[9,10,11,16,19,29,30]. Though much of the daily fluctuations of the apparent photosynthesis was reflected by irregularities in light intensity, the photosynthetic rate was generally shown plateau in figure about seven to nine hours in the mid-day. PEARSON[17] obtained similar results on single intact leaves of *Vicia faba* under the condition of the photoperiod of 16 hours, the temperature of 25°C, and a constant high light intensity. He stated that the net photosynthesis reached 95 % of the mean maximum rate within one hour in the start of photoperiod, and thereafter remained constant before declining the last of the photoperiod. He also stated that the loss of photosynthate-^{14}C from leaves exhibited a rapid phase which was fastest but shortest in the middle of the photoperiod and slower phase of much longer duration and that the maximum rate of the net photosynthesis was governed by either carboxylation reactions or transport of products away from the chloroplast. Although this experiment was undertaken in the natural day light and temperature, so-called mid-day depression[32] seemed to be the nature of broad bean plants.

The light compensation point was fairly good approximation among two experiments varing of temperature, growing stage, and section. But there had some divergence for the light saturation point among two experiments, especially in conjunction with the underground temperature[2]. It seems to be very important for broad bean cultivation in practice. As for the natural environmental trials of experiment II, however, the maximum photosynthetic rate throughout the whole stage was obtained similar value among four sections. This value was similar to those of C_3 plants[1,11,15,19], especially looked alike with crops which was grown from winter to spring as off-season cropping[11,19].

The average photosynthetic rate of leaves in four sections, of course, seemed to be varied correspondingly to the leaf age, and it was generally high in the upper younger leaves than the lower older ones. We have many reports about the relationship between photosynthesis and leaf expansion: the highest value of the photosynthesis has been recognized before[12] or at just time[31] of leaf full expansion with the differences in crop species. In this experiments, a considerable high value seemed to retain for a long period after reaching the completion of leaf expansion. It has shown by FINCH-SAVAGE et al.[4] the longivity varied from longer leaves of developed in the the early growing stage to shorter ones of late developed. However, though the longivity of leaves was different among four sections, those of 2nd section was excellent. Moreover, the leaf area, leaf thickness, and chlorophyll content of leaves retained high value in this section. Authors[26] have already reported that the carbohydrate content in the stem of 2nd section was most variable with the leaf removal trial. These facts seemed to have important meanings for the development of adjacent flowers and pods. Then these items, the important role in 3rd section came after to the 2nd one.

With regard to the variations of average photosynthetic rate, it was high at the flowering, them decreased as the growth advanced, finally increased again at the early stage of seed maturing when the development of seed rapidly progressed. This phenomenon was emphasized by leaves in the 2nd section. Thus, the photosynthesis of leaves in the 2nd section, which was adjacent to pod-bearing node order, seems to have a special important role for the later growing period. Indeed, the respiration of leaves in the 2nd section was correlatively higher than other ones.

The diurnal respiratory course of pods suggested to assure the vigorous activity of the metabolism within pods. A difference of the exhausted CO_2 from the last phase in the night time to the following early phase in the day time, just before and after the sunrise in the morning, was about 10 CO_2 mg, dm^{-2}, hr^{-1}, and this value showed a half of the photosynthetic rate of leaves. KUMURA et al.[12] examined that the green pods of the soybean plant have somewhat but small photosynthesis. Authors' unpublished data showed that the chlorophyll content measured on unit surface area of green pod of soybean plant was clearly low. On the contrary, in the case of the broad beans, it was not alike to that of soybean. Thus, in day time, with all the photosynthesis of green pod is considerably high in this plant, but the vigorous respiration of pods and inner seeds[5] seems to overcome it, because the respiration must have a important role for the translocation of the photosynthate.

From the facts mentioned above, it seems that the source ability, the photosynthesis, is related or governed with the sink ability, the translocation and accumulation of the photosynthate. Therefore, it may be pointed out that the function of leaves is controlled by the growth and the seed development or the consumption of the products.

