Coden:KDNKAO
ISSN:0453-0764

香川大学農学部紀要

第59号

1992年12月

MEMOIRS OF FACULTY OF AGRICULTURE
KAGAWA UNIVERSITY

No. 59, December 1992

STUDIES ON THE GROWTH HABIT AND ITS RELATIONS TO THE MECHANISM OF YIELDING PROCESS IN WINTER TYPE OF FABA BEAN (*Vicia faba* L.)

Kiyoshi KOGURE

香川大学農学部
香川県木田郡三木町
FACULTY OF AGRICULTURE, KAGAWA UNIVERSITY
Miki-chô, Kagawa-ken, Japan

香川大学農学部紀要

第59号

1992年12月　発行

各研究室の業績を発表するため，本学部は“香川大学農学部学術報告”と“紀要”を発行している．この“紀要”は研究の完成した比較的長い論文を発表するために発行されている．既刊の標題は最後のｉ－ｖ頁に記載されている．“学術報告”および“紀要”の交換または寄贈については，香川県木田郡三木町　香川大学農学部（〒761－07）あて照会されたい．

Memoirs of Faculty of Agriculture, Kagawa University

No. 59, December, 1992

The Faculty of Agriculture, Kagawa University publishes “Technical Bulletin” (Gakuzyutu Hōkoku) and “Memoirs” (Kiyō), and latter contains extended treatises. The titles of each number of “Memoirs” are printed on the pages i to v inside back cover. Correspondence concerning the exchange of publications should be directed to Faculty of Agriculture, Kagawa University, Miki-chō, Kagawa-ken, 761－07, Japan.

STUDIES ON THE GROWTH HABIT AND ITS RELATIONS TO THE MECHANISM OF YIELDING PROCESS IN WINTER TYPE OF FABA BEAN (*Vicia faba* L.)

Kiyoshi KOGURE

CONTENTS

INTRODUCTION

HISTORY OF CULTIVATION AND RESEARCH IN JAPAN AND BACKGROUND OF THIS STUDY

Until only four decades, faba bean (*Vicia faba* L.) seed has been a very important part of the diet of many Japanese, appearing in various forms such as main food item, subsidiary food items, protein curd, and fermented sauce and paste. Today, this become a more important food for many people throughout the developing countries.

It appeared that the cultivation of most of the pulses in the Old World began at about the same time as those of cereal crops. However, for faba beans there is controversy over the precise center of origin and when it was first domesticated.(32,152). In fact, Plitman(112) wrote that out of many cultivated crops the problem of the origin of *Vicia faba* was the most difficult. There is some evidence of the existence of this crop in the early Neolithic Age (ca. 5,000 BC) in the Near East region but this has not yet been fully substantiated. Evidence from the Bronze Age, however, showed that by 2,000 BC *Vicia faba* was already being cultivated throughout the entire Mediterranean basin, from Spain in the west to the Levant in the east. All the beans unearthed from this period have been of the small seed type (*V. faba* L. *var. minor*).

Zohary and Hopf(152) and Plitman(112) considered the progenitor of *Vicia faba* to be *V. galilea* Plitm. et Zoh. and this may help in predicting the place of origin of this crop. There is only scanty written evidence of the early cultivation of this beans in the East Asia region. Folk tales mentioned this crop plant in China about 100 BC and in Japan about 700 AD, but the first written description of this crop in China was not found until 1313. Other documents showed that the cultivation spread over the whole country in the early 15th century and that large seed types appeared by the end of the 16th century. However, in India, which is en route from the Near East to the Far East, there are no written descriptions of the early cultivation of this crop despite the existence of old names for the crop in Kashmir and Punjab regions(88).

The first description of this crop seed in Japan came from "Tashiki−Hen", a dictionary of plants published in 1631. The development of this crop in Japan took place in two or three stages. First to appear was the small seed type (*V. faba var. minor*), followed by the large seed type (*V. faba var. major*), both of which were introduced from China in the 16th century. Many new varieties of long pod and medium seed type (*V. faba var. medium* and *equina*) came from England, France, and Spain in the late 1800's. This explains both the present existence of three types of this crop plant in Japan and the seed contamination problems, and the cross pollination by bees.

The encyclopedia "Nogyou−Zensho" was published in 1697 and gave the first regular description of agriculture in Japan. The author, Yasusada Miyazaki, traveled throughout the whole country of Japan investigating the characteristics and peculiarities of many crops. He pointed out that this crop plant was grown as a winter crop in rotation with rice as summer crop on a moist and fertile soil, and that this crop was used as human diet because the maturing time was shorter than that of wheat or barley.

Most of the above observations could be applied to today's cultivation of this crop in Japan. In fact, the cultural practices used by farmers up to the end of the World War I were essentially based on this book. Since then, however, many studies have been made on the characteristics and adaptability of this crop. These studies were carried out by autoecological analysis of the relationship between plant growth and natural and artificial environmental conditions with the view of using the small and medium seed types as dry seed and the large seed types as green seed.

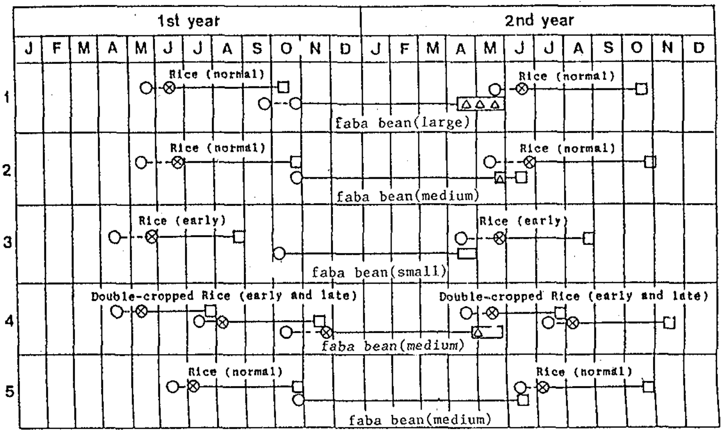

Fig. 1. Multiple cropping systems of paddy fields in Japan.

○ Sowing ⊗ Transplanting ☐ Harvesting (◬ immature green, ☐ dry seed)
----- Nursery
——— Field
1 Tokushima, Shikoku,
2—4 Kagawa, Shikoku
5 Saga, Kyushu

On the other hand, this crop has been cultivated as a winter crop in the multiple cropping system of paddy field as shown in Fig. 1. The development of the system as a whole has produced many local varieties as well as involving the nursery management and seedling transplantation techniques. Experience gathered over a long period revealed that though this crop is a good crop for fertilizing the soil and for improving other soil properties during the season of its cultivation, it can only be grown once every four or five years if "sick soil" is to be avoided. The most suitable crops for the intervening years are gramineous crops or rape. The ideal summer crop to follow this crop is late-maturing rice; other rice varieties are suitable as crops proceeding this crop.

The multiple cropping system enables fuller use of both the soil fertility and the sun light energy. For example, in Kagawa prefecture one field can produce good yields of this crop and hulled rice in the same year (Fig. 1, System 2). Multiple cropping system incorporating this crop plant seems to constitute a profitable agricultural practice in the temperate and subtropical zones. However, one problem associated with this system is that of soil moisture. Iinuma(42) has pointed out that seasonal fluctuations in rainfall resulted in agriculture being divided into humid zone and arid zone farmings. The date of planting or cultivation is strongly dependent on the amount of rain fall within summer and/or winter seasons. In view of the requirement for high soil moisture, it is difficult to envisage the route taken by this crop from its probable place of origin to the Far East. Since much of Central Asia is too dry to allow its cultivation, this is also true for the related species in the section Faba of the genus which also require high moisture, unlike certain other *Vicia* species in other sections such as *euvicia, cracca* and *ervum*(149).

In 1888 the scientific agricultural society was established in Japan following the foundation of the Society of Botany and Zoology. Since then, many pioneers have made efforts to promote scientific agriculture in Japan through agricultural education, research and compilation of agricultural statistics. Accompanying the development of scientific agricultural research, many specialized academic societies were established between 1910 and 1930 in the areas of Genetics, Breeding, Crop science, Horticultural science, Soil science and Plant nutrition, Phytopathology, and Applied entomology.

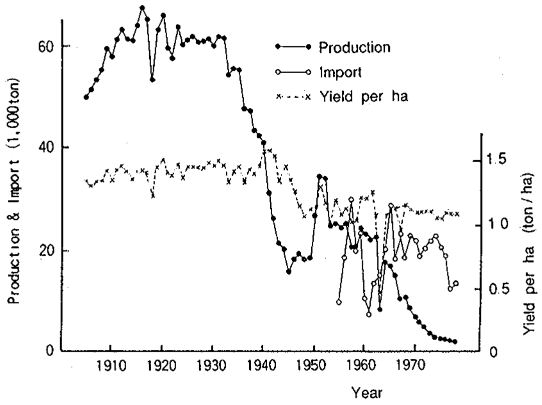

Fig. 2. Statistics of faba beans in Japan

Although the history of Faba bean cultivation in Japan goes back to over 1200 years, cultural practices used by farmers were not clarified until 1697 by Miyazaki's book, "Nougyou—Zensho". Farmers adopted these practices up to the end of the World War I when agricultural research had considerable effect on improving the old practices(65). Figure 2 shows the statistics of faba bean which were first officially recorded in 1905. Though the yield was about 1,400 kg／ha, it fell to about 1,000 kg／ha after the end of the World War II. Production together with the cropping area decreased rapidly since 1933 and the amount imported was higher than the locally produced quantity since 1960, so that today's situation in Japan is similar to that in all developed countries. However,this crop is one of the big six food legumes in the world, and China has by far the largest production, accounting for over half of total acreage and production(16,51,82,119,139,151).

From 1911 to 1979, there have been 236 scientific reports on this crop in Japan. The first study was carried out on the relationship between growth and soil reaction in 1912 (Table 1). The research history of each section can be summarized as follows:

1. Research in subject areas of genetics, crop husbandry, soil and fertilization, and insect damage began during the period 1912 to 1930. This included studies on the confirmation of chromosome number, problems in practices of winter cropping, soil reaction, inoculation of root nodule bacteria, and weevils.

2. In the next two decades, research developed in all subject areas except germination, virus disease, and seed quality and its processing. During this period, there were many studies on the characteristics of flowering and seed maturing habit of Japanese cultivars of winter type, including pollen germination, photoperiodism, vernalization, and adaptabilities to the environmental factors, especially the wet injury and

its counterplan in agricultural practices. Among the diseases, however, stem wilt began to cause severe damage of this crop, being closely related to winter cropping under wet conditions.

3. The efforts of researchers have produced a lot of reports in the following ten years (1951—1960) which contributed to the progress being made on the importance of phosphorus fertilizer, herbicides, mixed cropping, and the relationship between the germination and color of seed coat. Moreover, there were some valuable reports on the growth analysis, flowering and fruiting habit, and seeds, with reference to different producing regions or growing locations(1,125). These reports suggested the necessity of more research on the physiological analyses of the growth process which led to the initiation of this study.

Since then, though the research on this crop plant decreased steadily together with the decrease in local-production, there have been some important studies on this crop. These include studies on the karyotype analyses of *Vicia* species(149), dry matter production, physiological analyses of growth process including photosynthesis and respiration, and translocation of assimilated products(25,26,62,63,64,67,68,70,99,101,126,127,128,129,130,131,132,133), morphology and physiology of roots(136), and virus diseases.

Table 1. Research history of faba bean in Japan

Section & Subject		Number of Reports and Publications							
		1911-1920	1921-1930	1931-1940	1941-1950	1951-1960	1961-1970	1971-1979	Total
Breeding & Genetics		3	2	1	—	4	1	4	15
Physiology & Ecology	Germination	—	—	—	—	9	—	2	11
	Growing Process	—	—	2	3	15	7	18	45
	Flowering & Maturing	—	—	2	3	17	7	—	29
Crop Husbandry		—	2	5	7	22	3	1	40
Soil & Fertilizer		1	1	4	2	7	2	1	18
Disease Danage	Virus	—	—	—	—	7	8	7	22
	Others	—	—	3	4	8	1	2	18
Insect Damage		—	3	4	—	7	4	1	19
Seed Quality & Processing		—	—	—	—	9	3	7	19
Total		4	8	21	19	105	36	43	236

Despite the importance of this crop, its cultivation in Japan and perhaps in China has no good prospects. It is due to the overlap between the time of the harvest of this crop and the transplanting of subsequent rice resulting in its early cultivation. Moreover, it is very unfortunate that the reduction of winter cropping is spreading to warmer regions of Japan, despite the existence of favorable growing conditions. There are prospects for processing the green seed(48), whole plant fractionation and utilization of structural composition(22,71,72), in addition to the current uses as feed and green manure. Consequently, the need for the evaluation of the local varieties(69,73,74,75) and introduction of exotic varieties, especially determinate ones, cannot be overemphasized. Thus, though the cultivation and research of this crop plant has a long history, there still exist the need for more research to increase its production and consumption world wide(9,13,29,65,66,107).

In this study, the growth habit and its relations to the mechanism of dry matter production and seed yielding process in winter type of Japanese variety of faba bean was systematically analyzed. Firstly, the general growth and physiological status were studied. Also the physiological role of various organs and optimum population density for seed yielding process were discussed (CHAPTER I). Secondly, the characteristics of photosynthesis and respiration of individual plant and plant community were investigated (CHAPTER II). Thirdly, the translocating pattern of photosynthates was studied by means of $^{14}CO_2$-feeding techniques (CHAPTER III) and finally factors accounting for the determinate growth habit of Japanese cultivars of the winter type of faba bean plant were discussed.

CHAPTER I

GENERAL GROWTH OF WINTER TYPE AND PHYSIOLOGICAL ROLE OF VARIOUS ORGANS

CHAPTER I SECTION 1

GROWTH HABIT OF WINTER TYPE AND ITS RELATIONS TO CHEMICAL COMPONENTS OF VARIOUS ORGANS

For many years this crop has gained much popularity in Japan as mentioned in the introduction. Faba bean features prominently in Japanese diets both as dry seed and green seed. It is also used as whole plant for feeds or green manures in agricultural practices. On the other hand, this crop has been differentiated into many ecological types through the adaptation for long years, because this crop has an outstanding ecological adaptability to different agroclimatic conditions, and tolerating ability to both cold and soil moisture(65,75,126,127).

The physiological analysis of the growth process of this crop has been made systematically in last three decades(66). In this section, therefore, investigation was made firstly in order to describe the general characteristics of growth process, and their relationships to chemical components of various organs of this crop grown as a winter crop in warm region of Japan(66,126,127).

MATERIALS AND METHODS

The experiment was conducted in a non-heated glass house. The seeds of the cultivar "Sanuki-nagasaya" were sown with the root nodule bacteria in pots on November 4 and grown two plants per pot. The pots filled with paddy soil of precultivated rice as a summer cropping. The pots were received 5.5 kg N, 8.3 kg P_2O_5, and 8.8 kg K_2O per 10a as ammonium sulfate, calcium superphosphate, and potassium chloride, respectively, as basal dressing. At appropriate sampling times during the growing season, 4 to 6 plants were dug out from pots and washed. After the morphological characteristics measurements, the plants were separated into leaf blade, stem plus petiole, root including root nodule, pod, and seed, and weighed. These samples were dried in an oven at 90 ℃ for 30 minutes and then at 70 ℃ for 48 hours, weighed and ground finely with a Willey mill.

Analyses were made for carbohydrate and nitrogen components. The carbohydrates were extracted with water at room temperature. The reducing sugars were then determined directly, HCl hydrolyzed total soluble sugars and the insoluble portion of starch were determined by Micro-Bertrand method, and non-reducing sugar content was calculated. After extracting the nitrogen components by trichloro-acetic acid, soluble (soluble-N) and insoluble (protein-N) portions were determined by Micro Kjeldahl method.

RESULTS

Growing Process of Japanese Cultivar of Winter Type

The changes of dry weight with time in each organ are shown in Fig. 3. In winter, though the growth of the shoot was not remarkable except for the increase in numbers of branched stem, the root growth was remarkably vigorous. In spring, when we have longer days and increasingly high temperature, the shoot growth was accelerated. Flowering and pod setting were observed on the primary shoots at the lowest two nodes of the main shoot which branched at a very early stage of the growth in winter. Flowering started at the early stage of growth in spring, when the plant height was only half of that of matured stage and the dry matter was also a little. The first flower appeared at the 6th or 7th node in middle layer of each primary shoot, then flowering progressed upwards as the number of nodes increased till 20 to 25. However, pod setting was generally restricted to the range of firstly-flowering node to 3 or 5 nodes and upper flowers almost aborted. Therefore, the percentage of matured pods for total number of flowers was very low compared with other grain legumes(30,122,125). The development of vegetative organs reached maximum at green pod stage(93) which was about 30 days after the start of flowering and the following 30 to 40 days was necessary for seed maturity. Consequently, as the growth of this crop plant progresses competition between the vegetative and reproductive organs goes on for fairly long period.

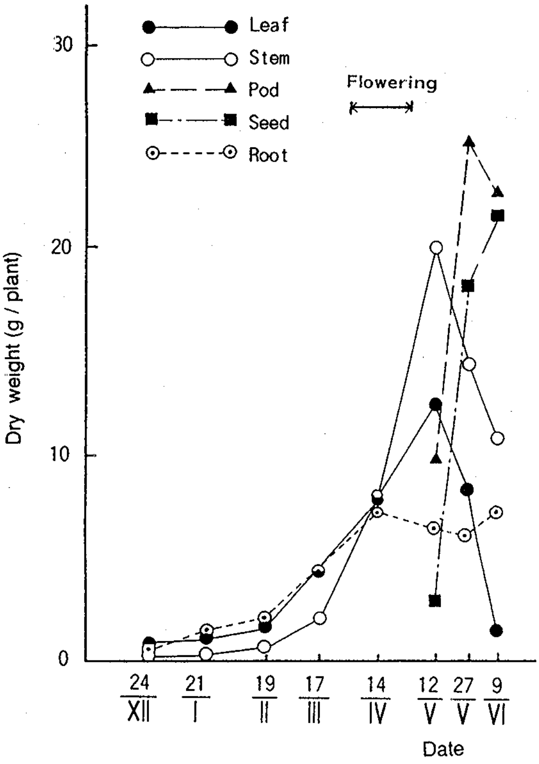

Fig. 3. Changes in dry weight of the tops and root of faba bean plant.

The shoot/root ratio which was about 1.0 during the early growth stage, increased accompanying flowering to 1.5 and at maturing to 3.1−5.7, suggesting that there is a complex but close relationship between shoot and underground growth.

Changes in Chemical Components in Various Organs with time

Changes in the carbohydrate components in various organs are shown in Figs. 4−1, 4−2, and 4−3. Reducing sugar content of leaf blade was high during the early growth stage in mid-winter and then declined. In the stem, it was generally high during the early growth to flowering stage, but became highest at the green pod stage. In the root including root nodules, however, it was generally low and changed little throughout the growing season. Those of pods and seeds were high at the early stage of development and then both of them declined rapidly with advancing maturity. On the other hand, the non-reducing sugar content in the vegetative organs was similarly high during the early growing stage in winter, then fell except a brief temporary rise at the green pod stage. Changes in the non-reducing sugar content in both of pods and seeds were almost the same as those in reducing sugar.

The starch content in leaf blade and root was generally low and increased in the later growth stage. In stem, though it was generally high, the change in contents before flowering and seed maturing stages were noteworthy. Starch content in seed finally attained more than 45 per cent which was higher than those in the other sugar contents. Consequently, the normal growth seemed to be supported by the physiological status; (1) the high carbohydrate content in vegetative organs during the stages of early growth in winter to early spring declined accompanying rapid progress in the development of both vegetative and reproductive organs, and (2) the temporary stored components in stem, root and later pod were translocated into seeds during the ripening stage.

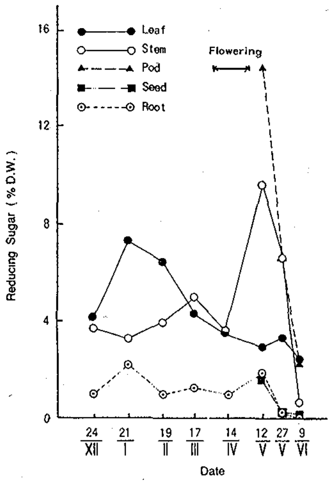

Fig. 4—1. Changes in reducing sugar contents in various organs.

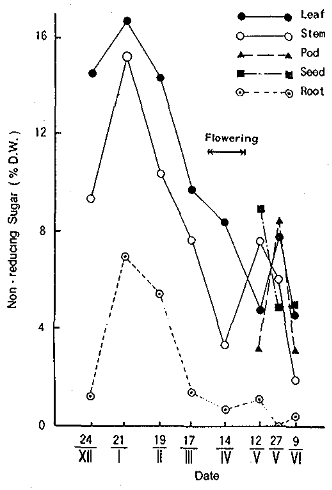

Fig. 4—2. Changes in non-reducing sugar contents in various organs.

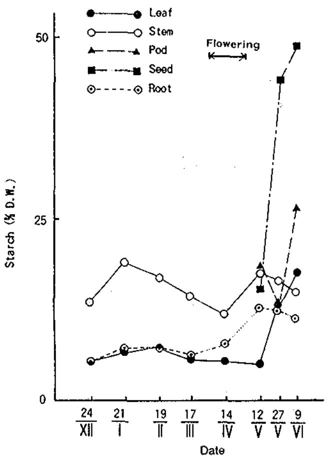

Fig. 4—3. Changes in starch contents in various organs.

The changes in soluble-N and protein-N contents (mg/g dry wt.) in various organs are shown in Figs. 5—1 and 5—2. Soluble-N contents were almost the same and changed little throughout the growing season among each organ. These were generally high in early growth stage and declined gradually towards maturity. On the contrary, protein-N contents fluctuated with growth and were different among organs. The high value was found in leaf blade during the period from early growth to flowering and at the flower bud formation stage in stem. The high value was also found in root including root nodules throughout the growing season. As for the contents of protein-N in the reproductive organs, it declined in pod as development progressed, but rapidly increased in seed and finally attained about 5.0 % compared with the 1.5 % of soluble-N content. Consequently, high nitrogen contents, especially the protein-N in the vegetative organs during the vegetative growth stage and in the underground organs throughout the growing season seemed to support the normal growth and seed production.

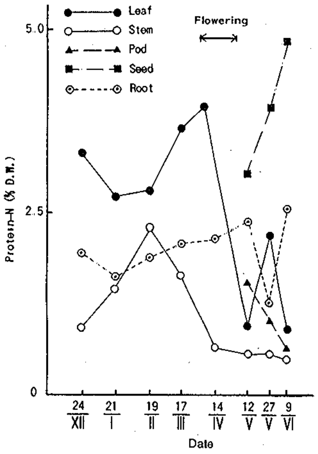

Fig. 5—1. Changes in Protein-N contents in various organs.

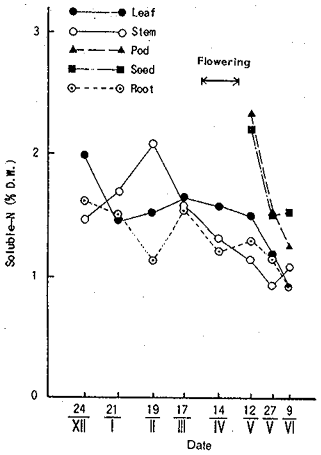

Fig 5—2 Changes in Soluble-N contents in various organs.

DISCUSSION

It is generally known that the growth process of crop plant is closely related to the surrounding meteolorogical factors(13,43,44,93,99,101,110,113,125,150). In this experiment, the results seemed to substantiate this fact and the close relationship between the growth process and the physiological status

In winter, the shoot growth was not remarkable except the branching(125), but the root growth was considerably vigorous. The high carbohydrate and nitrogen contents at this stage seemed to be closely related to the cold resistance(99,101,150) and to the development of new branched shoots, roots, and root nodules. Naka(99,101) reported that the chlorophyll content in the leaf, the osmotic pressure value of various organs, and the respiration of the shoot were very high at this stage. In early spring, this crop, which has vigorous vegetative and reproductive growth occurring simultaneously, had a special characteristics to require a large amount of chemical components, and was reflected in the rapid decline in previously stored carbohydrate during the former growth stage. These phenomena have been confirmed in defoliation(125,131) and shading(130,133) treatments.

After the pod setting in later spring, though the plant morphology had been established and large amounts of photosynthetic products synthesized, the total sink demands gradually exceeded the source supply. Considerable amounts of the assimilated products stored previously were, therefore, remobilized from vegetative organs and pods into seeds during seed filling stage. Similar fluctuations in carbohydrate contents of the vegetative organs and pods have been reported during the development of soybean seed(141), and potato tuber(100). Moreover, the starch was resynthesized from the remobilized sugars in seed as in the seed of other grain legumes(23,56). In addition, the results suggested that the consumption of large amounts of carbon is necessary to provide the energy and carbon skeletons for growth and development(104,147).

The root nodules were first found about one month after germination and developed gradually, and the bacteroid differentiated from bacteria in root nodule(24) even in cold winter. In early spring, high nitrogen content, especially protein-N in the underground organs, suggested high nitrogen fixation in root nodule continued until the time of senescence and its collapse during pod and seed ripening stage(143). However, it has been known that very large amounts of carbon are consumed in the root nodule formation and nitrogen fixation(105,147). Therefore, small amounts of carbonaceous and nitrogenous components seemed to remain in the lower nodes, resulting in a few numbers of matured pods concentrically at several nodes in middle layer of shoot(30,43,44,62,64,70,107,108,125,131), and none at upper nodes. It was also considered that this podding habit was a special characteristic of Japanese cultivars of winter type of this crop plant(69,75).