KUMURA et al.[12] examined with soybean that the total photosynthetic capacity increased with growth up to the beginning of ripening and then decreased, and that the dry matter production owed to those of middle leaves in connection with the duration of retaining the leaf area. It was substantially true in broad bean plants, and the high capacity at the flowering owed to the enlargement of the leaf area, and those at the early stage of seed maturing owed again to the retaining of the leaf area and/or the vigorous photosynthetic activity.

As shown in Fig. 12, though the total respiration/total photosynthesis ratio was about 5 % at the flowering, it became 40 % at the green pod maturing and finally 150%. Accordingly, accompanying with the development of both pods and seeds, the respiration increased and overcame the photosynthesis about two weeks before the time of maturity. With these results and the daily meteological data including the length of light duration and photosynthetically active radiation, the theoritical amounts of the daily carbon dioxide fixation per stem were calculated as starch and were accumulated throughout this experimental period. Figure 13 showed that there was a little difference between the theoritical value and experimental value with the exception of the behavior of the roots. FASHEUM et al.[3] stated that a growth efficiency value of incomming solar radiation with field beans(*Vicia faba* L) is amongst the largest values recorded for an annual C_3 crop. So, it seems that the conversion efficiency of carbon dioxide fixation into dry matter itself may be considerably high. However, INAKO et al.[8] reported that eight compound leaves supported only one

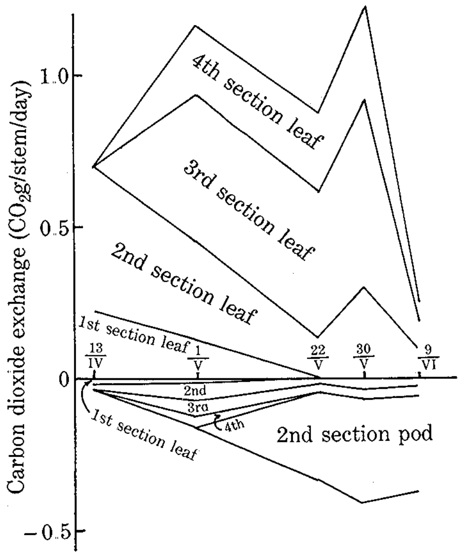

Fig. 12. Variations of carbon dioxide exchange.

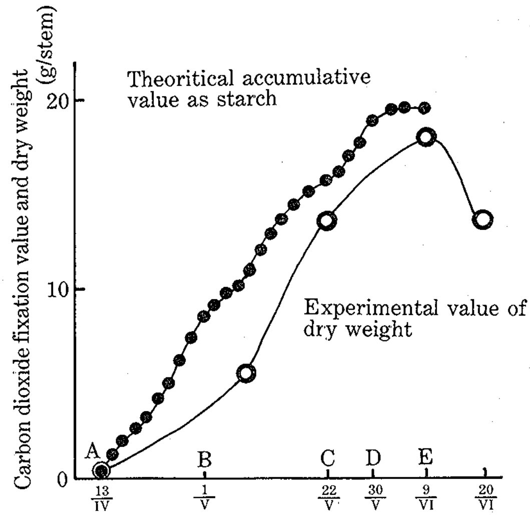

Fig. 13. Relationship between the carbon dioxide fixation value and dry weight.

mature pod in limitted stem on the late maturing large seed variety "Issun-soramame". It is well agree with the results in this experiment that 20 to 24 leaves yielded only about three or four mature pods of middle-size seed variety "Sanuki-nagasaya". Therefore, the photosynthetic capacity or dry matter productivity may be full act for the growth of vegetative and reproductive organs when the plant grows consisting of the limitted stems as this experiment.

From the facts, we may conclude that the shortage of the carbonaceous substances seems the most important critical factor for the growth of the broad bean plant from the ability of the photosynthesis and respiration. And we may also point out the leaves of the lower 1st section participate to the development of the vegetative organs of upper section in the early growing period and those of 3rd section do about a half and also those of 2nd and 4th section do every one-fourth to the pod and seed development after the green pod maturing stage, and that especially the activity of carbon dioxide exchange of leaves in the 2nd section behaves the most vigorously and long-lived among those of other sections throughout all of growing period.

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