The results suggest that: (1) Physiological and metabolic activities are considerably vigorous throughout the growing process, (2) The physiological role played by the vigorous plant organs changes at podding, (3) The stored carbonaceous and nitrogenous components in stem and root before flowering and pod setting, promote the rapid growth and development during subsequent periods and finally contribute to pod and seed formation, (4) In addition to such physiological characteristics, the productivity seems to be limited by the shortage of assimilated products throughout the growing season, (5) These physiological processes seem to explain the determinate growth habit and the necessity for high yielding Japanese cultivar of this crop.

SUMMARY

This investigation was undertaken to obtain information concerning the relationship between the growth habit and the carbohydrate and nitrogen contents of the shoot and underground organs during the entire growing period. The results obtained are summarized as follows:

(1) In winter, shoot growth was not remarkable but root growth was more vigorous. Flowering and podding in spring surpassed the latter, and this was followed by vigorous activity of shoots and roots, and nitrogen fixation by root nodules at maturation.

(2) The carbohydrate and nitrogen contents of the shoot were high at the early stage of growth, then decreased with accompanying flowering, however, a temporary increase occurred during the pod developing stage.

(3) In the roots, the variations of carbohydrate content were essentially the same as the growth of shoots. Though the changes in nitrogen content were related to the activity of bacteroid and senescence of root nodules, high nitrogen contents, especially protein-N, were found at almost all growth stages.

From the results, it may be concluded that the physiological role of the leaf as an assimilatory organ was closely related to the growth of the plant, and that the stem, root, and pod played the role of temporary storage organs for the chemical components of the seeds.

CHAPTER I SECTION 2

PHYSIOLOGICAL ROLE OF VEGETATIVE AND REPRODUCTIVE ORGANS

Faba bean plants, in common with many other grain legume crop plants, generally produce more flowers than mature pods(5,6,15,29,31,91,107). The following reasons have been proposed to account for this phenomenon; the insufficiency of available N, P, and K elements and water, the failure of pollination, and mainly the shortage of specific growth substances and carbonaceous components(69,73,74,75,122). This crop plant has the following characteristics: (1) vigorous vegetative and reproductive growth occur simultaneously after flowering, (2) the function of leaf blades as assimilatory organ is closely related to the growth of the plants, (3) the stems, roots, and pods play the role of a temporary storage organs for the chemical components in seeds.

The objective of this investigation is to examine the characteristics mentioned above in the various organs of four sections of shoot based on the pod bearing habit. The effects of partial defoliation at three growth stages on plant growth, the dry matter production, and the physiological status were undertaken in this experiment(131).

MATERIALS AND METHODS

The seeds of cultivar "Sanuki−nagasaya" were sown in nursery beds on November 2 and the seedlings were transplanted in the field on December 2 planting distance was 36 cm in the row and 76 cm between rows. Fertilizer application was made as follows: 27kg ammonium sulfate, 45kg calcium superphosphate, and 18kg potassium sulfate per 10a and plowed down.

Four primary branches per plant were used for this experiment and the others including main axis were cut off. With regard to the pod bearing habit of this crop plant, the primary branch generally produces 20 to 25 nodes and bears pods in a definite section. So, the stems could be distinguished into the following four sections by node order:

(1) no flowering, 1st to 6th node order (1st section), (2) first flowering and pod bearing, 7th to 11th nodes order (2nd section), (3) flowering but generally pod shedding, 12th to 16th node order (3rd section), and (4) no flowering, upside node order (4th section). Treatments were operated with leaflet removal for each section at the start(I T), end of flowering (II T), and green pod stage (III T). As shown in Fig. 6, plants were subjected to ten treatments including control.

Plants were sampled four times (A: the start of flowering, B: the end of flowering, C: the green pod stage, D: the time of maturity). The sampling techniques and the experimental details of chemical analysis were almost the same as described in Chapter I, Section 1. The chlorophyll was extracted with 85 % acetone and determined by the photoelectric colorimetric method for total chlorophyll. The dry matter productivity was measured on the leaf blades of the control plants grown in a pot by the twin-leaf method

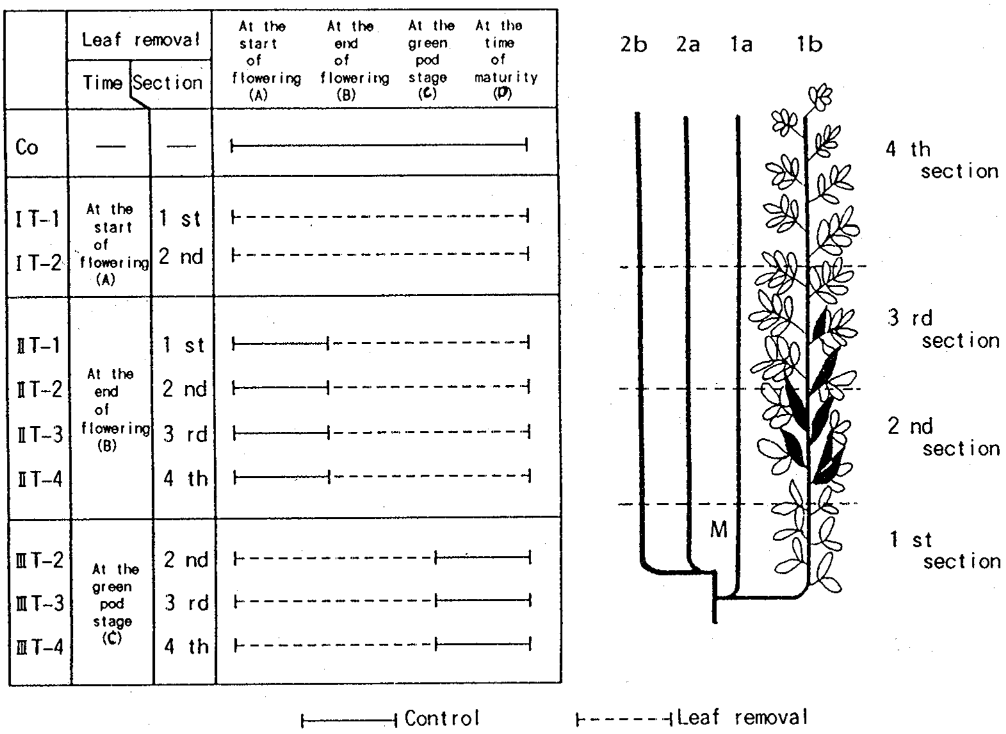

Fig.6. Experimental design and four sections of shoot.
M:Main shoot,
1a,1b : Primary shoot branched at 1st node of main shoot,
2a,2b : Primary shoot branched at 2nd node of main shoot,
1st section: 1st—6th node of shoot, no flowering,
2nd section: 7th—11th node of shoot, flowering and podding,
3rd section: 12th—16th node of shoot, flowering but pod-shedding,
4th section: 17th—20th and/or 25th node of shoot, no flowering.

RESULTS

Growing Process

The changes in stem length in each treatment are shown in Fig. 7. The elongation of stems was retarded by the leaf removal at the start of flowering, but the stem length of the plants treated at the later stage was similar to that of the control plants. Moreover, the treatment partially disturbed the stem elongation of the section which was vigorously lengthening at that time. The node number per stem at the time of maturity, was 24 in the control plants. On the other hand, plants treated at the start of flowering produced 24 nodes in the 1st section's leaf removal, but 21 nodes in the 2nd section's treatment. And afterwards, one, two, and three nodes were reduced by the 2nd, 3rd, and 4th section's treatments at the end of flowering, respectively, and one node was reduced by the 3rd and 4th section's treatments at the green pod stage.

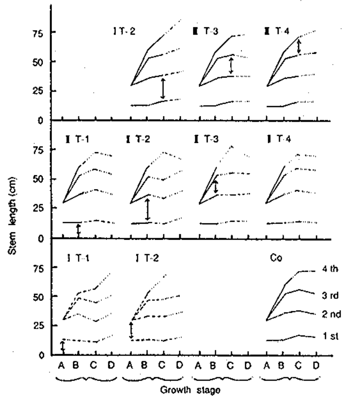

Fig.7. Changes in stem length of four sections. (Arrows show the treated section). Plots, (Co-IIIT) and growth stages, (A−D) are the the same as those Fig.6.

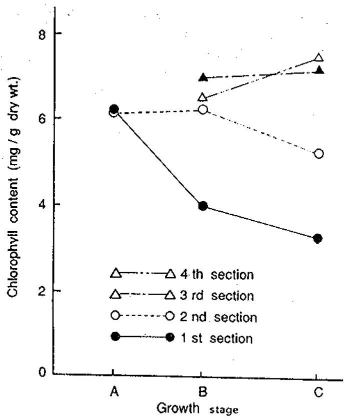

Fig.8. Changes in chlorophyll contents in leaf blade of each section. Plots, (Co-IIIT) and growth stages, (A−C) are the same as those in Fig.6

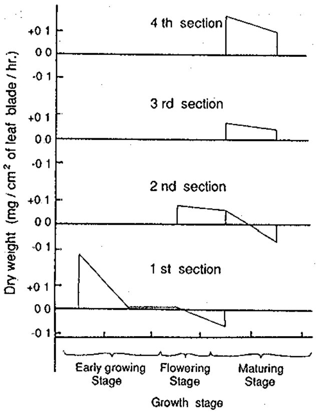

Fig.9. Dry matter accumulation rate per unit leaf area (mg／cm²／hr.) in each section.

The changes in the physiological status of the leaf blades with growth in each section was determined. The chlorophyll content (mg／g,dry wt.) is shown in Fig. 8. The content in the 1st section decreased after the start of flowering, but the contents in the other three sections seemed to maintain their values at leaf expansion. The dry matter accumulation rate per unit area (mg／cm²／hr.) of the leaf blade in each section is shown in Fig. 9. The photosynthetic activity of the leaf blades in the 1st and 2nd section seems to shift gradually from productive to consumptive status with the progress in growth, and that of the leaves in the 3rd and 4th section may play an important role in seed ripening during the later growth stage.

The dry weight of each organ per plant and its distribution in four sections at sampling times are shown in Fig. 10 and Table 2. The dry matter production in the vegetative and reproductive organs was lowered by the leaf removal, especially in the upper section' treatment. With regard to the leaf blades, stems, and roots, the leaf removal

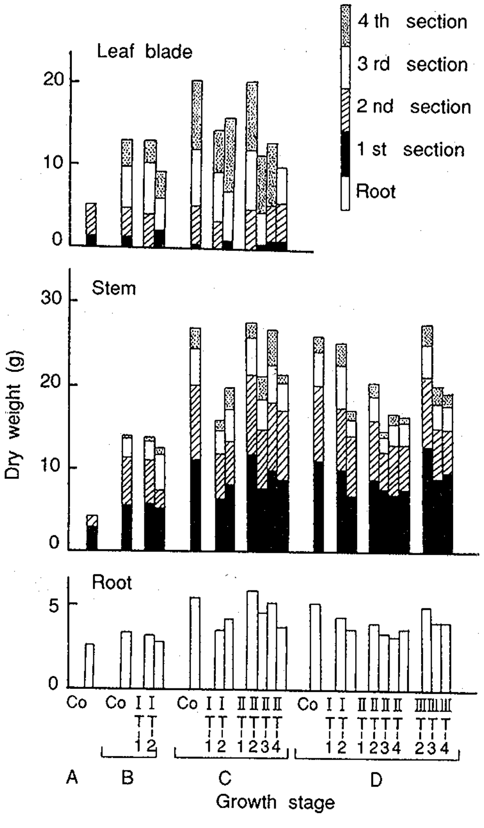

Fig.10. Changes in dry weight of each organ and the distribution in each section (per plant). plots, (Co-IIIT) and growth stage, (A−D) are the same as those in Fig.6.

Table 2. Effects of leaf removal on the flower, pod, and seed.
Plots, (Co−ⅢT) are the same as those in Fig.6.

	Section & Total	No.of flowers per stem	No.of pods per stem	Podding percentage (%)	Pod dry wt. per plant(g)	Seed dry wt. per plant(g)	100 seeds. wt. (g)
Co	II	21.9	7.0	32.0	30.6	73.2	91.4
	III	16.1	0.8	5.0	3.3	7.3	80.6
	Total	38.0	7.8	20.5	33.9	80.5	90.2
IT−1	II	23.1	6.1	26.4	19.3	41.4	71.4
	III	8.2	2.0	24.4	5.1	12.8	62.3
	Total	31.3	8.1	25.9	24.4	54.2	69.0
IT−2	II	19.6	3.2	16.3	16.0	37.2	93.2
	III	13.1	0.7	5.3	2.6	7.1	83.9
	Total	32.7	3.9	11.9	18.6	44.3	91.5
IIT−1	II	21.9	5.2	23.7	22.6	51.5	82.3
	III	16.1	0.1	0.6	1.0	2.9	88.6
	Total	38.0	5.3	13.9	23.6	54.4	82.6
IIT−2	II	21.9	5.4	24.7	15.8	36.2	82.3
	III	16.1	0.3	1.9	0.7	1.5	64.3
	Total	38.0	5.7	15.0	16.5	37.7	80.9
IIT−3	II	21.9	4.7	21.5	15.8	37.8	88.4
	III	16.1	0.4	2.5	1.5	2.4	79.2
	Total	38.0	5.1	13.7	17.3	40.2	87.7
IIT−4	II	21.9	4.5	20.5	14.0	39.3	84.8
	III	16.1	0.7	4.3	1.3	3.1	83.4
	Total	38.0	5.2	13.7	15.3	42.4	84.6
IIIT−2	II	21.9	6.5	29.7	22.0	66.8	89.3
	III	16.1	1.4	8.7	4.9	16.8	80.7
	Total	38.0	7.9	20.8	26.9	83.6	87.4
IIIT−3	II	21.9	6.2	28.3	17.8	52.6	80.5
	III	16.1	1.6	9.9	3.5	11.7	72.3
	Total	38.0	7.8	20.5	21.3	64.3	78.8
IIIT−4	II	21.9	6.8	31.1	20.0	61.5	81.6
	III	16.1	1.1	6.8	2.8	7.0	70.2
	Total	38.0	7.9	20.8	22.8	68.5	80.1

at the start of flowering retarded the dry matter accumulation at the green pod stage and the treatments at the end of flowering accelerated the dry matter degradation towards the time of maturity. On the other hand, the dry weight of pods was considerably lowered by the leaf removal in each treatment. Leaf removal of the start (I T) and end of flowering (II T) reduced seed weight remarkably. Moreover, among the four sections, the seed weight was influenced significantly by the upper three section's leaf removal at the end of flowering and by the upper two sections' treatments at the green pod stage. Although the seed development as shown by the 100-seed-weight was also retarded by the leaf removal, the results revealed more severe effects in later treatments. The podding percentages were generally lowered by the treatments, especially at the end of flowering.

Chemical Components

The chemical components in various organs were examined in the materials treated at the end of flowering (II T) with the exception of the 1st section's treatment. The results of carbohydrate content (mg/g,dry wt.) are shown in Figs. 11−1, 11−2, and 11−3. In the leaf blades of the control plants, the total sugar was generally high in the lower two sections (1st and 2nd section) and the starch content increased towards the green pod stage in each section. On the contrary, in the treated plants, though the total sugar contents varied, the starch contents were lower than those of the control plants in each section. The sugar and starch contents in stems were high at the green pod stage in the control plants. Similar trend was observed in all the four sections; the total sugar content was considerably high in the upper three

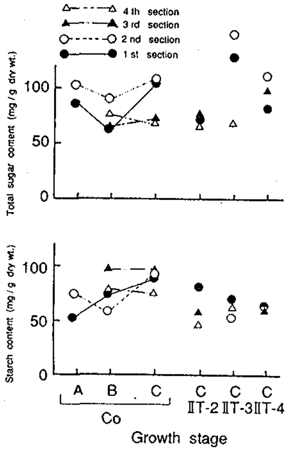

Fig.11−1. Changes in carbohydrate contents in leaf blade. Plots, (Co−IIT) and growth stages,(A−C) are the same as those in Fig.6.

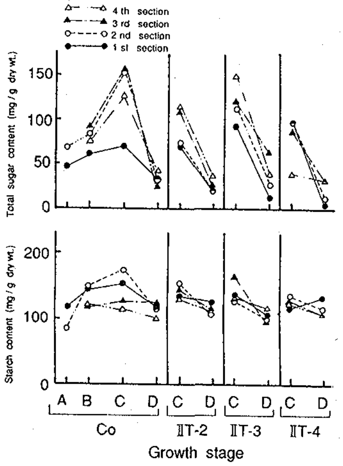

Fig.11−2. Changes in carbohydrate contents in stem. Plots, (Co−IIT) and growth stages, (A−D) are the same as those in Fig.6.

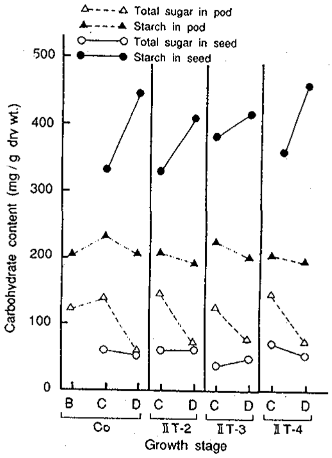

Fig.11−3. Changes in carbohydrate contents in pod and seed. Plots, (Co−IIT) and growth stages, (B−D) are the same as those in Fig.6.

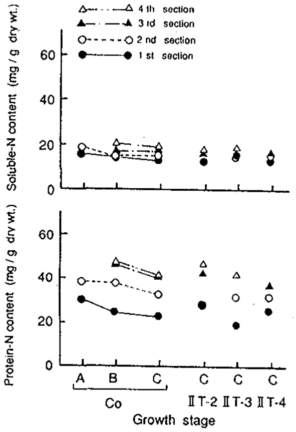

Fig.12−1. Changes in nitrogen contents in leaf blade. Plots, (Co−II T) and growth stages, (A−C) are the same as those in Fig.6.

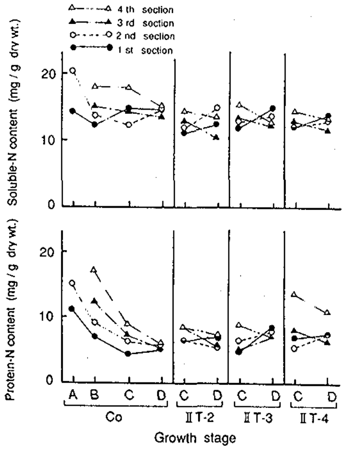

Fig.12−2. Changes in nitrogen contents in stem. Plots, (Co−II T) and growth stages, (A−D) are the same as those in Fig.6.

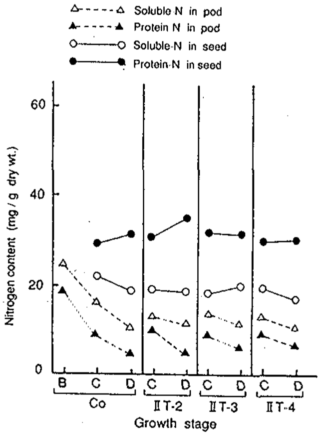

Fig 12−3. Changes in nitrogen contents in pod and seed. Plots, (Co−IIT) and growth stages, (B−D) are the same as those in Fig.6.

sections (2nd, 3rd, and 4th section) and the starch content was high in the lower two sections (1st and 2nd section). In the treated plants, the accumulation of the total sugars at the green pod stage was inhibited, especially in the treated section. Similar results were obtained on the starch content, especially in the 2nd section. With regards to the carbohydrate content in pods and seeds, though the leaf removal slightly reduced it, the reduction of the starch content in seeds was distinct in the plants treated in 2nd and 3rd section.

The nitrogen content is shown in Figs. 12−1, 12−2, and 12−3. In general, the soluble-N or protein-N in leaf blades and stems gradually decreased as the growth progressed, and the contents were high in the order, 4th, 3rd, 2nd, and 1st section. In the treated plants, the content in leaf blades and stems was approximately the same as the control plants except for the low soluble-N value in stems of all treatments at the green pod stage and the high protein-N value in stems of 4th section's treatment. The nitrogen content in pods and seeds of the treated plants, the slightly low soluble-N value in pods was observed of all treatments and the high protein-N value in seeds of the 2nd and 3rd section's treatment.

DISCUSSION

The present investigation was undertaken to obtain some information concerning the role or the physiological status of the leaf blades and four sections of the stem based on the pod bearing habit. The results of this experiment revealed differences in the production and distribution of photoassimilates between treated (leaf removal) and non-treated (control) plants. Can we realize the growth of plants treated with leaf removal to be normal? Therefore, I will discuss two flanks of leaf blades attached to or detached from the stem.

The effects of leaf removal on the vegetative and the reproductive growth were distinct accompanying the growing process. The leaf removal at the start of flowering caused a definite retardation in the development of vegetative organs as reported by Sugiyama et al.(125). Kuzunetsov et al.(81) indicated that the topping of fodder beans should be carried out 30 to 40 days before the harvesting time. In this experiment, the treatment at the end of flowering coincided with the experiment of Kuzunetsov et al.(81), prevented the accumulation of dry matter and chemical components, and reduced the podding percentage. Furthermore, the leaf removal at the green pod stage caused the reduction of seed yield. These results show that (1) the normal growth of this crop plant consists of the simultaneous development of both vegetative and the reproductive organs, (2) the reduction of the leaf area undoubtedly accounted for the flower-dropping and pod-shedding, and seed abortion, (3) the effective assimilating sections of the leaf blades and stems stepwisely rely on from the lower to upper parts.

Although this assumption supported the time trends of the chlorophyll content and photosynthetic activity of leaf blades in each section, the 2nd section's leaf blades had an outstanding feature of continuous physiological longevity. Many investigations have been reported about the defoliation experiments with corn(4,18,114), castor bean(61), soybean(27,28,78,148), and faba bean(81,125). These results indicated that defoliation was an unfavorable condition for the plant growth or yield. Generally, in partial defoliation trials, the lower leaves which expanded earlier had a close relationship to the development of the vegetative organs. Also, the removal of upper leaf of the soybean plants severely reduced the seed yield(27,28), but the corn plants the grain production was greatly reduced when the middle leaves were removed(18,114).

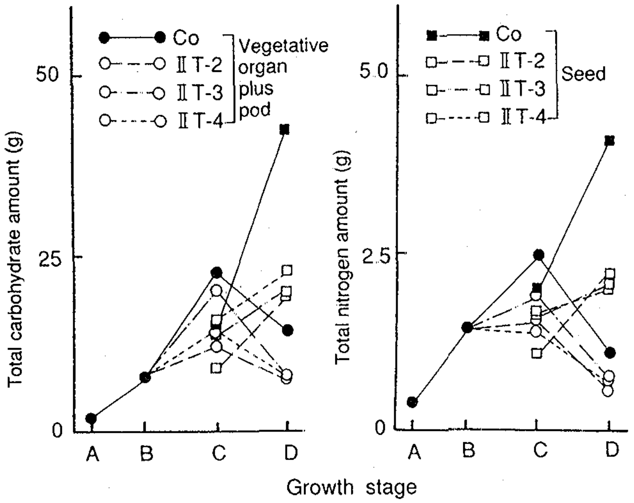

Fig.13. Changes in total carbohydrate and nitrogen amounts in the vegetative organs plus pod and seed (per plant).
Plots, (Co—IIT) and growth stages, (A—D) are the same as those in Fig.6

Table 3. Effects of leaf removal on the relative growth rate. (RGR, g/g/wk.)
Plots, (Co—IIT) are the same as those in Fig. 6.

	Co	IT-1	IT-2	IIT-1	IIT-2	IIT-3	IIT-4
At the start of flowering ↓ At the end of flowering	0.437	0.448	0.457	–	–	–	–
At the end of flowering ↓ At the green pod stage	0.348	0.272	0.336	0.336	0.249	0.349	0.298

With regard to the responses of the remaining leaf blades after the leaf removal, though reduction in starch was found, there were insignificant changes in the carbohydrate and nitrogen contents with a slight increase in reducing sugar. The stems adjacent to the section where the leaf was removed had a remarkable reduction in carbohydrate contents, especially the non-reducing sugars. Furutani et al.(27,28) reported that the defoliation in soybean plants resulted in the reduction of yield and that more deleterious effects occurred during the flowering to the mid-ripening stage when the starch contents were low in the stems. The results of McAlister et al.(89) also indicated that leaf removal reduced starch and sugar contents in the stems. Therefore, the results may emphasize that the compensation ability of the remaining leaf blades is not always vigorous.

On the other hand, as pointed out in Chapter I, Section 1 the stems, root, and pods played the role as a temporary storage organs for the chemical components in seeds. With this assumption, it is conceived that low seed production and chemical components were attributed to the reduction in vegetative organs by the leaf removal. Furthermore, in this experiment, it was clear that the leaf damage caused the degradation of the physiological activity not only as a whole, but also the treated section of stem. The degradations of the amounts of total carbohydrate and nitrogen in the vegetative organs, pods or seeds of the treated plants and the depression of the relative growth rate (RGR) due to the leaf removal further support the explanations mentioned above (Fig. 13, Table 3). Therefore, it seems that the function of the leaf blades is distinguished by the node orders, and that the 2nd section's leaf blades adjacent to the pod bearing node order situate as a key source of photosynthates. Accordingly, these growth characteristics are very important for the normal growth of this crop plant.

SUMMARY

The present investigation was undertaken to obtain some information concerning the physiological status of the vegetative organs in four sections of the shoot based on the pod bearing habit. The leaf removal was operated in four sections at the start and the end of flowering and the green pod stage. The effects on the growth, dry matter production, and chemical components are summarized as follows:

(1) The leaf removal at the onset of flowering inhibited stem elongation and the development of the vegetative organs, and subsequently the reproductive organs. The treatment at the end of flowering reduced the podding percentage and the accumulation of dry matter in the vegetative organs, especially in the 2nd section, and prevented the translocation of synthesized matter into seeds. The treatment at the green pod stage caused the reduction of the seed yield.

(2) The effects of leaf removal on the chemical components were examined for the plants treated at the end of flowering. The starch contents in remaining leaf blades and the total sugar contents in stems were lowered by the treatment, especially the non-reducing sugar contents in stems of the section adjacent to the treatment. The starch contents in seeds were reduced by the treatments at the 2nd and 3rd sections. But the nitrogen contents in all organs were approximately the same as those of the control plants.

Based on the results obtained in this experiment, it may be concluded that the role or the physiological status of the vegetative organs rely on the section from lower to upper accompanying plant growth, and the leaf blades of the 2nd section are very important for the normal growing process.

CHAPTER I SECTION 3

EFFECTS OF PLANTING DENSITY ON THE PLANT ARCHITECTURE, DRY MATTER PRODUCTION, AND SEED YIELD

In general, the seed yield of food legumes can be divided into the following four components; the number of stems bearing pod, number of pods per stem, number of seeds per pod, and size or weight of one seed. Many investigations have reported that the growth of this crop plant showed a high degree of plasticity and these yield components were all variable under various conditions such as soil moisture(2,97,128), soil fertility(63,129), light intensity or shading(1,49,130), and defoliation (81,89,125,131). 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.

Although there have been many reports on plant density(34,35,102,109,111,116), research on the performance of this crop in a competitive environment has received little attention. The objectives of the studies in this section are the effects of plant density on growth and seed production, and the nature of the competition and implications on dry matter partitioning into seed. In this experiment, the plant spacing was varied both between and within rows(132).

MATERIALS AND METHODS

The seeds of cultivar "Sanuki−nagasaya", were sown in the field on November 10 and the seedlings were grown as one plant per hill. Though the trials were consisted of four densities designed as shown in Table 4, the three densities high, medium, and low were used to compare the detailed analyses of the growth. Fertilizer application was made as basal dressing: 27 kg ammonium sulfate, 45 kg calcium superphosphate, and 18 kg potassium sulfate per 10a and were plowed down.

Table 4. Experimental design of planting density.

Density	Row width cm	Hill distance cm	No. of plants per sq. meter	Biological space per plant cm²
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 (A: the early growing stage, B: the start of flowering, C: the end of flowering, D: the green pod stage, E: the time of maturity). At the appropriate sampling time, the tops were clipped at every 10 cm height above the ground(54,92) and the roots were dug out in 25 cm depth and washed. Then the tops of every layers were separated into leaf blade, stem plus petiole, pod, and seed, and dried in an oven. At the same time, the leaf area was estimated by means of the blue print method.

The chlorophyll was extracted with 80 % acetone and total chlorophyll content(mg／cm²) was determined by the photoelectric colorimetric method. 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 Process

The growth status of plants of three densities are shown in Fig. 14, Tables 5 and 6. In winter, the growth of the shoots at three densities were not remarkable except branching. But some differences among three densities occurred in the elongation of stem or internode after the start of flowering when the stem length was 20 cm above the ground. The growth of branched stems decreased with decreasing spacing between and within rows; the number of stems per plant and percentage of the stem bearing pods declined. Moreover, the flowering of plants at the high density began a few days later than those of other densities, also the flowering of the 1st inflorescence started on the 7th node in contrast with the 6th in the low and medium densities. It was also noted that the height of the 1st flowering position was raised and the range of pod setting became wide in the high density. It followed the reduction in the number of nodes bearing pods in the high density because of the shedding of immature pod at the upper nodes. However, the nodal position of mature pod was unaffected by the plant density.

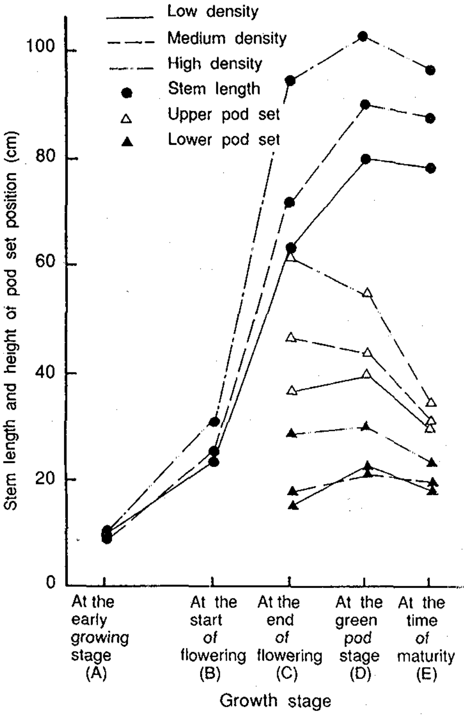

Fig. 14. Changes in stem length and height of pod set position.

Table 5. Effects of density on the flower, pod, and seed.

	Low density	Medium density	High density
No. of stem*1)	10.4	8.2	7.4
No. of stems bearing pods*2)	7.8	5.6	4.6
% of the stem bearing pods 2)／1)	75.0	68.3	62.2
No. of flowers*3)	156.6	160.5	150.0
No. of pods at muturity*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
No. of seeds per pod	3.6	3.7	3.8
100 seed wt. g	85.2	85.3	85.7

*per plant

Table 6. 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

The mutual shading of leaves increased as the growth progressed, started early in the high population density, and a part of lower leaves were defoliated. The number of flowers per plant was approximately the same in three densities, but the pod number per plant and the podding percentage were considerably lowered with increase in plant density. However, there were little differences among three densities for the pod length, the seed number per pod, and 100-seed-weight.

Dry Matter Production

The changes in dry weight of each organ per plant and per unit area (㎡) basis are shown in Figs. 15 and 16, respectively. With regard to the vegetative organs, the dry weight of leaf blade and stem attained maximum value at the end of flowering and at the green pod stage, respectively, but that of root was high during the end of flowering to the green pod stage. The dry weight of pod was maximum a the green pod stage and then decreased, but that of seed increased rapidly towards maturity. Within the range of densities used in this experiment, after the flowering period at when much mutual shading occurred, the dry weight per plant decreased consistently as the density increased. Contrary to the above results, on the basis of per square meter, the dry matter productivity was consistently high with increasing density.

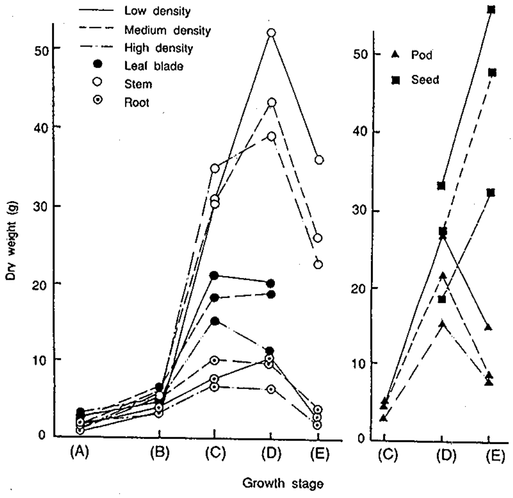

Fig. 15. Changes in dry weight of each organ (per plant).
Growth stages, (A−E) are the same as those in Fig. 14.

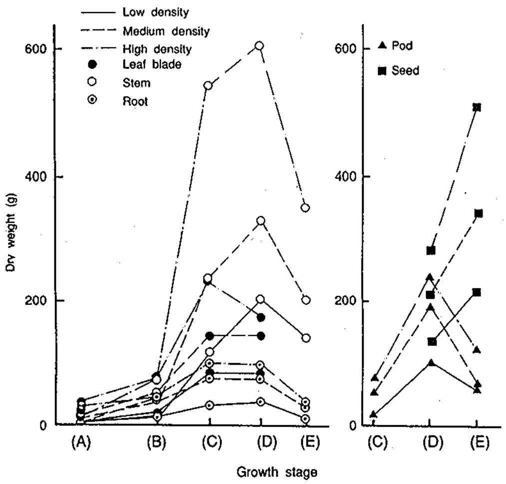

Fig. 16. Changes in dry weight of each organ (per sq. meter).
Growth stages, (A−E) are the same as those in Fig. 14.

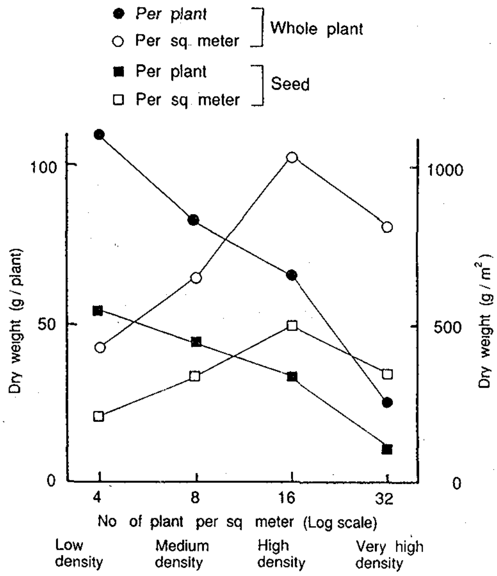

Fig. 17. Effect of density on dry matter production at time of maturity.

The dry weight of the whole plant and seed including very high density trial at the time of maturity is shown in Fig. 17. Those per plant were lowered with increasing density, especially in the very high density. But the dry weight per square meter became high in regular order of low, medium, and high density, but was again depressed severely when the density was beyond the range of this experimental "high".

Figures 18 and 19 show the differences of the productive structure at three plant densities obtained by stratifying every 10 cm clip method. In general, the vertical distributions of photosynthetic and non-photosynthetic system are the typical of broad leaf plants(54,92). The leaves distribution were similar at almost all the layers in three densities till the end of flowering. After then, the leaves in lower portions began to defoliate and the green leaves distribution was restricted to the upper portions. This fact was revealed earlier and clearer with increasing density. The pods were distributed in wide range due to the increase of internodal length.

Profile of Photosynthetic System

The differences in the vertical distribution of leaf area per plant and per square meter are shown in Figs. 20 and 21. As for the leaf distribution pattern of individual plants, the leaf, which was distributed mainly in the middle layers at the early growth stage, was stepwisely found in the upper part as the growth progressed. At high plant density, the maximum area per 10 cm layer was about 1,000 ㎠ at the end of flowering, then declined rapidly. But this was not found in the low and the medium densities. The leaf area per square meter, however, distributed higher in the order of high, medium, and low density at the end of flowering.

The leaf area indices (LAI) as shown in Fig. 22, increased with the growth and attained a maximum at the end of flowering in each plant density. After then, however, the LAI in low and medium densities of which the maximum values were 1.7 and 5.0, respectively, maintained until the green pod stage, but that in high density decreased from 9.1 to 5.0 during from the end of flowering to the green pod stage.

The profile of relative light intensities within canopies measured at three growth stages are shown in Fig. 23. Although the relative light intensity at the ground level was above 20 per cent at the start of flowering, but decreased along with the vigorous development of the vegetative organs, and became almost zero in the high and the medium plant densities at the end of flowering. At this time, the leaf-layer under 10 per cent of natural daylight intensity was at the first 10 cm above the ground in the medium density, and 30 cm height in the high density. These phenomena were more pronounced at the green pod maturing: the range under 10 per cent of light was 20 cm high in the low and the medium density, and 40 cm in the high density.

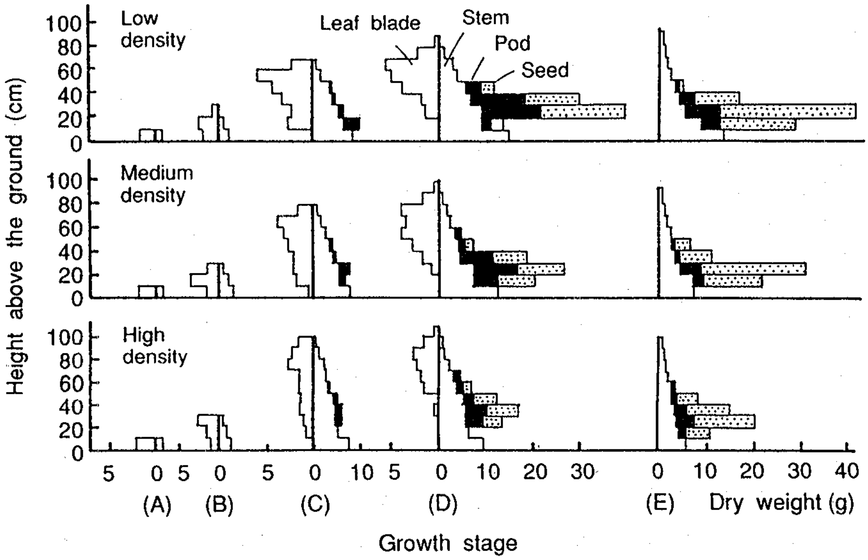

Fig. 18. Differences of the productive structure at three planting densities. (per plant)
Growth stages, (A−E) are the same as those in Fig. 14.

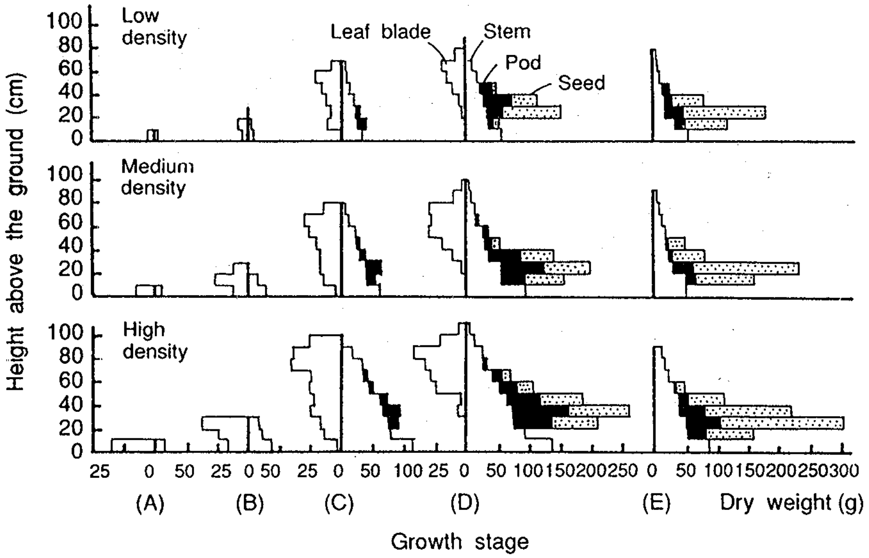

Fig. 19. Differences of the productive structure at three planting densities. (per sq meter)
Growth stages, (A−E) are the same as those in Fig. 14.

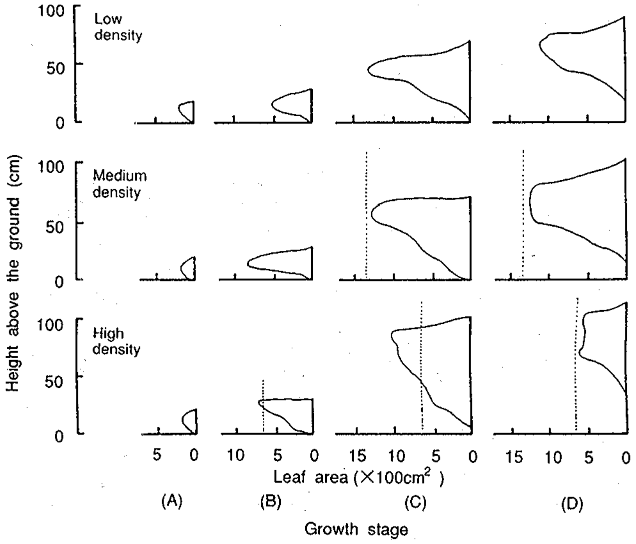

Fig. 20 Differences of the vertical distribution of leaf area (per plant)
Growth stages, (A—D) are the same as those in Fig. 14.
Dotted lines show the biological space.

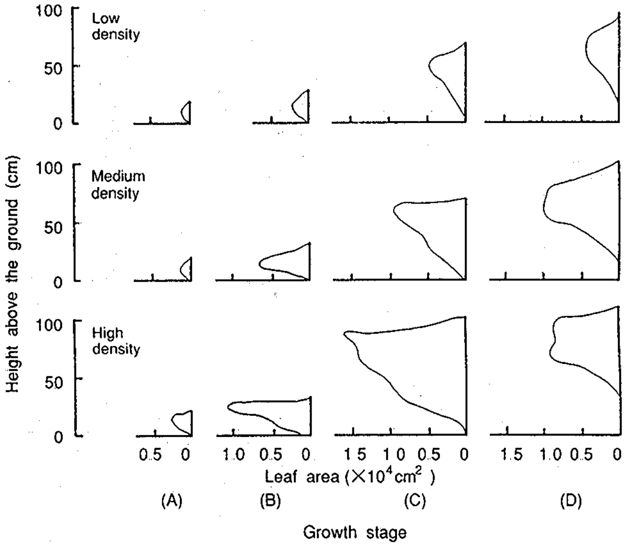

Fig. 21 Differences of the vertical distribution of leaf area (per sq. meter)
Growth stages, (A—D) are the same as those in Fig. 14.

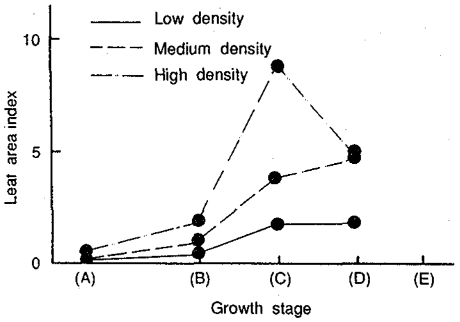

Fig. 22. Changes in the leaf area index of three planting densities.
Growth stages, (A—E) are the same as those in Fig. 14.

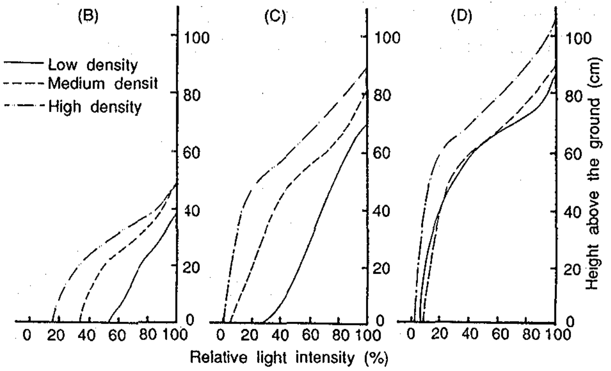

Fig. 23. Profile of the relative light intensity witihin canopies at three growth stages.
Growth stages, (B—D) are the same as those in Fig. 14.

DISCUSSION

Dantuma et al.(13,14) stated that the development and performance of the canopy are concerned with total dry matter productivity and its partition between reproductive and vegetative growth. In a plant density trial, any analysis on the nature of the competition must take a serious view of the biological space of individual plant. It is very important to consider how changing the planting rate or the plant arrangement correctly reveal the interrelationship between the growth and the plant number per unit area from the view point of whether the plant growth is uniform or not. In faba bean, Hodgson et al.(34,35), Picard et al.(109), and Riepma(116) have been revealed that the characteristics associated with the seed production had a close relation with the planting rate, but not with the planting arrangement, especially in the row width. Thus, in this experiment, though the row width in the low density was different from other densities, the results could be persuaded on the identical effects of the plant density.

Present results were in agreement with the results of other reports on this crop plant(34,35,102,109,116) and on soybean plant(83); the high density promoted the elongation of stem or internodal length, retarded the increase of the stem or node numbers, decreased the development of the reproductive organs, and had little effect on the seed size and/or weight or the seed number per pod. With regard to the elongation of stem or internodal length, Nagase et al.(98) pointed out that though soybean plants had usually a short internode in the upper and the lower layers, a long internode usually found in the middle layer transferred to the lower layer with increasing density. Such a phytosociological phenomenon was also recognized on this crop plant by increasing density.

With regard to the characteristics of leaves, this crop plant has usually 20 to 25 compound leaves per shoot and this compound leaf consists of two leaflets at the lower 6 or 7 nodes and 3 to 7 leaflets at upward node order. In this experiment, the leaf area per leaflet and chlorophyll content per unit leaf area at every 10 cm leaf layer are shown in Fig. 24. Though single leaf area was approximately among three densities, a rather small leaf on the upper and lower layers, and a large leaf in the middle layer, especially on the flowering nodes. The chlorophyll content, however, was similar among the each layer and three densities. Therefore, it seems that the leaves on middle layer and newly differentiated leaves on the uppermost layer have substantially similar activity, regardless of the different plant densities

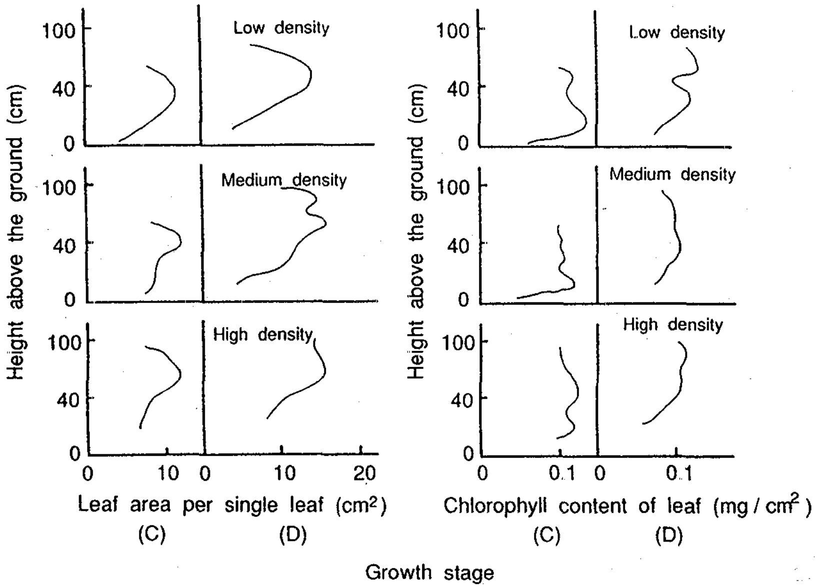

Fig. 24. Differences in leaf size and chlorophyll content of single leaf within canopies of three planting densities.
Growth stages, (C and D) are the same as those in Fig. 14.

The leaf canopy was accomplished primarily at the end of flowering accompanied with the establishment of plant architectural form. From this time toward the green pod stage, however, the changes of the vertical distribution in the leaf area became marked as shown in Figs. 19 and 20, and two decreased portions in the lower and the upper layers were recognized. With regard to the lower portion, leaves decreased at the green pod stage within a range which received under 10 per cent light intensity at former stage. This range was under 10 cm in height on the medium density and 30 cm in height on the high density. In Chapter II, Section 1, the light compensation point of this crop plant was found to be 10 per cent of daylight and the plant died within ten or twenty days in this light condition. Similar results of light compensation point of this plant were also reported by Blackman et al.(7) and Hodgson et al.(34,35). Nagase et al.(98) reported that the light compensation point of soybean plants and the range of yellowing of leaf were under 20 per cent of daylight in the field, but irrigation moved these effects under 10 per cent of daylight.

In the upper portion, leaves decreased at the green pod stage in the high and the medium densities. Then, the survived leaves were equally restricted in the same range. The land surface area available to the individual plant, was 2592, 1296, 648, and 324 ㎠ in the low, medium, high, and very high densities, respectively(Table 4). A dotted line in Fig. 20 shows the border of the biological space and at the same time indicates the limitation of the active leaf survivors. Figure 21 shows the variation of the leaf profile and the position of ㎡ leaf area as the dotted line, too. The process of such a typical decrease which was recognized with leaves within the range of the mutual shading(92) and the mutual contacting each other. It seems that such a physiological and physical defoliation are easily induceable on this crop plant community, and depends severely on the biological space(117).

Therefore, though the leaves of all layers differentiated and developed similarly during the early growth to flowering stage, thenceforth these leaves were gradually defoliated and established the final figure till the green pod stage. The leaf area index (LAI) in the medium and the high densities was 5.0 at that time, and this was the minimum value of published data(54) on the broad leaf plant community. Concomitant with increasing density, thus, the ratio of the photosynthetic organ was restricted in contrast with the ratio of the non-photosynthetic organs. Subsequently, this fact restrained the development of the reproductive organs during the maturing period as previously reported with the shading or defoliating trials (130,131).

Table 7. Effects of density on the crop growth rate (CGR, g／㎡／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 stage			

On the other hand, the crop growth rate (CGR) increased with increasing planting density throughout the whole stage till the green pod stage except for the high density (Table 7). With regard to the net assimilation rate (NAR) during the end of flowering to the green pod stage, the values were 0.45, 0.21, 0.20 g／100㎠／week in the low, medium, and high densities, respectively, calculated on the basis of survived leaf area. Accordingly, little differences in NAR were recognized between the medium and the high densities and seemed to relate to the status of CGR. Moreover, it was noteworthy that the translocation of synthesized matter previously stored in the stem, root, and pod seemed to be essentially the same among the three densities. Therefore, it is clear that the competition of tops of this crop plant at the high density begins at the start of flowering and the leaf area determined at the green pod stage by the defoliation of the lower and upper portions, and that though the seed yield per plant decreases, the high yield per unit area can be obtained at high density. Accordingly, potential of an individual plant to capture synthetic matter seems to be limited by the biological space and the optimum planting density exist at the level of the high density of this trial.

SUMMARY

Studies were carried out to obtain informations on the effects of plant density on growth, inter- and intra-plant competition and the efficiency of dry matter partitioning into economic yield of this crop. The experiment was conducted under four densities; low(3.8／㎡), medium(7.6／㎡), high(15.2／㎡), and very high (30.4／㎡). The results obtained are summarized as follows:

(1) The competition of tops began in the flowering period. The high density induced the elongation of stem or internodal length, but the retardation of number of stems, number of pods, podding percentage, and number of seeds per plant. As for the results per square meter, however, the growth of vegetative and reproductive organ increased with increasing density of low, medium, and high planting densities.

(2) With regard to the productive structures obtained with the stratifying 10 cm clip method, the photosynthetic systems varied from a status of being distributed in all layers at the flowering period to a status of being restricted to upper layers at the maturing period. This was more apparent and occurred early with increasing planting density.

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

From the results obtained in this experiment, it may be concluded that an individual potential seems to be limited by the biological space and the optimum planting density is the high density(15.2 plants／㎡) of this experiment.

CHAPTER II
PHOTOSYNTHESIS AND RESPIRATION

CHAPTER II SECTION 1
SIGNIFICANCE OF CARBON DIOXIDE EXCHANGE OF LEAVES AND PODS ON INDIVIDUAL PLANT

This crop plant produces generally much wasted reproductive organs such as immature pods or seeds in contrast with developing large vegetative organs. Soper(102) has suggested in review that the lack of specific growth substances and the shortage of carbonaceous and mineral substances accounted for this phenomenon.

On the other hand, it was pointed out that the role of the vegetative organs transmitted from lower to upper section and the existence of the 2nd section which was very important for the normal growing process described in Chapter I, Section 2. The objective of this section was to obtain the characteristics of carbon dioxide exchange of leaves and pods and the implications of the production and distribution of synthesized matter throughout the growing process(70).

MATERIALS AND METHODS

The seeds of 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 1.9g ammonium sulfate, 3.1 g calcium superphosphate, and 1.7 g potassium sulfate. Soil moisture was maintained at about 70 % of the field capacity.

Generally, though part of the main stem died during winter, the plants had four branched primary stems at first and second node order of the main stem and these stems grow similarly in spring. These stems could be divided into the four sections based on the flowering and pod bearing habits mentioned in Chapter I, Section 2 (Fig. 6).

Out of these primary stems, the first branched 1a was used, and middle three compound leaves in each section and pods in the 2nd section were measured for the photosynthesis and respiration. Measurements of CO_2 exchange were made by enclosing organs in a acrylic resin chamber, which was connected to an infra-red CO_2 gas analysis system (Fig. 25). At the same time the photosynthetically active radiation was measured with the photosynthetically active radiometer.

Experiment I; In order to obtain the general characteristics of photosynthesis and respiration of this crop plant, experiments were conducted on the leaves of 4th section at the flowering and green pod stages. Measurements were made in the growth chamber, the temperatures of air and underground were maintained at 15 to 30 ℃ with temperature controlled air flow and water bath in which pots dipped, and under the range of 2 to 100 % of natural daylight intensity by covering cheese cloth.

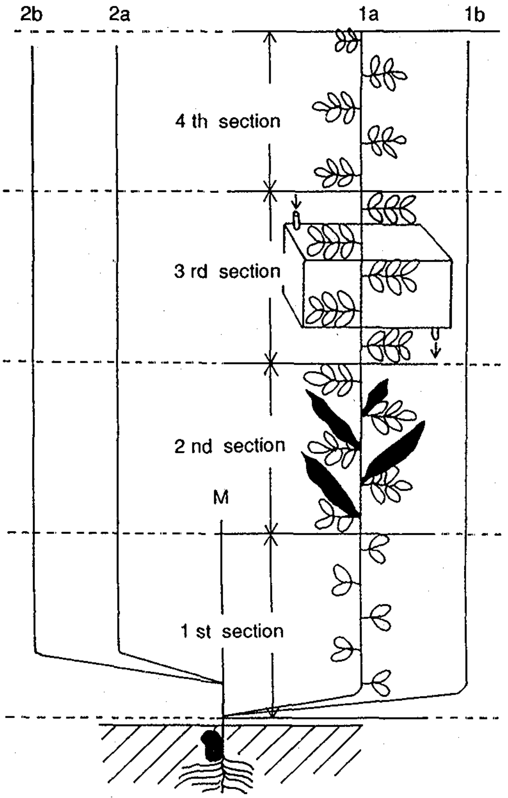

Fig. 25. Flowering and pod-bearing habit of faba bean plant and attaching methods of CO_2 measuring apparatus.
Shoots, (M,1a, 1b, 2a, 2b) and Sections, (1st, 2nd, 3rd, 4th) are the same as those in Fig. 6.

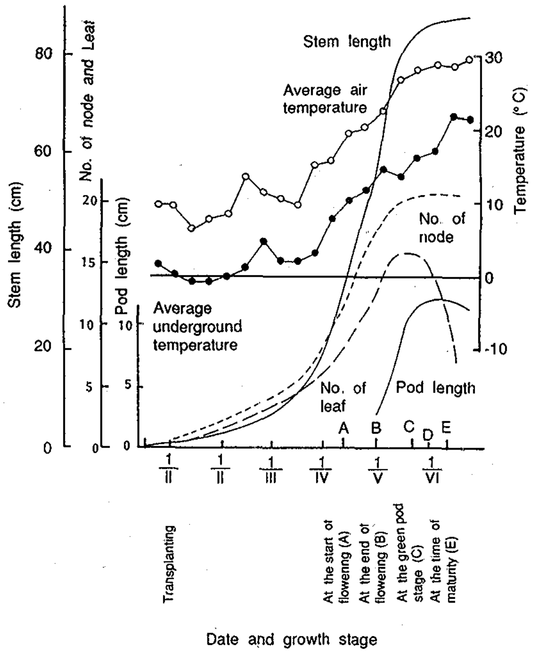

Fig. 26. Changes in morphological characteristics and temperature during the growing process.

Experiment II; In order to obtain the differences in CO_2 exchange rate and capacity of leaves in each four section and pods in 2nd section, experiments were carried out five times; at the start of flowering, 0 day(A), 20 days after that time(B), 40 days, the green pod stage(C), and 50(D) and 60(E) days, the time of seed maturity (Fig. 26). Measurements were made outdoors under the natural condition. In this case, temperature which was measured by thermojunction was about 5 ℃ 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 separated into the measured part and others on each section, then divided into leaf blades, stem plus petiole, root, and seed. These organs were dried in an oven and weighed. The leaf area and pod surface area were measured, and the chlorophyll was extracted with 85 % acetone and determined by the photoelectric colorimetric method as total chlorophyll.

RESULTS

Growing Process of Plants used for Measurement of CO_2 Exchange

The growing status of plant and the changes in air and underground temperature are shown in Fig. 26.

The length of stem and number of leaves per stem increased rapidly in April and flowering which began in late March, continued for about one month. The flowers of 2nd section developed into matured pods: it required about 40 days to reach green pod stage and another 30 days for the seed maturity. Consequently, the development and competition between vegetative and reproductive organs occurred simultaneously for considerably long period.

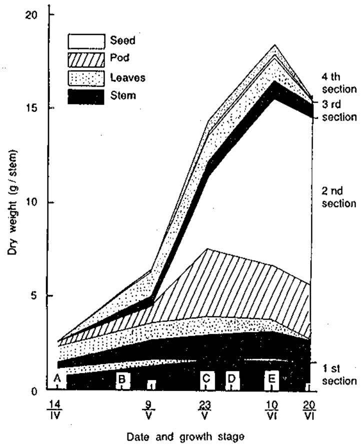

Fig. 27. Changes in dry weight of each organ (per stem).
Growth stages, (A−E) are the same as those in Fig. 26.

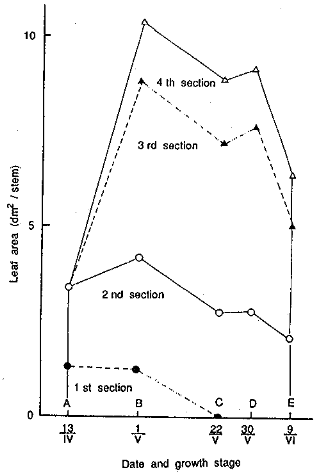

Fig. 28−1. Changes in accumulation with leaf area of each section. (per stem)
Growth stages, (A−E) are the same as those in Fig. 26.

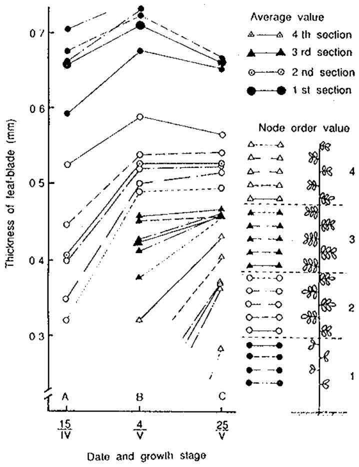

Fig. 28−2. Changes in thickness of leaf blade in each section.
Growth stages, (A−C) are the same as those in Fig. 26.

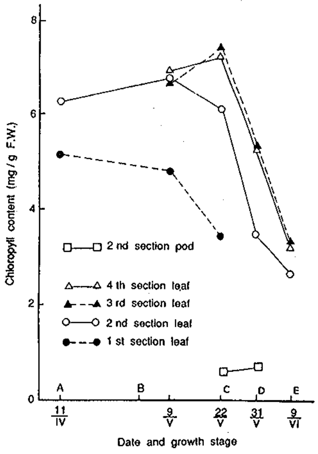

Fig. 28−3. Changes in chlorophyll content of leaf blade in each section.
Growth stages, (A−E) are the same as those in Fig. 26.

The dry weight of each organ per stem and in the four sections is shown in Fig. 27. The weight of total leaves was maximum at green pod stage and especially those of 2nd and 3rd sections occupied about 60 to

70 % throughout the pod and seed developing period The maximum value of stem weight, however, was recognized later and those of each section declined from lower to upper one. But, the dry weight of root did not vary during the flowering to pod maturing stage as mentioned in Chapter I, Section 1. The dry weight of pods in the 2nd section was maximum at the green pod stage and decreased progressively. The seed weight increased up to the time of maturity.

Figures 28—1, 28—2, and 28—3 show the status of leaves in the four sections. The total leaf area had two peaks at 20 and 50 days after the start of flowering and a large part of leaf area was occupied in 3rd and 2nd sections. However, the thickness of the leaf blade in the lower section was clearly superior to those of the upper sections. The chlorophyll content of leaves was generally high in upper section and decreased as the leaf age progressed, but the delay in its decline was noteworthy in the 2nd section.

Photosynthesis and Respiration

Experiment I: The relationship between the light intensity and photosynthetic rate at the green pod stage is shown in Fig. 29. Regardless of air and underground temperature, the light-response curve had hyperbolic shape and the highest value was 15℃ and generally in the order of 15>20>25>30℃. Though the light compensation point varied with underground temperature, it was 0.010 to 0.012 cal.㎠,min^{-1} of photosynthetically active radiation except for 15℃ and high value at high temperature. The light saturation point varied from 0.20 to 0.30.

Figure 30 shows the relation between the temperature and CO_2 exchange rate The optimum temperature was found to be comparatively low and within a narrow range at the flowering stage However, the optimum temperature and its range increased from the flowering to the green pod and seed maturing stage. Thus, this crop plant seems to be adaptable to a wide range of environmental temperatures accompanying with the aging of plant. On the other hand, the respiration showed an exponential increase as rising temperature at the flowering, but changed to a parabolic curve Consequently, faba bean seems to have a wide range of elasticity for temperature from the view point of CO_2 exchange.

Experiment II: The diurnal changes in CO_2 exchange rate of leaves in four sections and pods in the 2nd section are shown in Fig. 31. The apparent photosynthesis of leaves began at sunrise and reached almost 100 % of the daily maximum within 2—4 hours Throughout the following 9—7 hours the photosynthesis maintained relatively constant value, subsequently it declined in the last 2—3 hours of the day time Though the photosynthetic rate of leaves was different among four sections throughout the growing process, similar light compensation and the saturation point with Experiment I were observed Respiration, however, was observed immediately after the sunset and the rate was less variable throughout the night time.

For pods, no apparent photosynthesis was observed, but the diurnal course of respiration was unique. At the green pod stage, the high respiration in the night time suddenly decreased upon receiving sun-light at the time of sunrise and soon reached minimum value. After maintaining this value for a few hours, it again increased for the rest of day time. In the night, however, it became temporarily high value after the sunset, and declined gradually toward the following morning

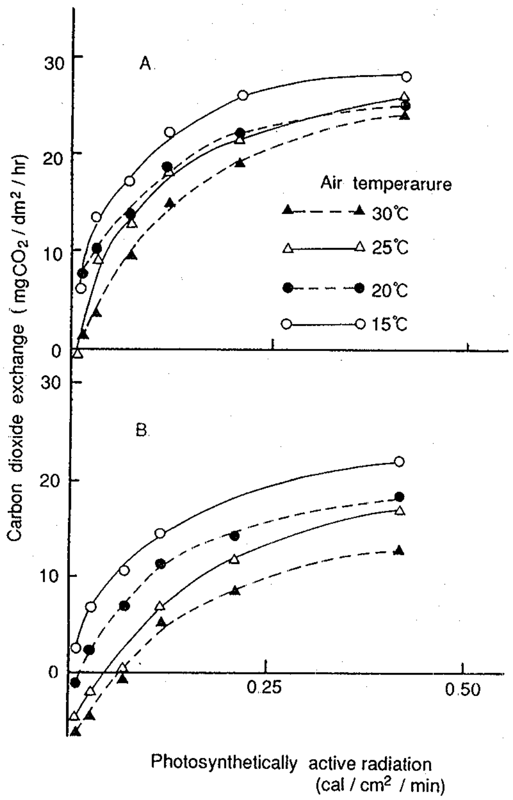

Fig. 29. Relationship between light intensity and photosynthetic rate.
A:underground temperature, 25℃.
B:underground temperature, 15℃

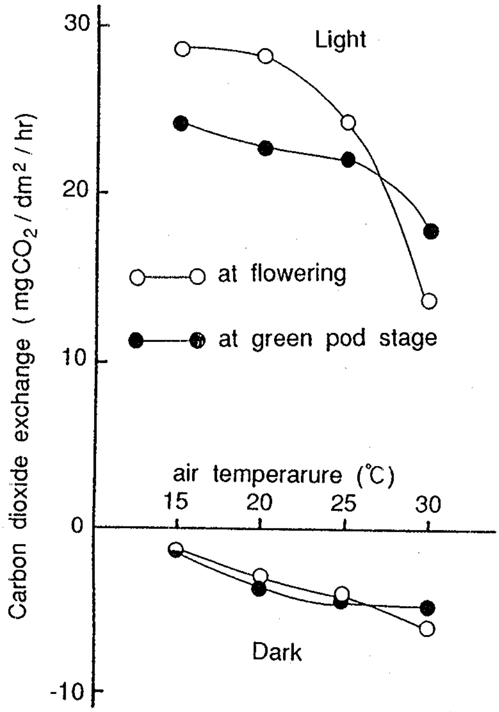

Fig. 30. Relationship between temperature and carbon dioxide exchange rate. (underground temperature, 15℃)

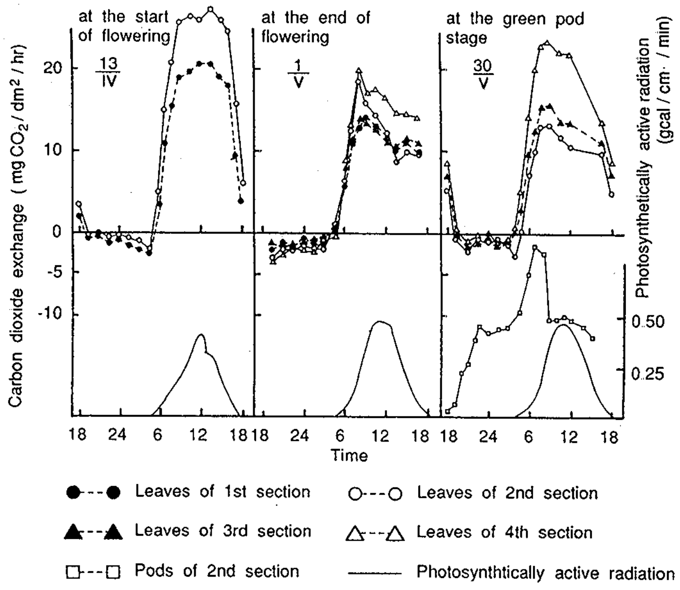

Fig. 31. Diurnal changes in carbon dioxide exchange rate of leaves and pods.

The changes in the average apparent photosynthetic rate of leaves in four sections are shown in Fig. 32−1. Throughout the whole stage it was always high in the upper section which was composed of young leaves at every time. Photosynthetic rate was high in the 1st and 2nd section at flowering but declined temporarily as the pods development progressed. Then it increased again at the early stage of seed maturation; the value of this stage was 11.8, 14.1, and 22.6 mgCO_2, dm^2,hr^{-1} in the leaves of the 2nd, 3rd, and 4th sections, respectively.

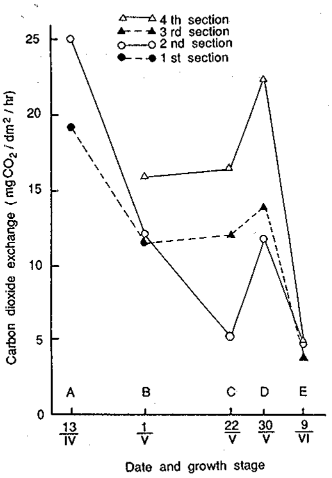

Fig. 32−1. Changes in the average photosynthetic rate in four sections.
Growth stages, (A−E) are the same as those in Fig. 26.

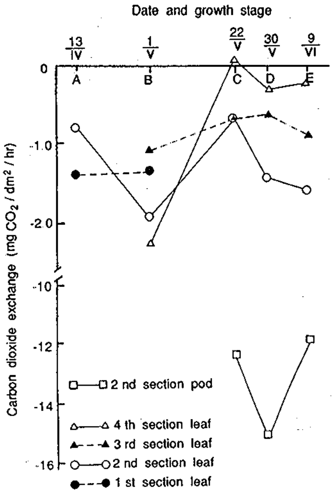

Fig. 32−2. Changes in the average respiratory rate of leaves in four sections during the night time and pods in the whole day.
Growth stages, (A−E) are the same as those in Fig. 26.

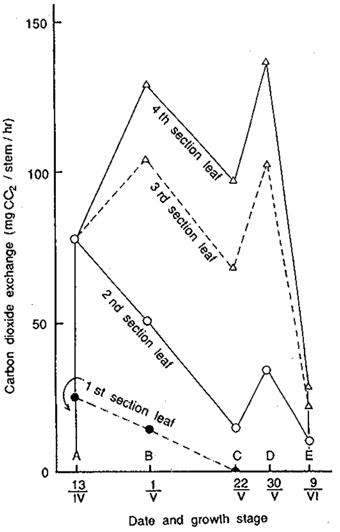

Fig. 33−1. Changes in photosynthetic capacity of leaves in each section and the cumulated values.
Growth stages, (A−E) are the same as those in Fig. 26.

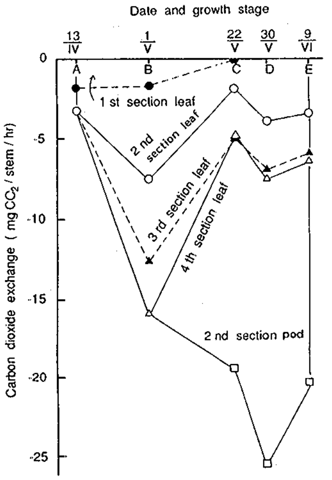

Fig. 33−2. Changes in respiratory capacity of leaves in each section and pods in 2nd section, and the cumulated values.
Growth stages, (A−E) are the same as those in Fig. 26.

The changes in the average respiratory rate of leaves in the night and those of pods in the whole day are shown in Fig. 32—2. The respiratory rate of leaves was less variable throughout the whole stage but it was generally high in the 2nd section which was pod-bearing one. The respiration of pods was remarkably higher than that of leaves. However, in contrast with the average value in the night time, it was considerably low in the day time(Fig. 31). This fact suggests a high photosynthesis of the green pod surface for a few hours.

The changes in the apparent photosynthetic and respiratory capacity of leaves and pods per stem are shown in Figs. 33—1 and 33—2. Total photosynthetic capacity had two peaks at the end of flowering and the early stage of seed maturation. At the end of flowering stage, leaves in 3rd and 2nd sections contributed immensely to total photosynthesis. At the latter stage, leaves in the 3rd section accounted for about a half of total photosynthetic capacity and those of the 2nd and 4th sections accounted for a quarter of total photosynthetic capacity. The respiratory capacity of leaves attained a maximum at the end of flowering, then decreased, and was the highest in the 2nd and 3rd sections throughout the experimental period. On the contrary, that of pods was remarkably higher than leaves just before the time of maturity. Consequently, total respiration of plant seemed to be maintained very high value after the green pod stage.

DISCUSSION

With regard to an influence of the light intensity and temperature on the growth of faba bean, Schroder(120) stated that there found a few differences among varieties depending on the adaptability and dry matter productivity. As for an optimum air temperature for the photosynthesis, the results of having relatively wide range was different from that of other *Vicia* spp. plants, common vetch (*Vicia sativa*)(95), especially at the later stage. Murata et al.(95) stated that there was difference in the response of photosynthesis to temperature between winter-grown and summer-grown northern type of C_3 plants; the former is more resistant to low temperature and less resistant to high temperature compare with the latter plant of the same species. This crop plant which was grown in winter season, however, seems to gain some high photosynthetic ability even under high temperature in the later growth stage. Similar results were reported by Fukuyama et al.(25) using a large seed variety of this crop in warm region of Japan. Consequently, this fact may explained by considering the "thermo-adaptation phenomenon" together with "source-sink relationship".

The diurnal course of CO_2 exchange of leaves generally agreed with those observed in leaves of other crops(49,52,76,79,103,121,137,138). Although much of the daily fluctuations reflected the irregularities in natural daylight intensity, the photosynthetic rate generally shown a plateau in the figure about 7-9 hours in the day time. Pearson(106) obtained similar results on single intact leaves of *Vicia faba* under a photoperiodic condition of 16 hours and a temperature of 25 ℃ and constant high light intensity. He stated that the net photosynthesis reached 95 % of the mean maximum rate within one hour at the start of photoperiod, and thereafter remained constant before declining during the last stage of the photoperiod. Although this experiment was conducted in the natural condition, the so-called mid-day depression(146) might to be a common characteristic of this crop plant.

The light compensation point was fairly a good approximation between the two experiments varying with temperature, growth stage, and section. But there had some divergence for the light saturation point between the two experiments, especially in conjunction with the underground temperature (11). It seems to be very important for cultivation of this crop in practice. Similar maximum photosynthetic rate throughout the whole stage was observed among the four sections. This value was similar to those of other C_3 plants(8,76,94,95,121), especially crops which are grown from winter to spring during the off-season. The average photosynthetic rate of leaves in the four sections, which was generally high in the upper younger leaves than the lower ones seemed to be varied correspondingly to the leaf age. There were many reports about the relationship between photosynthesis and leaf expansion: the highest value has been recognized before(79) or at just time(144) of leaf full expansion with the different plant species. On the other hand, Finch-Savage et al.(19) showed that the longevity varied from longer leaves which developed in the early growing stage to late developed shorter ones. In this experiment, the value seemed to retain for a considerably long period after reaching a leaf full expansion. But the longevity of leaves was different among the four sections and was the longest in those in the 2nd section. The leaf thickness and chlorophyll content were also retained high value till later stage in the 2nd section. These facts seemed to have very important implications to the development of adjacent flowers and pods. It was also confirmed that the importance of these factors in the 3rd section came after those of the 2nd section.

With regard to the changes in the average photosynthetic rate, it was high at the flowering, then decreased as the growth advanced, but finally increased again after the green pod stage when the development of seed rapidly progressed, especially on leaves of the 2nd section. Thus, the photosynthesis of leaves in the 2nd section, which was adjacent to pod-bearing node order, seems to play an important role in the later growth period. Indeed, the respiration of leaves in the 2nd section was correspondingly higher than others.

The diurnal respiratory course of pods indicates the vigorous metabolic activity within pods. The difference between the CO_2 released during the last phase of the night time and the following early phase in the day time, i.e. just before and soon after the sunrise in the morning, was recognized about 10 $mgCO_2{,}dm^2{,}hr^{-1}$, and this value was half of the photosynthetic rate of leaves. Muntz et al.(96) reported that the photosynthetic incorporation of $^{14}CO_2$ by the pod itself was maximal at 3 weeks after the anthesis and declined rapidly on *Vicia faba*. Kipps et al(59,60), however, found that the carbon activity of the seed was only one-tenth of that of the subtending leaf on the same plant even under the light supplying condition. Kumura et al.(79) observed that the green pods of the soybean plant had somewhat but small photosynthetic activity. Unpublished data of myself showed that the chlorophyll content based on unit surface area of green pod of soybean plant became low in short term after reaching high value. On the contrary, this crop plant behaved differently from soybeans. Consequently, though the photosynthesis of green pod surface was considerably high, the vigorous respiration of pods and inner seeds(20) seems to overcome it. So, the respiration must have an important role in the translocation of the photosynthates and for the change to the seed components such as starch. From the facts mentioned above, it seems that capacity of the leaf-source for photosynthesis is related to or governed by the existence and activity of sink.

Kumura et al.(79) examined that the total photosynthetic capacity of soybean increased with growth up to the beginning of ripening and then decreased, and that the dry matter production depended on those of middle leaves and the remaining duration of leaves. It is substantially true on this crop plant, and the high capacity at the flowering stage is supported by the enlargement of the leaf area, and those at the early stage of seed maturing due to the retention of the leaf area which had vigorous photosynthetic activity.

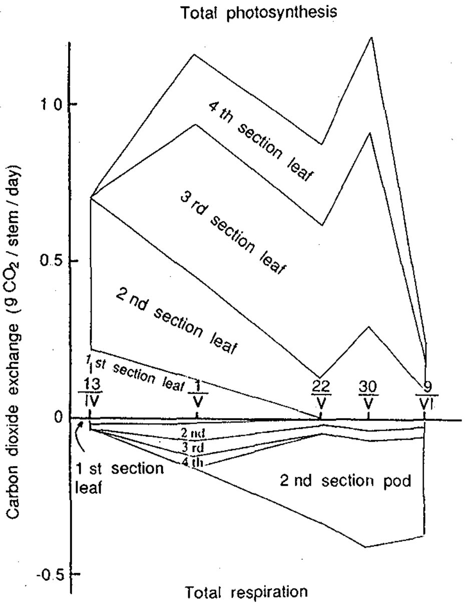

Fig. 34. Time trend of carbon dioxide exchange in stem.
Date of growth stage are the same as those in Fig. 26.

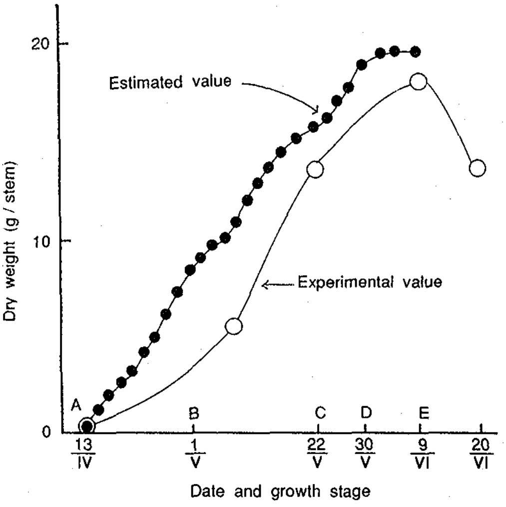

Fig. 35. Relationship between the estimated value of carbon dioxide fixation as starch and experimental value of dry weight
Growth stages, (A−E) are the same as those in Fig. 26.

As shown in Fig. 34, though the total respiration/total photosynthesis ratio was 5.0 % at the flowering, it rose to 40 % at the green pod stage and finally reached 150 %. Accordingly, accompanying the development of both pods and seeds, the respiration increased and exceeded photosynthesis about 3-2 weeks before the time of maturity. Using these results, the daily light duration, and photosynthetically active radiation, the theoretical amounts of the daily stationary CO_2 fixation per stem were calculated and compared with the estimated value of starch that accumulated throughout this experimental period. Figure 35 showed that there was a little difference between the theoretical value and experimental value. Fasheum et al.(17) stated that a growth efficiency value of incoming solar radiation in field beans (*Vicia faba*. L) is the largest values recorded for a annual C_3 crops. So, the conversion efficiency of CO_2 fixed into dry matter itself might be considerably high. However, Inako et al.(44) reported that eight compound leaves supported only one mature pod in limited stem on the large seed "Issun" variety. This agrees with the results in this experiment as 20 to 25 compound leaves yielded only three or four mature pods on middle seed variety. Therefore, the photosynthetic capacity or dry matter productivity may be fully supported the vegetative and reproductive growth *in this experiment*.

From the facts, it may conclude that the shortage of the carbonaceous substances seems to be the most important factor for the growth of this crop plant from the ability of the photosynthesis and respiration. And it may also pointed out the leaves of the lower 1st section contributed to the development of the vegetative organs of upper section in the early growing process, those of the 3rd section contributed about half, whereas each of those 2nd and 4th sections contributed every one-fourth to the pod and seed development after the green pod stage. The activity of CO_2 exchange of leaves in the 2nd section behaved most vigorously and were long-lived in the whole growth stage.

SUMMARY

This investigation was undertaken to obtain some informations concerning the relation between the changes in carbon dioxide exchange of leaves and pods *in four sections of shoots based on the flowering* and pod-bearing habits and its implications to dry matter production and partitioning. The results obtained are summarized as follows:

(1) The photosynthesis of leaves was adopted to a wide range of temperatures(15-30 ℃), especially high temperature at the later growing period. Within this range of temperature, the light compensation and saturation point were 0.01 and 0.20－0.30 cal.cm^2,min^{-1} of photosynthetically active radiation, respectively. The maximum photosynthetic rate was about 20 mgCO_2,dm^2,hr^{-1}, and the photosynthesis of leaves showed a mid-day depression.

(2) Although the leaves seemed to maintain their photosynthetic capacity for a considerable long hours *after reaching high value, it followed closely* the physiological age of leaves and with the existence of pods or not. The photosynthesis was high at the flowering and the early stage of seed maturing. Though the respiration of leaves in the night time was generally low, it was high *in the 2nd section of the stem which* carried pods and next to the 3rd section. The respiration was high at same stage concomitant with photosynthesis.

(3) The respiration of pod was high throughout the day and development. The diurnal course of the respiratory rate was unique; the high value at the night time declined very rapidly with sunrise but ceased soon after. Accordingly, though the green pods seemingly had photosynthetic activity, this was masked by the high respiration, the translocation and distribution of the photosynthates.

From the results it may be concluded that the insufficiency or shortage of photosynthates is an important critical factor for the plant growth and seed yield stability, and that the role of leaves in the 1st section was to support developing vegetative *sinks and those of the 2nd and the 3rd and* upper the 4th section move up stepwisely favoring partitioning to the pods and seeds development, especially those of the 2nd section is the most important.

CHAPTER II SECTION 2

EFFECTS OF PLANTING DENSITY ON CARBON DIOXIDE EXCHANGE

As a first approach to explain the changing pattern of competition which followed alteration of plant density, detailed analyses were made in Chapter I, Section 3. The competition of tops begins after the start of flowering and the leaf area was determined at the green pod stage by the defoliation of the lower and upper portions The results confirmed that the optimum planting density was 15.2 plants per square meter.

On the other hand, there have been reports on the photosynthesis and respiration(3.70.106) and the effect of leaf removal trials (35.90,131) on this plant. In Chapter II, Section 1, it was clarified that the activity of photosynthesis and respiration of leaves can be distinguished into four sections based on the flowering and pod bearing habit. It was also proved that the physiological status of the vegetative organs of the 2nd section, which was adjacent to pod bearing nodes, was very important for the normal plant growth. These results suggest that the seed yield instability is closely related with the insufficiency and shortage of the carbonaceous substances.

The objective of this section was to supplement these researches on the nature of competition. The effects of planting density on CO_2 exchange of leaves and pods and the implications on the dry matter production and seed yield(62) were investigated.

MATERIALS AND METHODS

The seeds of cultivar "Sanuki—nagasaya", were sown in a field on November 6 and seedlings were grown as a plant per hill. Fertilizer was applied as basal dressing; 27kg ammonium sulfate, 45kg calcium superphosphate, and 18 kg potassium chloride per 10a and plowed down. The experimental design was the same as described in Chapter I, Section 3, excluding medium density (Table 4).

The measured portion is shown in Fig. 25, 1a. Three compound leaves in each section and pods in the 2nd section were used for the photosynthesis and respiration measurements. The apparatus was the same as mentioned in Chapter II, Section 1, and the measurement of CO_2 exchange was made under natural condition

The plant growth survey was carried out three times; at the start (0 day), and end of flowering (20 to 30 days), and at the seed maturing (50 to 60 days). The CO_2 exchange measurement was undertaken at the end of flowering and the seed maturing. At the appropriate sampling time, tops were divided into the measured part and other sections, then separated into leaves, stem plus petiole, root, pods, seeds, which were dried in an oven and weighed. At the same time, the leaf area and pod surface area were measured by means of the blue print method.

RESULTS

Growing Process

The morphological changes, distribution of leaf area and dry weight measured at harvesting times are shown in Figs. 36, 37, and 38. The results were essentially the same as those of Chapter I, Section 3. Though branching was approximately the same among the three densities in winter, 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 in number of stems, pods, and seeds, especially number of stems bearing pod per plant.

As the growth progressed, leaves reduced in much mutually shaded portions and this phenomenon occurred early at high and very high planting densities. Thus, the dense leaves began to defoliate in the upper mutual contacted section and in the lower shaded section. At the very high planting density, vigorous growth and development of stems and leaves in the upper 4th section was accelerated secondarily.

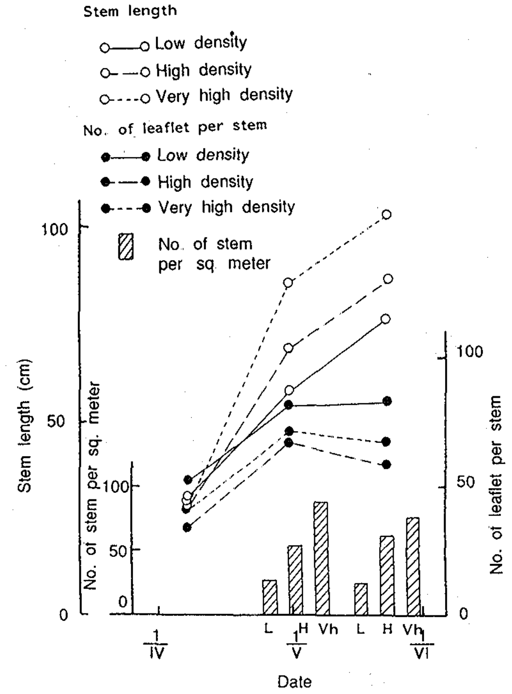

Fig. 36. Changes in stem length, number of stems(per ㎡) and number of leaflets (per stem) at three planting densities.
L:Low density, H:High density, Vh:Very high density.

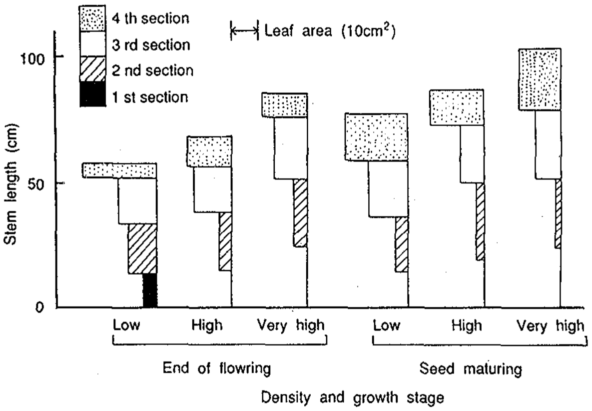

Fig. 37. Mode of distribution of leaf area per stem in each section.

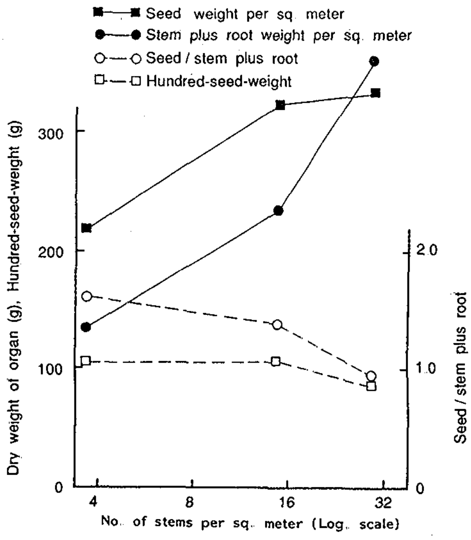

Fig. 38. Effect of density on the dry weight of vegetative and reproductive organs at the time of harvesting.

The profile of photosynthetic system, the distribution of leaf area in the four sections was clearly different among the three densities. The leaf area indices (LAI) were 2.29, 3.75, and 5.45 in low, high, and very high densities, respectively, at the beginning of seed maturing. The dry weight of whole plant also increased with increasing planting density. However, the abnormal plant form finally resulted in poor seed development and less seed yield which contrasted the development of the huge vegetative organs in very high density.

Photosynthesis and Respiration

Diurnal changes in apparent CO_2 exchange of leaves and pods at the seed maturing stage are shown in Fig. 39. The diurnal course showed a similar tendency among the three planting densities of two measuring times These features were essentially similar to the results which were measured on individual plant described in Chapter II, Section 1. A fairly good approximation of photosynthesis was found in leaves of the uppermost 4th section among the three planting densities. However, the duration of the photosynthesis varied among the four sections of the three planting densities accompanied with the increase of day length Although the duration of the lower section was almost the same at the start of flowering, it became shorter accompanying with increase of densities even on the 2nd section The decreasing hours of photosynthesis of lower section was recognized about one hour at both sunrise and sunset at the seed maturing stage. It was emphasized in the very high density by the increase of shading sphere

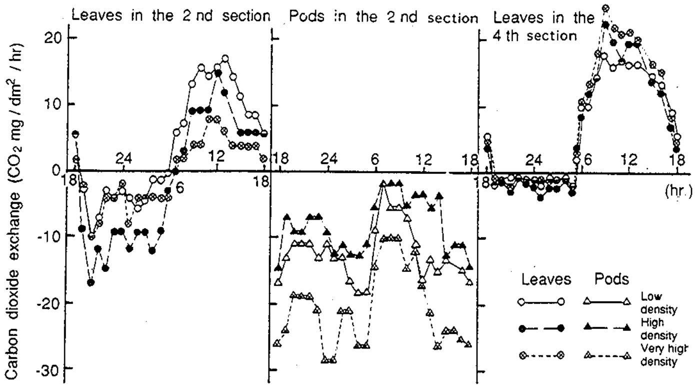

Fig. 39 Diurnal changes in carbon dioxide exchange rate of leaves and pods at the seed maturing stage.

The differences in the photosynthetic and respiratory rate of leaves and pods among each section are shown in Fig. 40. The photosynthetic rate of leaves of the lower section, at the end of flowering, was generally superior to those of the upper section and was also superior in low density. But, it became low in the lower shaded section and high in the upper section at the seed maturing stage. On the contrary, the respiratory rate of leaves in the night time was accelerated in the lower section as the growth advanced, especially at the high planting density. Though the average value of respiratory rate of pods was high throughout the day and night time, it was high in the night time particularly at the very high planting density.

Figure 41 shows the differences of photosynthetic and respiratory capacity and the amount of stationary fixed CO_2. At the end of flowering, though the shaded leaves began to defoliate in the lower section of high and very high densities, the photosynthetic capacity was considerably high in the 2nd section as shown typically at low planting density. It was rather high in the 3rd section with increasing planting density After that stage, an important role of photosynthesis successively transmitted to the upper section, especially in very high density. On the contrary, the respiratory capacity became high in leaves at high planting density and in pods at very high planting density. The amount of daily fixed carbon dioxide per square meter increased with increasing planting density at the end of flowering. Such a tendency still existed at the seed maturing.

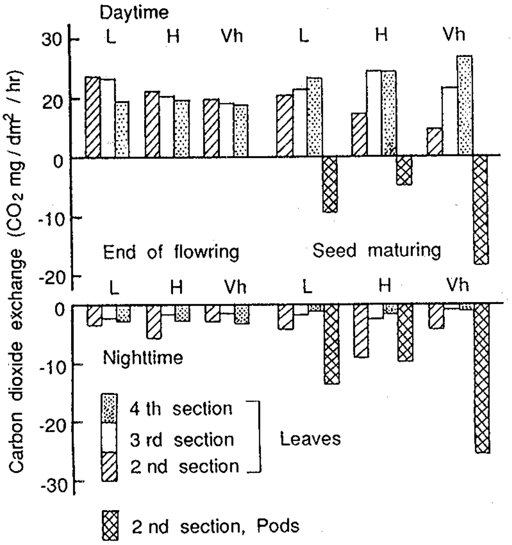

Fig. 40. Differences in photosynthetic and respiratory rates of each section among three planting densities.
Densities, L,H,Vh are the same as those in Fig. 36.

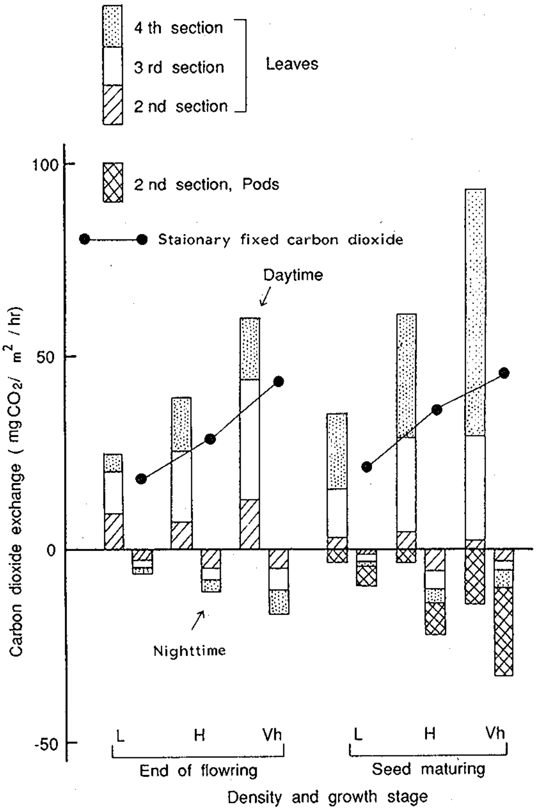

Fig. 41. Differences in photosynthetic and respiratory capacity and the amount of stationary fixed carbon dioxide among three planting densities.
Densities, L,H,Vh are the same as those in Fig. 36.

DISCUSSION

In planting density trials, such phytosociological phenomenon as the elongation of stem- or internodal length has been well known in leguminous crops(34,35,83,98,132). The results of this experiment were in agreement with the long internodal part usually located in the middle layer of shoot and moved to the lower ones with increasing density. Moreover, the long internode was also observed on the upper 4th section of very high planting density. Therefore, it seems to occur at different stages from the flower bud development to flowering among the different three planting densities.

The light intensity within plant community declined more early and severely with increasing competition. What affects the physiological status of leaves in four sections? Here, various effects should be related on (1) the process of defoliation, (2) the duration of photosynthesis, (3) the activity of photosynthesis and respiration, and (4) finally the inter-relationship among these factors and the production and partitioning of dry matter.

Accompanying to the progress of competition, compound leaves decreased in two portions of the lower and upper in the same manner as described in Chapter I, Section 3. The defoliated lower portion coincided with the range which previously did not receive even 10 per cent of daylight and the defoliated upper portion also coincided with the unavoided range of the mutual shading and contacting leaves. Thus, leaves seemed to retain about 5.0 of LAI value even at very high planting density. In connection with leaf behavior, the apparent photosynthetic duration of leaves was short in the lower shaded portion. At the seed maturing, though the difference between the lower 2nd and the upper 4th sections was only 0.5 hour at low planting density, it increased to three times even at high planting density. The photosynthetic rate of upper younger leaves was generally superior to those of the lower older ones on individual plant in Chapter I, Section 1. In this trial, the photosynthetic rate of leaves in the upper section seems to accelerate with increasing plant density. Therefore, leaves of plant grown in dense population in the upper-most section might gain the sun-leaf characteristic, as compared with leaves in the lower section possessing shade-leaf characteristic(10,94,118). Many researchers have reported that the light saturation point was increased in leaves located at higher position in the crop canopy(10,80,132). With this experiment, it was ascertained that though the light saturation point was 0.20 cal.cm^{-2}.min^{-1} of photosynthetically active radiation in low density, it was 0.30 in very high density.

On the other hand, it was established that the relationship between the photosynthetic activity of leaves and other factors such as the respiration(94,103,142) and source-sink relationship(131,134) was very important. In this experiment, the respiratory rate of leaves in the 2nd section and of pods with inner seeds in the 2nd section were very high. The high photosynthesis seemed to be accompanied or supported by vigorous respiration at high and very high planting densities. It was suggested that the photosynthetic activity of the source was related to the sink strength for translocation and resynthesis of photosynthates, as already explained in Chapter I, Section 2, and Chapter II, Section 1.

Although the daily fixed CO_2 per square meter was clearly high at very high planting density, the total respiration／total photosynthesis ratio was 37.6, 41.8, and 51.1 % at low, high, and very high planting densities, respectively, at the seed maturing stage. With regard to the distribution of synthesized assimilates from leaves to reproductive organs, especially in seeds, it was relatively low at very high planting density as shown in Fig. 38. Moreover, the seed／top plus root ratio and 100-seed-weight also declined at very high planting density. In connection with this fact, the close source-sink relationship has been found between leaves in the 2nd and 3rd sections and reproductive organs of pods plus seeds in the later Chapter III, Section 2 by $^{14}CO_2$ feeding trials. It was also found that leaves in the upper-most 4th section played an important role via maintaining of root activity. In this experiment, the fact seemed to be true in low density. However, such a relationship between leaves of the 4th section and root is not always detected at the very high planting density, and much fixed stationary photosynthates by upper leaves seemed to be consumed mainly for the preservation of huge vegetative organs including root and vigorous respiration of pods and seeds in the very high planting density.

Consequently, a considerably high photosynthetic activity of leaves may be essentially retained for a long period, especially in the 2nd section. And these functions seem to be governed by the consumption of synthesized matter for growth and the seed development of plant encountered under unfavorable condition such as severe competition. And the existence as a adequate quantity of leaves as in high planting density in the middle 2nd and 3rd sections assures to prove the critical important condition for the stability of seed yield.

It may be concluded that the function of leaves transmits from lower to upper section accompanying with leaves assembled in the upper shoot with increasing plant density, and those leaves behaved like those of sun plants having high photosynthetic activity. But at the same time, plants consume much photosynthates for wasteful building of vegetative organs and vigorous maintenance of respiration. Accordingly, the high density (15.2 plants／㎡) is again recognized as the optimum planting density from the view point of carbon balance of this crop plant.

SUMMARY

The effects of plant density on CO_2 exchange of leaves and pods were studied to further assess the nature of competition. The experiment was conducted at three planting densities of low(3.8／㎡), high(15.2／㎡), and very high(30.4／㎡). The results obtained are summarized as follows:

(1) The competition began after the onset of flowering stage. Stems elongated and leaves defoliated by mutual shading and physical contact, the higher the plant density, the more early and severely the growth retarded and resulted in poor seed development and less seed yield.

(2) 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 night time was heightened in the lower section especially at high planting density. The respiration of pods became high at very high planting density as growth advanced.

(3) The daily fixed CO_2 per square meter was high with increasing planting density, but the respiration／photosynthesis ratio was simultaneously increased. Though the close source-sink relationship was recognized between leaves of 2nd and 3rd section and pods at low planting density, such a phenomenon was not found between the huge amount of leaves in the upper 4th section and pods at very high planting density, accounting for the poor seed development and reduction in seed yield.

From the results, it may be reconfirmed that high planting density of this experiment is optimum from the view point of source-sink carbon balance and seed yield

CHAPTER III
BEHAVIOR OF PHOTOSYNTHETIC PRODUCTS ASSOCIATED WITH GROWTH AND SEED PRODUCTION

CHAPTER III SECTION 1
BEHAVIOR OF ^{14}C PHOTOSYNTHETIC PRODUCTS

Out of the many factors which determine the seed yield of crops, the assimilation and movement of carbonaceous substances in plant are of vital importance. Though the physiological status of plant varies with the growing process, detailed data of the translocation, accumulation, distribution, and consumption of photosynthates assimilated at various growth stages is necessary to analyze the seed production mechanism. In this aspect of the physiology of the growing process, many tracer experiments have been made on cereal and pulse crop plants(20,36,37,45,46,47,53,77,84,85,86,87,115,124,134,140,145)

In former chapter, it was suggested that unstable yields were attributed to shortage of carbonaceous substances of this crop plant, especially those grown under undesirable conditions.

The objective of this section is to clarify qualitatively and quantitatively the behavior and role of photosynthesized carbonaceous substances assimilated during the flowering to seed maturing stage with special reference to the seed formation, using ^{14}C as a tracer(64).

MATERIALS AND METHODS

The seeds of cultivar "Sanuki-nagasaya" were sown in nursery bed on November 7, and two seedlings per pot were transplanted on December 11. Each pot received 2.9 g ammonium sulfate, 4.8 g calcium superphosphate, and 1.9 g potassium sulfate. Soil moisture was maintained at about 70—75 % of the field capacity.

Whole plants were exposed to $^{14}CO_2$ gas at three stages of growth: the start of flowering (Treatment I, 0 day), the end of flowering (Treatment II, 25 to 30 days), and the seed maturing (Treatment III, 60 days)(Fig. 42—2). The underground part of plants were enveloped with vinyl film and transferred into a chamber. Then, plant was enclosed in vinyl film bag and exposed to $^{14}CO_2$ which was liberated from ^{14}C-carbonate by adding excess amounts of 0.1 N HCl. The initial CO_2 concentration was 450 ppm and $^{14}CO_2$ feeding was done for 2 hours under the natural sun-light conditions.

Plants were sampled at the time of $^{14}CO_2$ feeding, 7th day after feeding, the green pod stage, and the time of maturity in Treatment I and II, and also the time of feeding, 7th day, and the time of maturity in Treatment III. At each sampling time, after the root was washed out, (1) plants were killed in boiling water and made into herbarium specimen for autoradiography, and (2) other plants were separated into various organs and powdered them. For ^{14}C radioactivity meseaurement, sample was treated by the wet combustion method with Lindenbaum's apparatus and then determined by a liquid scintillating counter with toluene solution containing hyamine, P.P.O., and P.O.P.O.P.

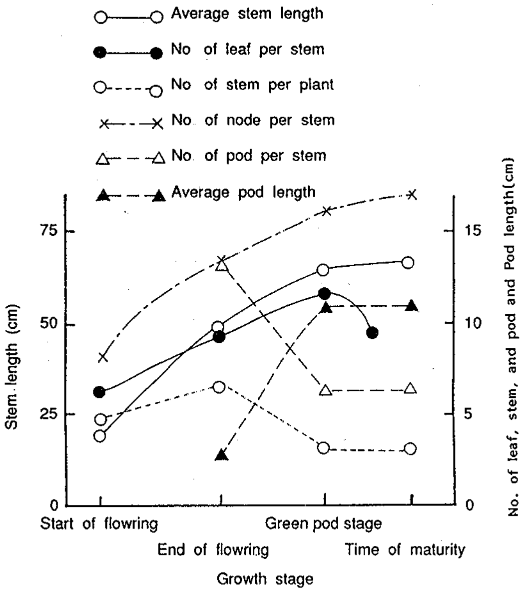

Fig. 42—1. Changes in morphological characteristics.

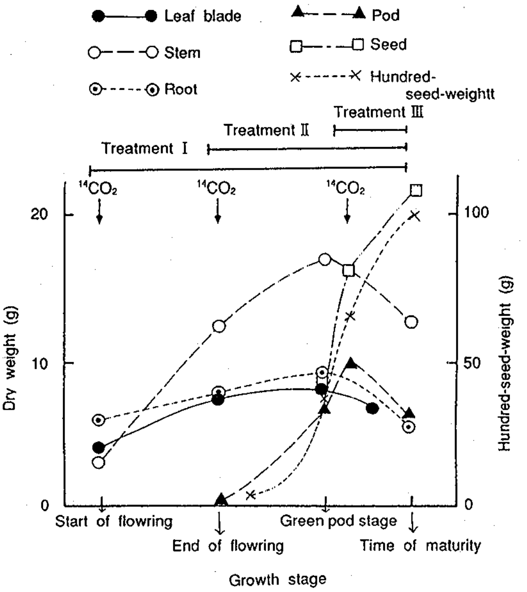

Fig. 42—2. Changes in dry weight of organs per plant and hundred-seed-weight, and the time of $^{14}CO_2$ feeding.

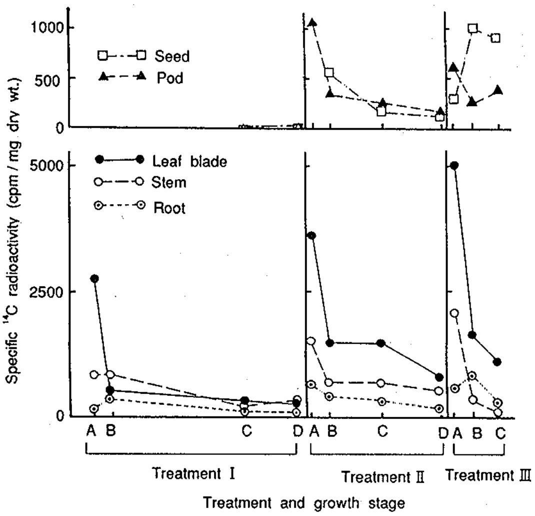

Fig. 43. Changes in specific ^{14}C radioactivity in each organ.
A:at the time of $^{14}CO_2$ feeding.
B:at the 7th day after feeding.
C:at the green pod stage.
D:at the time of maturity.

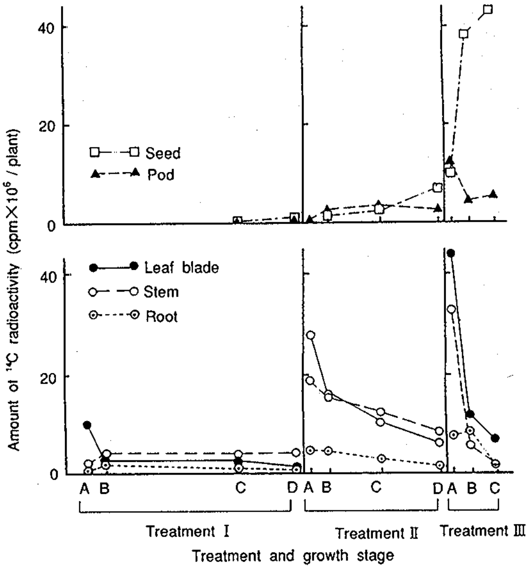

Fig. 44. Changes in the amount of ^{14}C radioactivity in each organ.
Stages,(A—D) are the same as those in Fig. 43.

RESULTS

Growing Process

Figures 42—1 and 42—2 show the morphological changes of plants sampled for the analysis. The stem length, number of leaves, and weight of vegetative organs at the start of flowering, in general, were only half of the maximum value. The growth of reproductive organs, the rapid elongation and development of pod, was not recognized until 30 days from the start of flowering, when many fertilized pods began to decrease in 3 to 5 per stem. More 10 to 20 days later from this stage, seeds began to develop in shape and component till 70 to 80 days from the start of flowering. Therefore, the role of photosynthetic products in plant is supposed to vary with various growing processes.

Behavior of ^{14}C Products

The changes in the specific ^{14}C radioactivity in each organ are shown in Fig.43. At $^{14}CO_2$ feeding, practically two hours after assimilation, the activity in leaf blades was superior to other organs throughout all treatments of the three stages. It was also high in those of later treatment and in the upper and/or younger sections (Fig. 47). Within 7 days after $^{14}CO_2$ assimilation the activity declined rapidly in various organs excluding the stems and roots of Treatment I and roots and seeds of Treatment III. However, the behavior of specific radioactivity from 7th day to the time of maturity showed, in general, the tendency of gradual decline in various organs.

Figure 44 shows the changes in the amount of the assimilated ^{14}C in each organ per plant. In Treatment I, much of the ^{14}C were translocated from leaf blades to stems and roots within 7 days after the assimilation followed retaining in vegetative organs in minute quantity and was distributed in pods and seeds at maturity. On the contrary, the continuous decrease in ^{14}C activity in leaf blades, stems, and roots, and the increase in seeds were found in Treatment II and III. This tendency was emphasized along with Treatment III as shown in Fig. 48.

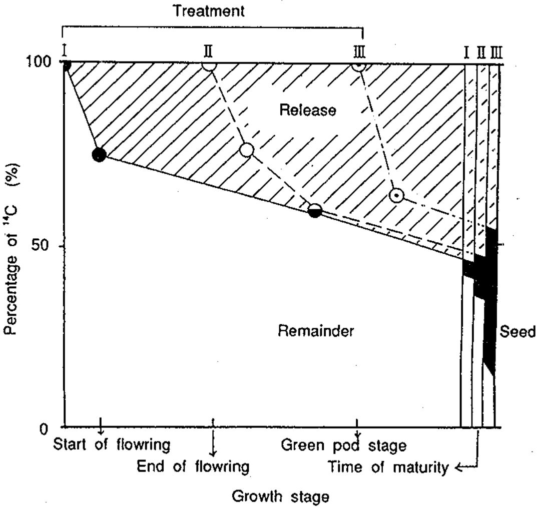

Fig. 45. The fate of ^{14}C assimilated at three stages of growth.

The fate of assimilated ^{14}C at three stages of growth is shown Fig. 45. So far as the pod was made almost entirely in shape, of total ^{14}C assimilated, over 50% was released or disappeared and the remainder was translocated mainly to the vegetative organs, especially in stems (Treatment I). While, after this process, the amount of ^{14}C retained which was under 45 or 50 %, seemed to move directly from blades into seeds, especially in Treatment III.

Figure 46 shows the changes in the distribution percentage of dry matter in various organs and those of ^{14}C assimilates throughout the growing process. With regard to the distribution of dry matter, a high percentage was found in stem from the end of flowering to the green pod stage, and thenceforth, it favored the seeds. The ^{14}C distribution percentage was high in stems with plants fed $^{14}CO_2$ of Treatment I, but the distributed ^{14}C concentrated in seeds with those of Treatment III As for the changes in the distribution percentage of ^{14}C assimilates for roots, however, it was approximately the same among plants treated at the three stages.

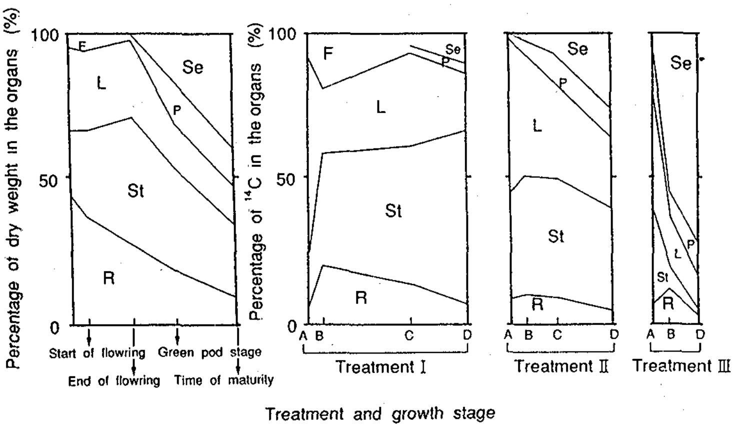

Fig. 46. Changes in distribution percentage of dry matter and ^{14}C assimilates throughout the growing process.
L:Leaf blade, St.:Stem, R:Root,
F:Flower, P:Pod, Se:Seed.
Stages, (A—D) are the same as those in Fig. 43.

DISCUSSION

It has already pointed out that (1) In order to build up the new vegetative organ and simultaneously develop flowers and pods during the flowering to pod setting period, a considerable amount of chemical components which were previously stored in vegetative organs were used. (2) The chemical components in seeds consisted of two parts of mostly assimilated during the seed maturing period and of partially translocated from vegetative organs and pods(126,127,128,129 130,131,133). Accordingly, in order to support the temporary storing in the vegetative organs, translocation and resynthesis in seed components, a large amount of assimilated carbon is supposed to be necessary for these physiological phenomena including the respiration(84,147).

The specific ^{14}C radioactivity of leaf blades and stems was unlike among node orders at each $^{14}CO_2$ feeding time as shown in autoradiograph of Fig. 47. These results reconfirmed the different photosynthetic activity of leaf blades described in Chapter II, Section 1 and 2.

The present experiment showed that a large proportion of ^{14}C was released from plants; 50—55 % of the total ^{14}C with plants fed $^{14}CO_2$ at the start and the end of flowering (Treatment I and II), and 45 % at the seed maturing (Treatment III). A large proportion of the ^{14}C released occurred very rapidly soon after ^{14}C-assimilation whenever was $^{14}CO_2$ fed to plants. The amount of ^{14}C released from plants within a short period of 7 days, was 40—45 % of the total released when plants assimilated at the start and end of flowering (Treatment I and II). In plants treated at the seed maturing, however, it was contrastively over 80 % (Treatment III). With this connection, it has already pointed out that the respiration of pods including inner seeds was considerably high in Chapter II, Section 1. Therefore, the physiological implications of the released or consumption by respiration seemed to vary functional with process of chemical component synthesis in each organ as the growth advanced, especially with seed maturation.

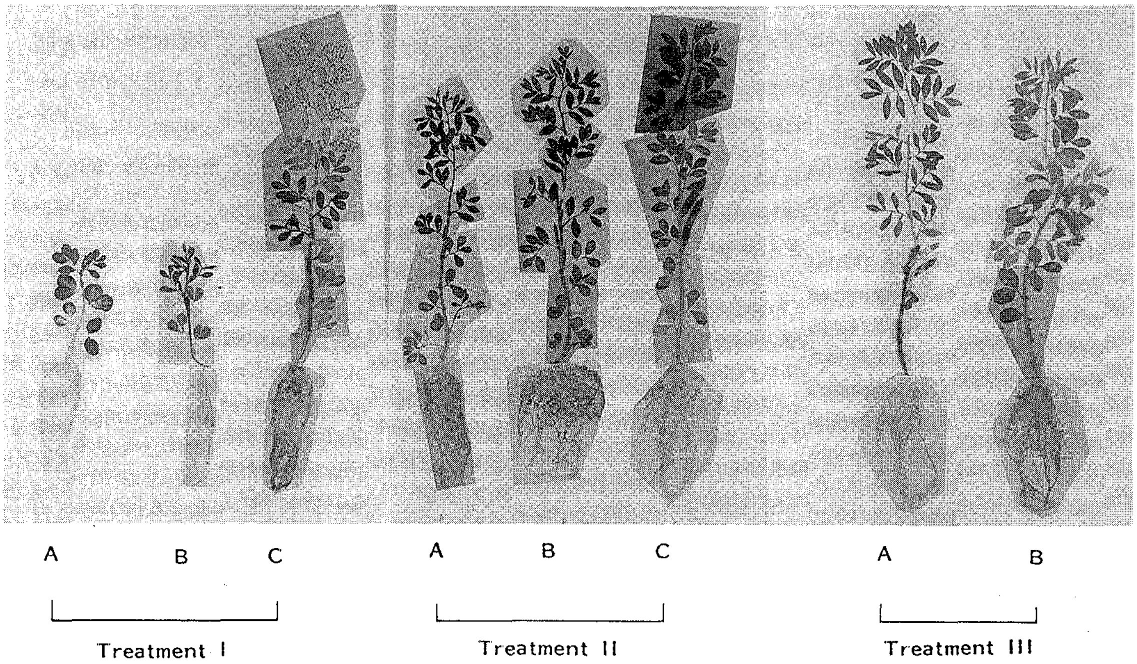

Fig. 47. Autoradiograph: Behavior of ^{14}C in each organs treated at three stages of growth.
Stage,(A−C) are the same as those in Fig. 43

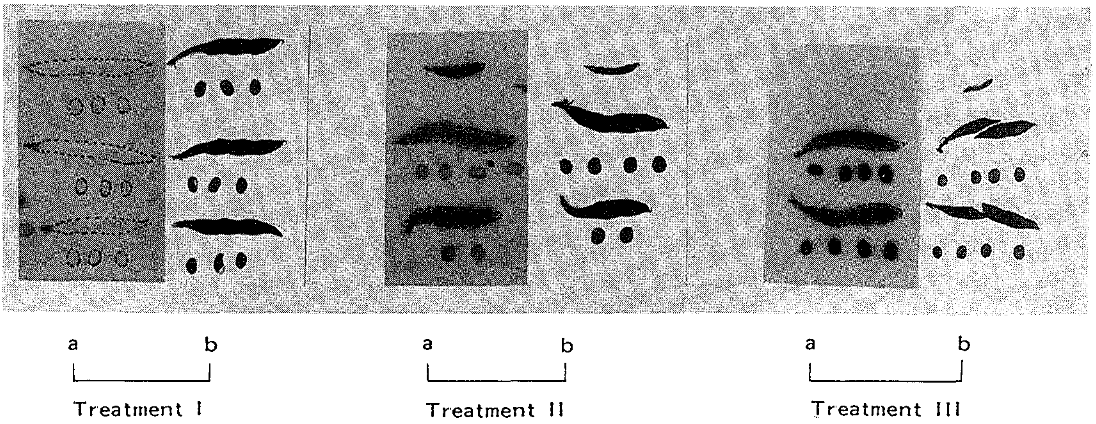

Fig. 48. Autoradiograph: ^{14}C in pods and seeds at the time of maturity.
a: autoradiograph, b: herbarium specimen.

The behavior of the remaining carbon and the translocation of photosynthetic products in plants, are very closely related to the interrelationship between the source and sink at various growing processes. With regard to the sink activity at each $^{14}CO_2$ feeding time, at flowering period (Treatment I) the stem and root were the active sinks, whereas during pod developing period(Treatment II) the root, pod, and later seed were the active sinks. And finally the sink was mainly the seed and root in Treatment III at seed developing period (Fig. 48). Though there are various sinks with different kind and size, and distance from the source organ, the sink activity seems to depend upon the existence of sink despite of whatever the kind may be different among plant species and growth stage (36,37,38,39,55,57,58,139). As for the ^{14}C accumulation into roots, there have had many papers with plants of sweet potato(55), tomato (57,58), rice(84), wheat(115), pea(20), kidney bean (87,134,135), and faba bean(38,39). The leguminous crops, above all, must be continuously supplied with the carbonaceous materials to support nitrogen fixation. So, roots are very important sink throughout the growth, especially the later growing process of seed maturing as shown in this experiment. This fact might be of vital importance to this crop plant. Moreover, high ^{14}C-radioactivity of pods was found soon after the time of $^{14}CO_2$ feeding, indicating that pods had some photosynthetic activity as described in Chapter II, Section 1 and 2.

Thus, ^{14}C-assimilates temporary stored in stems, roots, and later pods, seemed to be retranslocated into seeds accompanying the development of the reproductive organs. Finally, the percentages of ^{14}C retained at the time of maturity in stems plus roots out of the total ^{14}C-assimilates, were 30.4, 18.6, and 2.9 in plants of Treatment I, II, and III, respectively. On the contrary, those translocated in seeds were 5.1, 12.0, and 40.4. The percentages of retranslocated ^{14}C-assimilates from vegetative organs plus pods into seeds were 19.2, 40.3, and 41.1 in Treatment I, II, and III, respectively.

Therefore, it may be reconfirmed that the photosynthates assimilated during the flowering to early stage of pod developing are mainly concerned with the building of vegetative organs, and thenceforth photosynthates contribute mainly toward the seed production including the remobilization of stored assimilates from vegetative organs.

SUMMARY

An analytical study on the behavior and role of ^{14}C-photosynthates by $^{14}CO_2$ feeding at three stages of the start (Treatment I), the end of flowering (Treatment II), and the seed maturing (Treatment III) was conducted. The results obtained are summarized as follows:

(1) The specific 14C radioactivity of leaf blades at the time of $^{14}CO_2$ feeding was superior to other organs and was high in each organ as the growth advanced. The activity of organs generally declined, and the release of ^{14}C, which occurred within 7 days, finally was 55% (Treatment I), 50% (Treatment II), and 45% (Treatment III).

(2) The translocation of ^{14}C photosynthetic products from leaf blades was found mainly in vegetative organs when plants fed $^{14}CO_2$ at the flowering (Treatment I) and in turn in pods and seeds accompanying later $^{14}CO_2$ feeding trials (Treatment II and III), with the exception of constant accumulation in roots.

(3) The retranslocation of temporarily stored ^{14}C-products in stems, roots, and later pods into seeds varied

with the various growth stages: the amounts retranslocated expressed as percentages of the total ^{14}C assimilates were 19, 40, and 41 in plants of Treatment I, II, and III, respectively.

The results of this experiment further substantiated the fact that the photosynthates assimilated during the flowering to pod developing stage are mainly concerned with building of the vegetative organs and the setting of young pods and thenceforth these contributed to the seed production.

CHAPTER III SECTION 2

BEHAVIOR OF ^{14}C-PHOTOSYNTHATES SYNTHESIZED IN FOUR SECTIONS OF THE SHOOT

It has been established that the stems, roots, and later pods played the role of temporary storage organs for the chemical components in seeds, and that the shortage of carbonaceous substances was an important factor for the normal plant growth and seed yield stability of this crop plant. These factors were also found to be closely connected with the photosynthetic and respiratory ability of vegetative and reproductive organs in four sections of the shoot based on flowering and pod bearing habits.

Therefore, the main objectives of this section are to investigate the behavior of photosynthetic carbon assimilated during the flowering to seed maturing stages with leaves in four sections and the relation between source leaves and possible sink organs with special reference to seed formation using $^{14}CO_2$ as a tracer.

MATERIALS AND METHODS

The seeds of cultivar "Sanuki-nagasaya" were sown in nursery bed on November 8 and seedlings were transplanted two plants per pot on December 11. Each pot received 2.9 g ammonium sulfate, 4.8 g calcium superphosphate, and 1.9 g potassium sulfate. Soil moisture was maintained at about 70 % of the field capacity.

Out of the three or four primary stems, the first branch 1a (Fig. 25), was used for this experiment. Labeling treatments of $^{14}CO_2$ were done on each of the four sections which were divided on the flowering and pod bearing habits mentioned in Chapter I, Section 2 and 3.

The middle three compound leaves in each section were labeled with $^{14}CO_2$ by enclosing them in an acrylic rasin chamber which has been described in Fig. 25 of Chapter II, Section 1 for one hour under natural day light conditions. Treatments were carried out at three stages of growth: the flowering stage (Treatment I, 1T), the pod development stage (30 days after the start of flowering, Treatment II, 2T), and the seed maturing stage (50 days, Treatment III, 3T) (Fig. 49—3).

Plants were sampled at the time of $^{14}CO_2$ feeding, seven days after feeding, the green pod stage, and the time of maturity. At the appropriate sampling time, while one plant was killed in boiling water and made into herbarium specimen for autoradiography, the other plants were divided into four sections and separated into the various organs. These organs were oven-dried, powdered, and the ^{14}C activity determined by the method described in Chapter III, Section 1.

RESULTS

Growing Process

At the start of flowering, plant height, number of leaves, and dry weight of vegetative organs were only half of the maximum value. Thereafter, the vegetative growth in 3rd and 4th sections and reproductive

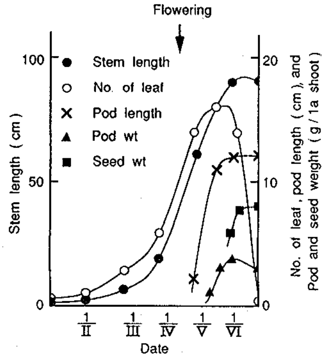

Fig. 49−1. Changes in morphological characteristics of plants used for the analysis.

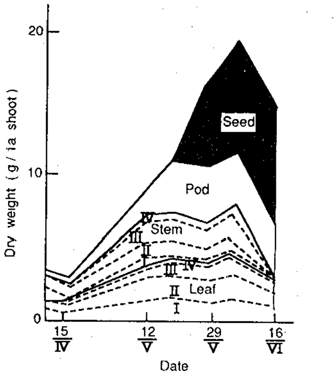

Fig. 49−2. Changes in dry weight of various organs in four sections. Numbers in figure, (I−IV) show the four sections.

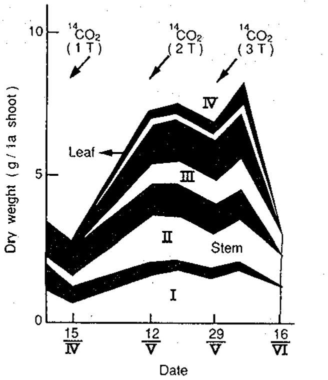

Fig. 49−3. Changes in dry weight of leaves and stem in four sections and $^{14}CO_2$ feeding time. Number in figure, (I−IV) show the four sections.

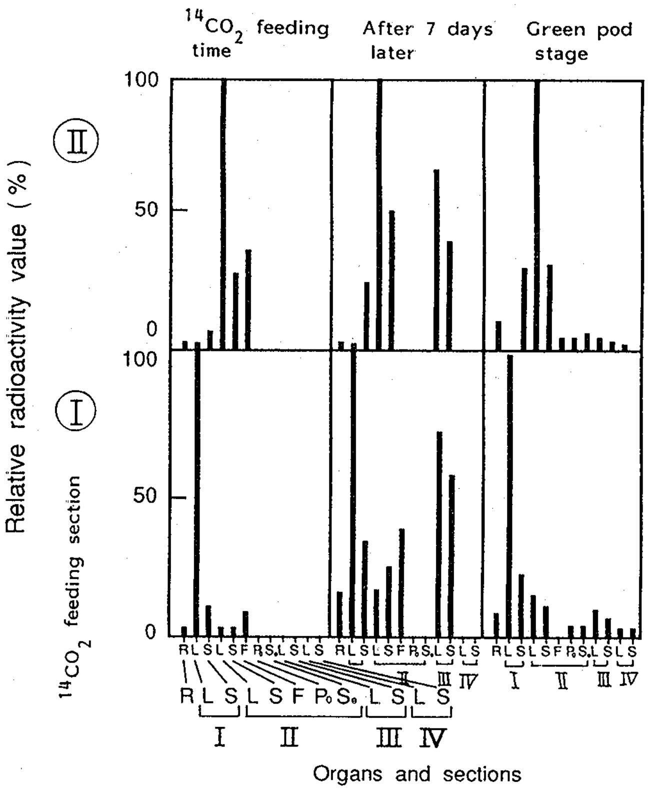

Fig. 50−1. Changes in the specific ^{14}C radioactivity of various organs of four sections and root (Treatmet I, 1T)
Radioactivity values are expressed as the percentage of relative value to 100 % of $^{14}CO_2$ fed section's leaves at each sampling time.
I. II, III, IV: Number of section.
R: Root, L: Leaves, S: Stem,
F: Flower, Po: Pod, Se: Seed.

growth were observed simultaneously for a fairly long time of 30 to 40 days till the green pod stage (Figs 49—1, 49—2, 49—3).

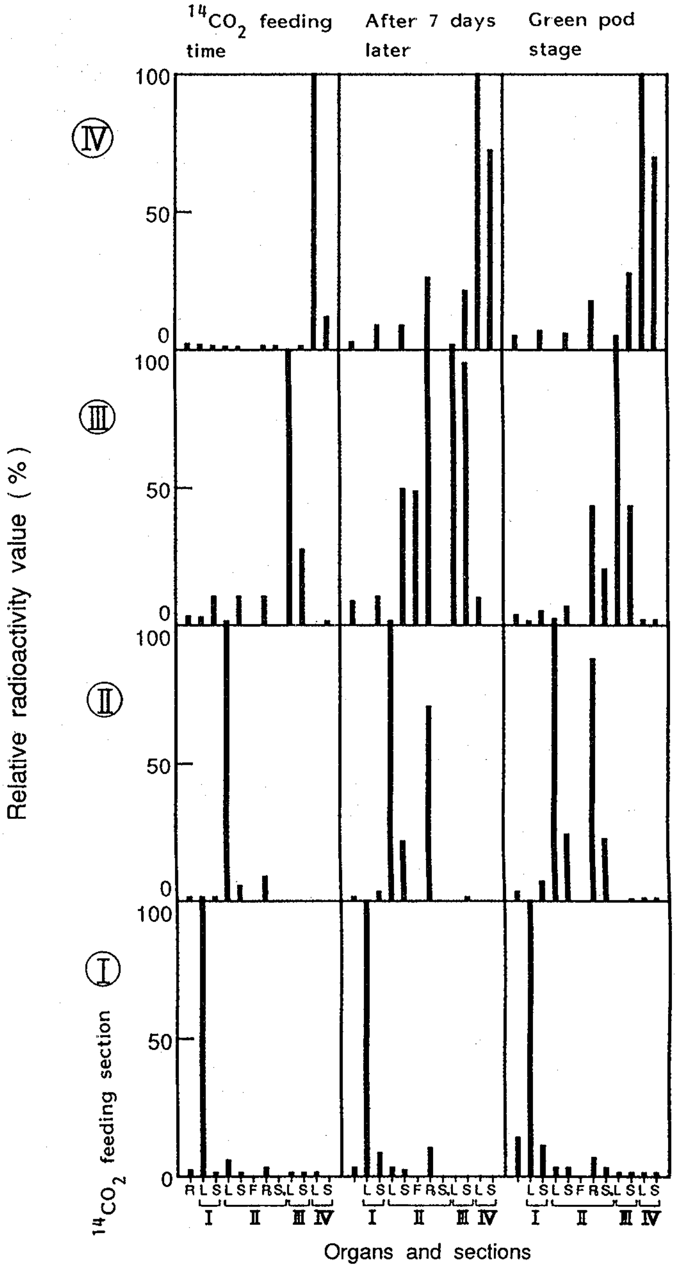

Fig 50—2 Changes in the specific ^{14}C radioactivity of various organs in four sections and root (Treatment II, 2T)
Explanation of figure is the same as those in Fig 50—1

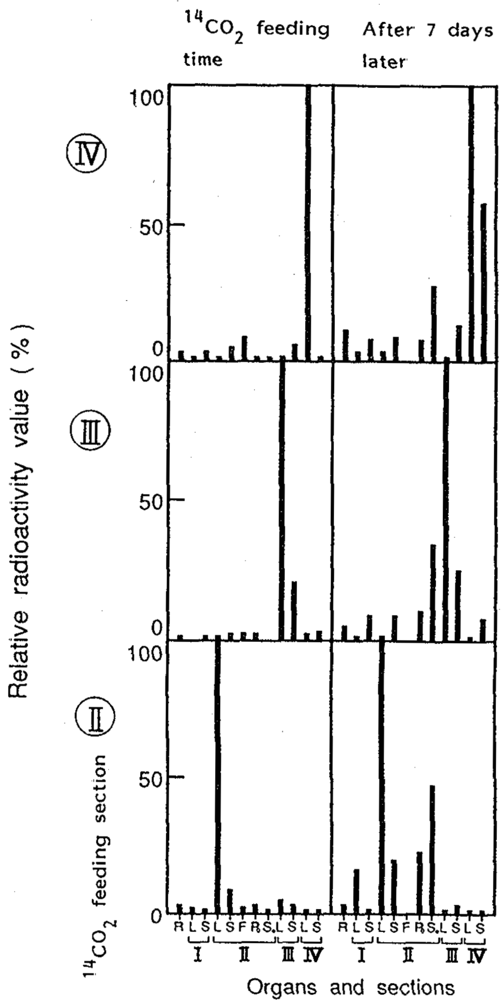

Fig. 50—3. Changes in the specific ^{14}C radioactivity of various organs of four sections and root (Treatment III, 3T)
Explanation of figure is the same as those in Fig. 50—1.

Behavior of ^{14}C Products

Figure 50 shows the changes in the specific ^{14}C radioactivity of various organs in four sections and root. It was expressed as relative value(%) to $^{14}CO_2$ fed section's leaf at each sampling time.

The ^{14}C-photosynthates assimilated by the leaves in the 1st and the 2nd sections at the flowering stage (1T) were translocated to throughout the whole plant of roots and vegetative organs of upper and younger sections, especially to the root. The ^{14}C translocation from the 1st section to developing reproductive organs was relatively low compared with those of leaves of the 2nd section. When the $^{14}CO_2$ was fed at the pod development stage (2T), translocation and retention of ^{14}C-photosynthates were mainly observed in pods and seeds. Radioactivity of pods and seeds were highest at $^{14}CO_2$ fed leaves of the 2nd section and declined in the 3rd, 4th, and 1st sections in that order. The translocation pattern of ^{14}C-photosynthates from fed leaves of different sections were also clearly distinguished; ^{14}C-photosynthates from the leaves of the 1st section was found to be higher in the roots, those of the 2nd section were mainly found in the organs adjacent fed section, those of the 3rd section were present in all vegetative organs, and those of the 4th section were found in the upper new shoots. At the seed maturing stage feeding(3T), ^{14}C activity was observed mainly in the seed, which was highest in the 2nd section, and decreased in the order of the 3rd and 4th sections. However, the labeled carbon of the fed 4th section at this stage was found in the stem and root, especially in the root, is noteworthy

Figure 51 shows the distribution percentage of the amount of ^{14}C at various organs in each section. The direction of translocation of ^{14}C-photosynthates changed from shoot development to pod and seed development as the growth progressed. Thus, though ^{14}C-photosynthates in the seeds at the time of maturity seemed to result from remobilization of stored assimilates of the vegetative organs and pods, the most parts were those synthesized in the 2nd, and the 3rd sections after the end of flowering stage(Table 8).

Table 8. Differences in the contribution of ^{14}C assimilates at each section among different growth stages.

		$^{14}CO_2$ feeding stage		
		1 T	2 T	3 T
Sections	Ⅳ	——	12.0	16.9
	Ⅲ	——	13.7	46.6
	Ⅱ	1.3	33.4	27.7
	Ⅰ	5.8	25.6	——
Sum.		7.1	84.7	91.2

DISCUSSION

Although the material used in this experiment was a typical Japanese cultivar of winter type with a determinate growing habit (69,75), the vegetative and reproductive growth preceded concurrently for a fairly long time(126,127). Therefore, the role of photosynthates synthesized in the leaves at different section of the shoot changed as growth advanced.

In Chapter I, Section 2, it was pointed out that the leaves and stems of the 2nd and 3rd sections played a major role in the development of reproductive organs and final seed yield. The present experiment confirms this phenomenon, as shown in Table 8. The highest percentage of labeled carbon translocated into seeds was observed in the 2nd section of Treatment II and the 3rd section of Treatment III. In Chapter II, Section 1, it was also suggested that the consumption of synthesized carbon through respiration affects the development of vegetative and reproductive organs, seed formation and the composition of chemical components of the seeds. The proportion of ^{14}C consumed was calculated by subtracting the proportion present at sampling from the amounts at feeding time. The amounts consumed were 65.4, 72.3, and 75.8 % for the 3rd and 4th section of Treatment II and the 4th section of Treatment III, respectively. These values were higher than those on other sections. The results seem to suggest that the physiological importance on the release or consumption of synthesized carbon and on the long distance translocation of chemical components between source and sink.

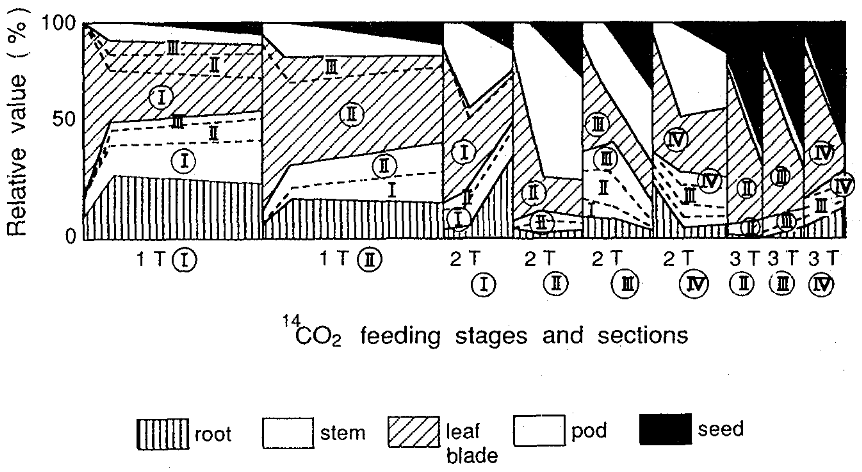

Fig. 51. Distribution percentages of ^{14}C-amount of organs in four sections.
Solid lines show the every organs and dotted lines show the four sections.
(I).(II),(III), and (IV) show $^{14}CO_2$ fed section's organs.

There have been reports on the translocation patterns of ^{14}C photosynthates, in tomato(134), phaseolus bean(135,145), soybean(53,77), and faba bean(12,45,46,47,50,59,60,134). Crompton et al.(12) observed that in faba bean, the developing seeds were strong sink for assimilates during later growing process, though the distribution patterns for assimilates varied widely. Sprent et al.(123), however, demonstrated that there was a weak relation between sink and source. These contrasting results were due to the fact that Sprent et al. used a determinate variety, whereas Crompton et al. used an indeterminate one. The results of this experiment suggest that the high sink activity of reproductive organs of 2nd section directly influenced the translocation from the vegetative organs of adjacent section. The upper leaves on the 4th section played the role of supporting and maintaining the root activity and nitrogen fixation in the later growth stage(105). The results of this experiment confirm the findings of Fritz(21) that the translocation away from a leaf occurs in both upward and downward directions within the same vascular bundle. The autoradiographs as shown in Fig. 52 better explains the behavior of synthesized carbon.

Thus, the role of leaves of the lower section at preanthesis can transmit to the upper section. However, after anthesis the demand for photosynthates of the 2nd section soon reaches the critical status for carbon economy as a whole plant. Thereafter, there is a division of source functions: the leaves of the middle 2nd and 3rd sections, adjacent to the pod, assume the important role of supporting seed development. Those of the upper-most section supported the normal plant growth, root and nodule activity in the later growth stage. These results suggest, therefore, that the determinate growth habit of Japanese cultivars of winter type of faba bean seemed to be physiologically induced.

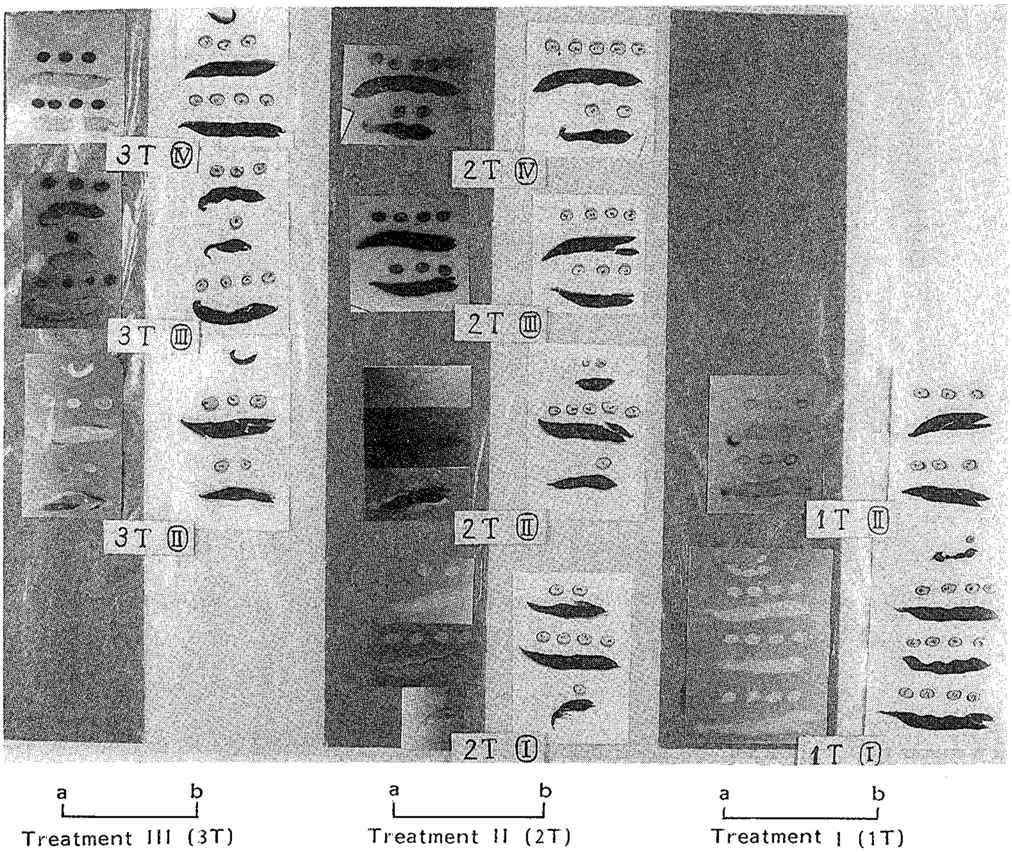

Fig. 52 Autoradiograph: ^{14}C in pods and seeds at the time of maturity.
a: autoradiograph, b: herbarium specimen.
Treatments, (1T,2T,3T) are the same as those in Fig. 49—3
(I), (II), (III), and (IV) show the $^{14}CO_2$ feeding section.

SUMMARY

A study on the behavior and role of ^{14}C-photosynthates from the leaves of four sections based on the flowering and pod bearing habits at flowering (Treatment I), pod development (Treatment II), and seed maturing (Treatment III)stages of growth was conducted. The results obtained are summarized as follows:

(1) The ^{14}C-photosynthates from the leaves of the lst and the 2nd sections were translocated to the root and upper shoot at the flowering stage. While those from leaves of the 1st section supported the roots, those of the 2nd and 3rd sections were related to the pod and seed developments at the pod development stage. After this stage those of the 2nd and 3rd sections were directly translocated into the seed.

(2) The ^{14}C-photosynthates from the leaves of the upper 4th section supported the roots and nitrogen fixation by root nodules, in addition they supported the growth of whole plant at later stages.

From the results, it can be deduced that the role of the photosynthates assimilated in the leaves of the four sections of the shoot differentiates after anthesis into supporting developing pods and seeds, maintaining the physiological status of normal growth including root and nodule activities.

CHAPTER III SECTIN 3

MUTUAL TRANSLOCATION OF ^{14}C-PHOTOSYNTHATES AMONG SHOOTS

This crop plant, which is generally cultivated during the autumn to spring season in warm region of Japan, show no remarkable top growth of main shoot but profusely development of branched shoot in winter (126,127). In spring, this type of faba bean plant has usually dead main shoot and many branched shoots on late maturing varieties and less on early maturing varieties. We sometimes counted over ten shoots per plant, which decrease with increasing plant density(132). With branched shoots in such cases, the low percentage of shoots bearing pods and unstable seed yield seem to due to the shortage of assimilates (62,69,70,75,122,126,127,128,129,130,131,133). Moreover, each shoot seems to be independent from the view point of the source-sink relationship between leaves and reproductive organs.

Therefore, in this section, studies were conducted to obtain the information on the characteristics of the independency of each shoot and the translocation ability of photosynthates among shoots with or without the leaf-source and pod-sink(67).

MATERIALS AND METHODS

The pot trials on the behavior of ^{14}C-photosynthates assimilated at 45 days (Stage I) and 65 days (Stage II) after the start of flowering were carried out using the cultivar "Sanuki-nagasaya". Three shoots of 1a, 1b, and 2a, which branched and developed at the first and the second node on the main shoot were used for this experiment, and other branched shoots were cut off. Each shoot had 20 to 25 leaf blades and/or nodes and some pods in the 2nd section as described in Chapter I, Section 2. The flowering began firstly on 1a shoot, followed on 2a and next on 1b, at two or three days intervals, and this order was similar within the same branch. In this experiment, the pollination was carried out by hand trip-pollinating method on every 2 days at successive nodes. Before $^{14}CO_2$ feeding, the pretreatments were given to remove the leaf-source on 1a shoot for Plot 4 (P_4) and Plot 5 (P_5), and also to remove the pod-sink on 1b and 2a for Plot 3 (P_3) and Plot 5 (P_5) as shown in Fig. 53.

For labeling with ^{14}C, after the covering the pods with small vinyl-film bag, the whole shoot was enclosed in a large vinyl-film bag and exposed to $^{14}CO_2$ for about 20 minutes. Leaves on 1a shoot for Plot 1 (P_1), and those on 1b and 2a shoots for P_2 of non-pretreated plants and for P_3, P_4, and P_5 of pretreated plants were fed with $^{14}CO_2$. Plants were subjected to five plots as shown in Fig. 53. At maturity, each organ, especially pod and seed were sampled, oven-dried, and powdered. The ^{14}C activity was measured by Gas Flow-meter and the value was calculated per weight of unit carbon. With regard to measuring the respiration of pods, it was conducted by the method described in Chapter II, Section 1

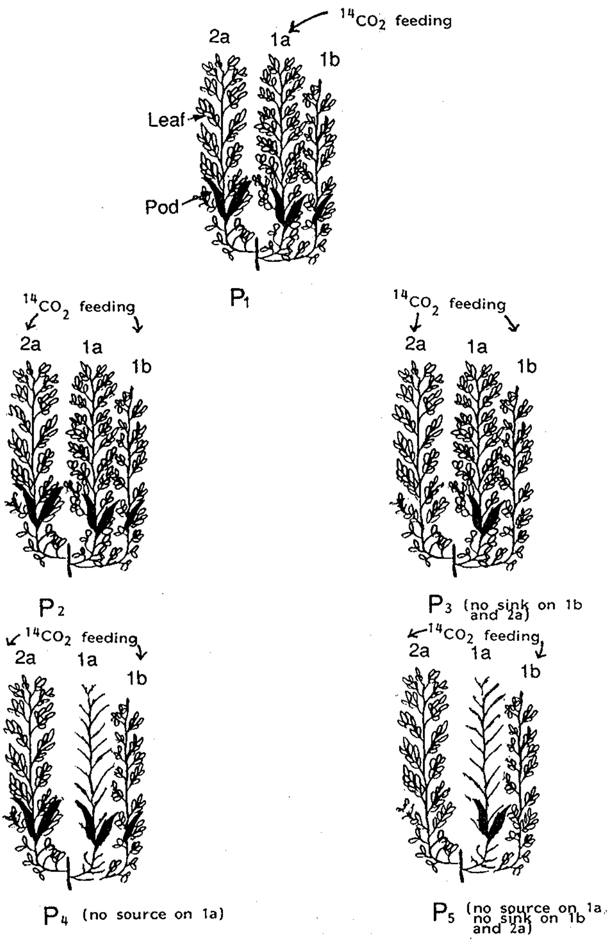

Fig. 53. Experimental design of $^{14}CO_2$ feeding and pretreatments of leaves and/or pods removal.
Numbers of pod: 1a and 2a: 2pods, 1b: 1pod.
P_1:Control, $^{14}CO_2$ fed on 1a, P_2:Control, $^{14}CO_2$ fed on 1b and 2a.
P_3, P_4, P_5: Tretment, $^{14}CO_2$ fed on 1b and 2a.
P_4, P_5: Pretreatment, leaves removal on 1a.
P_3, P_5: Pretreatment,pods, removal on 1b and 2a.

RESULTS

Growing Process

The dry weight of pods and seeds and the 100-seed-weight at maturity are shown in Table 9. Although pod and seed weight of 1a shoot on P_2 plants were generally lower than those of pretreated, total seed weight in P_4 were the highest. As for the filling degree of seed, expressed as a percentage of 100-seed-weight of 1a with non-pretreated P_2, it was similarly low value with P_3, P_4, and P_5 of pretreated at Stage I. However, it became 111.8, 93.5, and 83.6 % with P_3, P_4, and P_5, respectively, at Stage II. The results showed that the presence of leaf-source and sink on the same shoot has a key for the translocation of synthesized matter and finally seed yield. These facts have an very important meanings to the characteristics of shoot having substantially independence but occasionally translocation of the synthesized matter occurred among shoots.

Table 9. Differences in dry weight of pods and seeds, hundred-seed--weight at the time of maturity among treatments.

	Stage	Shoot	Plot			
			P_2	P_3	P_4	P_5
Pod dry wt. (g)	I	1a	4.06	4.54	4.06	3.76
		1b, 2a	6.80	—	7.44	—
	II	1a	5.09	6.63	5.66	4.45
		1b, 2a	7.07	—	5.26	—
Seed dry wt. (g)	I	1a	9.64	10.96	9.11	12.54
		1b, 2a	13.53	—	19.30	—
	II	1a	12.50	13.56	17.43	12.54
		1b, 2a	16.31	—	14.16	—
100 seeds wt (%)*	I	1a	100.0	85.6	88.9	90.0
		1b, 2a	100.7	—	100.5	—
	II	1a	100.0	111.8	93.5	83.6
		1b, 2a	101.0	—	103.0	—

* : 100-seed-weight is expressed as the percentage of relative value to 100 % of P_2 on 1a shoot of Stage I and II.

Behavior of ^{14}C Products

The activity and the amount of ^{14}C in pods and seeds were shown in Figs. 54 and 55. As already mentioned in Chapter I, Section 1, the development of the vegetative organs almost ceased and the pod was the predominated sink at Stage I After 20 days, the sink was completely only seeds at Stage II. As for the translocation of ^{14}C-photosynthates among shoots, however, the sink activity of pods and seeds seemed to be directly linked with the hand trip-pollinated order. In P_1, where the 1a shoot was fed with $^{14}CO_2$, almost all of ^{14}C-photosynthates were distributed to the pods and seeds attached to 1a shoot, and not found in those of shoots of 1b and 2a. However, ^{14}C-photosynthates was slightly distributed in pods and seeds on 1a shoot when $^{14}CO_2$ was fed to leaves of other shoots of 1b and 2a in P_2.

Similar trend was generally found with the sink on 1a shoot in other plants. The ^{14}C activity and the amount were lower in sink of 1a shoot in P_3 of removed sink on other 1b and 2a shoots than in P_5 of removed leaf-source on 1a shoot, and the difference between P_3 and P_5 was high in Stage I treatment The translocating degree of ^{14}C in the sink of 1a shoot on P_2, compared with P_4 of removed leaf-source on 1a shoot, was retarded by the presence of sink of 1a shoot. Moreover, ^{14}C-photosynthates seemed to translocate easier or stronger within the same nodal branched shoot, compared with the translocation ability among shoots of different nodal branched ones.

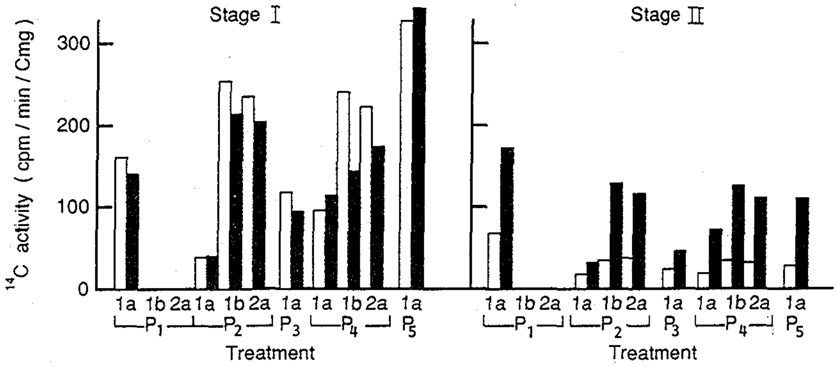

Fig. 54. ^{14}C activity in pods and seeds at the time of maturity.
StageI: $^{14}CO_2$ fed at 45 days after the start of flowering.
StageII: $^{14}CO_2$ fed at 65 days after the start of flowering.
Plots, (P_1-P_5) and shoots, (1a, 1b, and 2a) are the same as those in Fig. 53. ☐ :Pod, ■ :Seed.

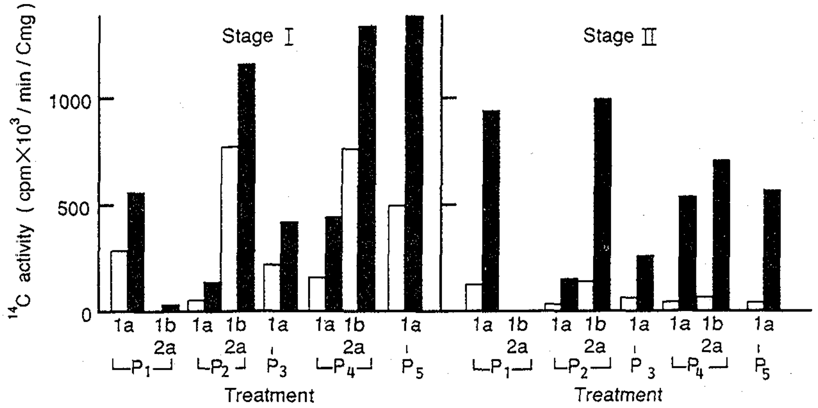

Fig. 55. ^{14}C amount in pods and seeds at the time of maturity.
Stages, (I and II), Plots, (P_1-P_5), and shoots, (1a, 1b, and 2a) are the same as those in Fig 54. ☐ :Pod, ■ :Seed.

DISCUSSION

The results explain the vigorous sink ability of pods and/or seeds and the strong competition among the sink within the same shoot of plant. The establishment of competitive ability seems to depend on the order of hand trip-pollination among pods within the same shoot. By what means does this phenomenon occur? The respiration of pods including seeds on 1a shoot at 50 days after the start of flowering were 12.9, 11.7, and 14.4 % higher with P_3, P_4, and P_5, respectively, than that of P_2. But there were no distinguished differences among the three Plots. Therefore, in this experiment, similar activity of respiration of pod on P_3, P_4, and P_5 seemed to be related to the carbon consumption accompanying the translocation of assimilates from source of other shoot into sink of pods. With regard to this, however, reports (20,62,70) have suggested that though pod surface respiration of leguminous plants seemed to be superior to their photosynthesis, a high activity of CO_2 fixation in inner tissue of pods by utilizing effluxed CO_2 from seeds, so called "recycled CO_2 fixation" phenomenon might resolve it.

Defoliation studies have often provided valuable help towards the interpretation of the general hypothesis of translocation and the mechanisms of relationships between sources and sinks by Hartt et al. on sugar cane(33), Lovell et al. on pea(85,86). With the similar point of view, Kokubun et al.(77) conducted experiments to determine the efforts of debranching on the translocation and utilization of ^{14}C-assimilates during reproductive growth of soybean. As for the reciprocal transfer of radiocarbon in faba bean plant, Ismail et al.(46) suggested that the reciprocal exchange between a lateral branch and its parent shoot is indicative of the complexity of the relationship between source and sink, and also that reciprocal transfer is simultaneously able to occur by the different defoliation trials.

Therefore, though the respiratory rate of pod is accelerated by removing source on the same shoot, the physiological activity of pods-sink is very strong and substantially similar among treatments. And it assures that the pulling activity of sink for the photosynthates have a tendency of 1a>2a>1b, and that this characteristic owe to the order of developing shoots following that of pollinating pods The results show that the characteristic of seed maturing habit having a complete source-sink relationship as a whole shoot is based on the independency of each shoot on Japanese type of this crop plant.

SUMMARY

A study on the translocation behavior of assimilated products from leaves of shoot into sink of reproductive organs was conducted by feeding of $^{14}CO_2$ at 45 and 65 days after the start of flowering. The experiment consisted of five plots using three branched shoots combined with pretreatments of removing leaf-source and pods-sink. The results obtained are summarized as follows:

(1) The major sink was the pods at 45 days after the start of flowering when the development of vegetative organs ceased, and following more 20 days later the sink became completely only seeds. Translocating activity of ^{14}C-products was high on the sink of 1a shoot and followed in the order of 2a and 1b shoots alike with the order of flowering and pod setting among shoots.

(2) The leaves played the main role as a source for the sinks attached on the same shoot and occasionally played supplementary role of mutual translocation of products for the sink of another shoots.

(3) The respiratory rate of sink was approximately similar among the treated plots despite of presence of sources and/or sinks. It seemed that the sink activity for the translocation of products was similar among the sinks within the same and another shoot.

From the results, it may be concluded that each shoot behaves essentially independent on the carbon balance between supply and demand, and makes a source-sink relationship within one shoot, and this is a special characteristic of Japanese variety of winter type.

CONCLUSION

Although the origin of *Vicia faba* is not yet clear, the cultivation might have spread in four directions from its probable center of origin on near East. These are (1) west to the Mediterranean basin, (2) north to Europe and (3) south to north Africa, and (4) east to the Far East including China and Japan. On the way of dissemination, two ecological winter and spring types seem to differentiate : the former is now being cultivated in southern region of China and Japan, and Mediterranean basin, the latter in high altitude and high elevation region of Europe, Africa, and China.

With regard to the flowering and pod bearing habits, pods put concentrically in the middle layer of many shoots with the increase in the number of nodes is being restricted to the plants of winter type compared with the node develops indeterminately and the podding sporadically in whole layer of few shoots of spring type. The yield per unit land area of winter type is generally lower than that of spring type. The yield, however, is not always stable, especially on indeterminate spring type.

It is known that though the growth habit of the two types is considerably different, the characteristics of this crop plant is substantially indeterminate in both types. The reasons which account for the determinate growth habit of Japanese cultivars is questionable. The objective of this study is to examine the growth habit and its relations to the mechanism of dry matter production and yielding process in winter type of Japanese cultivars of this crop plant.

A series of experiments was carried out to obtain the relationship between general growth of individual or plant community and (1) the physiological status of various organs, (2) changes in carbon dioxide exchange, and (3) behavior of photosynthates. The studies have revealed the following informations:

(1) The physiological role of leaves as the assimilatory organ is closely related to the growth habit of plant, and the stem, root, and later pod play the role as a temporary storage organs for the chemical components of seeds. The physiological status or role of various organs transmit in turn from lower to upper section accompanying with the progress of growth and the leaves on the 2nd section which attached concentrically pods together are most important for the normal growing process. Moreover, the potentials of individual plant among plant community is limited by the biological space and the most desirable plant growth is made under a density of 15 plants per square meter.

(2) As for the photosynthesis, the role of leaves in the 1st section participates in the following developing and those in the 2nd, 3rd, and upper 4th section move up stepwisely participating in the later development of vegetative organs and of pods and seeds, and those in the 2nd section play the most important role throughout the growing process. However, the shortage of the substances, especially carbonaceous one, is a critical factor for the growth and seed yielding stability. Besides, the optimum density mentioned above is ascertained from the view point of source-sink balance of carbon economy of plant and composing seed yield.

(3) The behaviors of photosynthates are competitively concerned in building the vegetative organs and in bearing young pods during the flowering to pod developing stage, and thenceforth mainly contributes to

the seed production. However, the role of the photosynthates assimilated in leaves of four sections is different following the development of pods and seeds. It assures that the activity of the 2nd section is very important for seed yield and that of the 4th section in later stage is the most important via supporting the function of roots and root nodules. Moreover, it is found that though the synthesis in leaves and utilization in seeds of the carbonaceous substances generally integrate independently within one shoot, sometimes play a supplementary role through mutual translocation of assimilates among shoots.

From the results of this series of studies, it was concluded that (1) though pod setting is high, pod and seed development are restricted by availability of assimilates, (2) the shoot has an integrated source-sink relationship as a whole, (3) however, the balance between the production of photosynthates and its use, for building of the vegetative organs and development of the reproductive organs, is not always stable, (4) consequently, the shortage of carbonaceous substances might reveal that the determinate growth habit of the Japanese cultivar seemed to be physiologically induced.

Improvement in seed yield and stability of this crop plant in future seems to depend on the changes in some genetical and physiological systems: firstly, a determinate type cultivar is more valuable than indeterminate one because the wasteful building of vegetative organs and damage caused by lodging are avoided; secondly, more research is needed on the reduction in the proportion of initiated abscission of flower and young pod; thirdly, much effort is required for the retardation of the abscission rate of leaves and the retainment of photosynthetic ability and root activity till the later stage of growth.

ACKNOWLEDGMENT

The author wishes to express his sincere gratitude to Dr. Kimio NAKASEKO, Professor of Hokkaido University, for his encouragement throughout this work and critically reading through the manuscript. The author also expresses his gratitude to Dr. Junzaburo NAKA, Emeritus Professor of Kagawa University for his guidance throughout the course of this work. He is greatly indebted to late-Dr. Keisaku TAGUCHI and Dr. Kanji GOTO, both Emeritus Professors of Hokkaido University, Koh-ichro ASANUMA and Akihito KUSUTANI, both Associate Professors of Kagawa University. The author thanks Miss Hana KAWAI, Former vice-President of Keisen Jogakuen Junior College for reading the manuscript.

It is indeed a pleasure for the author to express his gratitude to the students of Crop Science Laboratory, Faculty of Agriculture, Kagawa University for their earnest assistances in the course of these experiments.

LITERATURE CITED

(1) Aihara,S.: Studies on the flower dropping of broad bean, (1) Influences of the light deficiency on the dropping of flower, *Tech. Bull. Miyagi Pref. Agr. Exp. Sta.*, (28), 6−10 (1960).*

(2) ………: Ibid. (2) Influence of the soil moisture on the dropping of flower, *Ibid.*, (29), 1−4 (1962).*

(3) Andreeva,T.F.,Iguen Tkhyu Tkhyok, Vlasova,M.P., Nichiporovich,A.A.: Effect of N nutrition on photosynthetic activity in the leaves of different tiers and on the productivity of *Vicia faba* plants, *Fiziologiya Rastenii*, 19, 265−272 (1972).

(4) Asanuma,K., Naka.J., Tamaki.K.: Effects of topping on growth, the translocation and the accumulation of carbohydrates in corn plants, *Proc. Crop Sci. Japan*, 36, 481−488 (1967).*

(5) Aufhammer,Isabella Gotz, Peter,M.: Yield performance of field beans (*Vicia faba* L.) in relation to interactions between inflorescences at different nodes, *Jour. agric. Sci.*, 108, 479−486 (1987)

(6) ………, Nalborozyk,E., Barbara Geyer, Gotz, Isabella, Mack Carola, Paluch,S. : Interactions between and within inflorescences in relation to the storage capacity of field beans (*Vicia faba*), *Ibid.*, 112, 419−424 (1989).

(7) Blackman,G.E., Black,J.N.: Physiological and ecological studies in the analysis of plant environment, XI. A further assessment of the influence of shading on the growth of different species in the vegetative phase, *Ann. Bot.*, 23, 51−63 (1959)

(8) Bohning,R.H., Burnside,C.A.: The effect of light intensity on rate of apparent photosynthesis in leaves of sun and shade plants, *Amer. Jour. Bot.*, 43, 557−561 (1956).

(9) Bond,D.A., Lawes,D.A., Hawtin,G.C., Saxena,M.C. Stephens,J.H.: Faba bean (*Vicia faba* L.), Eds. Summerfield, R.J., Robierts, E.H., Grain Legume Crops, 199−265 (1986).

(10) Brown,R.H., Cooper,R.B., Blaser,R.H.: Effects of leaf age on efficiency, *Crop Sci.*, 6, 206−209 (1966).

(11) Cornillon,P.: Root temperature, growth and development of plants, *Annls. agron.*, 32, 63−84 (1980).

(12) Crompton,H.J., Lloyd-Jones,C.P., Hill-Cottinham.D.G.: Translocation of labeled assimilates following photosynthesis of $^{14}CO_2$ by the field bean, *Vicia faba*, *Physiol. Plant.*, 51, 189−194 (1981).

(13) Dantuma,G., von Kittlitz,E., Fraven,M., Bond,D.A.: Yield, yield stability and measurements of morphological and physiological characteristics of Faba bean (*Vicia faba* L.) varieties grown in a wide range of environments in western europe, *Z. Pflanzenzucht.*, 90, 85−105 (1983).

(14) ………: Whole-crop physiology and yield components, The Faba Bean, Hebblethwait, P.D., 143−158 (1983).

(15) El-Fouly,M.M. : Flower and pod drop, Eds. Hawtin,G., Webb,C., Faba Bean Improvement, 177−184 (1982).

(16) FAO : FAO Production yearbook, 43, 145−159 (1989).

(17) Fasheum,A., Dennett.M.D.: Interception of radiation and growth efficiency in field beans (*Vicia faba* L.), *Agric. Meteoro.*, 26, 221−229 (1982).

(18) Fawzi,A.L., Iskandar,A.Z., Gouda,A.A.E.: Effectiveness of stripping and topping on yield of maize, *Agric. Res. Rev., Cairo*, **41**, 76—83 (1963).

(19) Finch-Savage,W.E., Elston,J.: The death of leaves in crops of field beans, *Ann. Appl. Biol.*, **85**, 463—465 (1977).

(20) Flinn,A.M., Pate,J.S.: A quantitative study of carbon transfer from pod and subtending leaf to the ripening seeds of the field pea (*Pisum arvense* L.), *Jour. exp. Bot.*, **21**, 71—82 (1970).

(21) Fritz,E.: Microautoradiographic investigations on directional translocation in the phloem of *Vicia faba*, *Planta*, **112**, 169—179 (1973).

(22) Fujihara,T., Ohshima,M.: The feed value on ensiled fibrous residue left after the extraction of broad bean (*Vicia faba* L.) leaf protein in sheep, *J. Japan. Glassl. Sci.*, **28**, 209—216 (1982).

(23) Fujii,H., Konno,Y., Abe,Y., Onuma,T., Aragaki,K. : Accumulation of nitrogen and carbohydrates in each organ of high yield soybeans at successive stage of growth, *Jour. Sci. Soil Manure, Japan*, **58**, 316—322 (1987).*

(24) Fujita,T.: Studies on the root nodules of the broad bean, *Vicia faba*, *Proc. Crop Sci. Soc. Japan*, **20**, 106—108 (1951).*

(25) Fukuyama,T., Sato,T., Kawai,M. : Studies on dry matter production of broad bean, 1 Photosynthesis and respiration of green broad bean, *Report of Shikoku Branch, Crop Sci. Soc. Japan*, (14), 25—29 (1978).*

(26) ………,………,………: Ibid., Effects of seeding time on the growth and yield, *Ibid.*, (15), 29—35 (1979).*

(27) Furutani,Y., Kukii,M.: On the fruiting habits of soybeans, II. The effects of defoliation at the different stages at the pod and seed development, *Kyushu Agric. Res.*, (8), 51—52 (1951).*

(28) ………,………: Ibid. IV. Effects of partial defoliation and solid planting on pod development, *Ibid.*, (9), 47—48 (1952).*

(29) Gates,P., Smith,M.L., Boulter,D.: Reproductive physiology of *Vicia faba* L., The Faba Bean, Ed. Hebbelthwait, P.D., 133—142 (1983).

(30) Gondo,S.: Studies on the fruit age of broad bean, *Kyushu Agric. Res.*, (6), 57—58 (1950).*

(31) Grover,Anil, Koundal,K.P., Sinha,S.K.: Senescence of attached leaves: Regulation by developing pods, *Physiol. Plant.*, **63**, 87—92 (1985).

(32) Hanelt,P.: Zur geschite des anbaues von *Vicia faba* L. und ihrer Verschiedenen Formen, *Die Kulturpflanze.*, **20**, 209—223 (1972).

(33) Hartt,C.E., Kortshak,H.P., Burr,G.O.: Effects of defoliation, deradication and darkening the blade upon translocation of ^{14}C in sugar cane, *Plant Physiol.*, **39**, 15—22 (1964).

(34) Hodgson,G.L., Blackman,G.E.: An analysis of the influence of plant density on the growth of *Vicia faba*, I. The influence of density on the pattern of development, *Jour. exp. Bot.*, **7**, 147—165 (1956).

(35) ………,………: Ibid. II. The significance of competition for light in relation to plant development at different densities, *Jour. exp. Bot.*, **8**, 195—219 (1957).

(36) HOZYO,Y., KOBAYASHI,H., ODA, K.: Studies on the stiffness of culms in barley plants (*Hordeum sativum* JESSEN), II. Physiological studies on the stiffness of culms by ^{14}C tracer method (1), *Proc. Crop Sci. Soc. Japan*, 34, 171—180 (1965).*

(37) ………,………: Tracer studies on the behavior of photosynthetic products during the grain ripening stage in six-rowed barley plant (*Hordeum sativum* JESSEN), *Bull. Nat. Inst. Agr. Sci. Japan*, D20, 35—77 (1969).*

(38) HUMPHRIES,E.C.: Dependence of net assimilation rate on root growth of isolated leaves, *Ann. Bot.*, 27, 175—183 (1963).

(39) ………, THORNE,G.N.: The effect of root formation on photosynthesis of detached leaves, *Ibid.*, 28, 391—400 (1964).

(40) ICARDA: Determinate faba bean, *Ann. Rep.* 1987, 32—33 (1987).

(41) IDLE,D.B: Studies in extension growth, II. The light-growth responses of *Vicia faba* L., *Jour. exp. Bot.*, 8, 127—138 (1957).

(42) IINUMA,J.: Arid zone farming and humid zone farming: a historical and geographical study, *Jour. Humanistic Sci.*, 27, 1—54 (1955).*

(43) INAKO, Y., HAMADA.K., FUJIKURA,T.: Fruiting habit of "Issun" broad bean (I) Effect of date of planting on the fruiting habit, *Jour, Japan. Soc. Hort. Sci.*, 26, 215—222 (1957).*

(44) ………, SAKAI,T.: On the fruiting habit of "Issun" broad bean (part 3), I. Relation between the number of young pods and weight of harvested pods, II. Differences of the number of leaves and their located places on the fruiting habit, *Bull. Chiba-ken Agric. Exp. Sta.*, (6), 133—144 (1965).*

(45) ISMAIL,A.M.S., SAGAR,G.R.: The influence of leaf age, leaf position and sinks on the rate of export and partition of ^{14}C at different stages of development following assimilation of $^{14}CO_2$ by a single leaf of *Vicia faba* L., *Jour. Hort. Sci.*, 56, 55—63 (1981).

(46) ………,………: The reciprocal transfer of radio carbon between a lateral branch and its parent shoot under normal and stress conditions in plants of *Vicia faba* L., *Ibid.* 56, 155—159 (1981).

(47) ………: The movement of ^{14}C-labeled products from source leaves during the growth and development of broad bean, *Exp. Agric.*, 20, 311—318 (1984).

(48) IWATA,T., OGATA,K.: Time-temperature tolerance for keeping quality of fresh fruits and vegetables I. Differences of time-temperature tolerance among strawberries, peas, broadbeans, asparagus, and cherries, *Jour. Japan. Soc. Hort. Sci.*, 40, 434—443 (1971).*

(49) IYAMA,J., MURATA,Y., HOMMA,T.: Studies on the photosynthesis of forage crops, III. Influence of the different temperature levels on diurnal changes in the photosynthesis of forage crops under constant conditions, *Proc. Crop Sci. Soc. Japan*, 33, 25—28 (1964).*

(50) JAQWERY,R., KELLER,E.R.: Beeinflussung des Fruchtansatzes bei der Ackerbone (*Vicia faba* L.) durch die Verteilung der Assimilate, *Angew. Botanik*, 52, 262—276 (1978)

(51) JING HUANZIAN : A survey of the cropping systems of Faba bean (*Vicia faba*) in China, *FABIS*, (4), 9—10 (1982).

(52) KANEMASU,E.T., HIEBSH, C.K.: Net carbon dioxide exchange of wheat, sorghum, and soybean, *Can.*

Jour. Bot., **53**, 382—389 (1975).

(53) Karen,E. Koch, Larry,E. Schraper: ^{14}C-photosynthates partitioning and translocation in soybeans during reproductive development, *Plant Physiol.*, **75**, 1040—1043 (1984).

(54) Kasanaga,H., Monsi,M.: On the light-transmission of leaves, and its meaning for the production of matter in plant communities, *Jap. Jour. Bot.*, **14**, 304—324 (1954).

(55) Kato,S., Hozyo,Y.: Translocation of ^{14}C-photosynthates in several growth stages of the grafts between improved variety and wild type plants in *Ipomoea*, *Bull. Nat. Inst. Agr. Sci. Japan*, D(25), 31—58 (1974).*

(56) Kawamura,S., Suzuki,H., Matsumoto,T.: The relation of maturity to the composition of broad bean seeds, II On the carbohydrates, *Tech. Bull. Kagawa Agric. Coll.*, **7**, 81—86 (1955).

(57) Khan,A., Sagar,G.R.: Alteration of the pattern of distribution of photosynthetic products in the tomato by manipulation of the plant, *Ann. Bot.*, **33**, 753—762 (1969).

(58) ··········,··········: Changing patterns of distribution of the products of photosynthesis in the tomato plant with respect to time and to the age of a leaf, *Ibid.*, **33**, 763—769 (1969).

(59) Kipps,A.E., Boulter,D.: Carbon transfer from the node leaf to the fruit of *Vicia faba* L., *New Phytol.*, **72**, 1292—1297 (1973).

(60) ··········,··········: Origin of the amino acids in pods and seeds of *Vicia faba* L., *New Phytol.*, **73**, 675—684 (1974).

(61) Kittock,D.L., Willima,J.H.: Effect of leaf removal at four stages of growth on yield of castorbeans, *Agron. Jour.*, **59**, 489—490 (1967).

(62) Kogure,K., Otoi,T., Naka,J.: Physiological studies of the growing process of broad bean plants, X. Effects of plant density on carbon dioxide exchange of leaves and pods, *Tech. Bull. Fac. Agric., Kagawa Univ.*, **28**, 1—9 (1977).

(63) ··········, Asanuma,K., Naka,J. : Ibid., XI. Effects of amounts of fertilizer, especially P application on the growth and seed production, *Ibid.*, **29**, 1—9 (1977).

(64) ··········, Naka,J., Asanuma,K.: Behavior of ^{14}C photosynthetic products during the reproductive growth in broad bean plant, *Ibid.*, **30**, 1—8 (1978)

(65) ··········: Broadbeans in Japan: Origin and development, *FABIS*, (1), 11—14 (1979).

(66) ··········: Faba beans in Japan, a history of research, *Ibid.*, (2), 12—13 (1980).

(67) ··········: Transport of ^{14}C photosynthate in faba bean branches with or without pods, *Ibid.*, (3), 31—32 (1981).

(68) ··········, Naka,J. Asanuma,K.: Effects of after-ripening practices on the seed yield and quality of broad bean (*Vicia faba* L.), *Tech. Bull. Fac. Agric., Kagawa Univ.*, **36**, 85—93 (1985).*

(69) ··········: Ecophysiological analysis on mechanisms of seed production of faba beans differentiated in different regions of the world, *Poster Abstr. 1986 International Food Legume Research Conference*, 32 (1986).

(70) ··········, Yoshihara,S., Wada,H., Naka,J.: 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, *Tech. Bull. Fac. Agric., Kagawa Univ.*, 37, 85−96 (1986).

(71) ………, Ohshima,M.: Studies on the fractionation and utilization of structural composition of green crops, Ⅰ. On the effects of different dressing conditions of nitrogen for faba bean plants, *Ibid.*, 43, 1−10 (1991).*

(72) ………,………: Ibid. Ⅱ. On the effects of amount of fertilizer for faba bean plants, *Ibid.*, 43, 97−109 (1991).*

(73) ………, Asanuma,K., Kusutani,A.: Photosynthesis of different node order on the indeterminate and determinate types of faba bean plants, *Poster Abstr. 2nd International Food Legume Research Conference*, 45 (1992).

(74) ………,………,………: Mobility performance of chemical components on the indeterminate and determinate types of Faba bean plants, *Proc. 1st European Conference on Grain Legumes*, 233−234 (1992).

(75) ………: Difference of seed productive mechanism between the varieties of Japanese and north European types of faba bean ── On the autumn and spring sowing with small seed varieties ── *Tech. Bull. Fac. Agric., Kagawa Univ.*, 44, 1−9 (1992).*

(76) Koh,S., Kumura,A.: Studies on matter production in wheat plant, Ⅰ. Diurnal changes in carbon dioxide exchange of wheat plant under field conditions, *Proc. Crop Sci. Soc. Japan*, 42, 227−235 (1973).*

(77) Kokubun,M., Asahi,Y.,: Distribution and utilization of ^{14}C-labeled assimilate in debranched soybeans, *Japa. Jour. Crop Sci.*, 54, 353−358 (1985).

(78) Kouta,S., Inoue,H.: Effects of defoliation at the last stage in soybean on yield and chemical compounds, *Sci. Rep. Miyagi Agric. Coll.*, (5), 1−5 (1958).*

(79) Kumura,A., Naniwa,I.: Studies on dry matter production of soybean plant, Ⅰ. Ontogenic changes in photosynthetic and respiratory capacity of soybean plant and its parts, *Proc. Crop Sci. Soc. Japan*, 33, 467−472 (1965).*

(80) ………: Studies on dry matter production in soybean plant Ⅴ. Photosynthetic system of plant population, *Proc. Crop Sci. Soc. Japan*, 38, 74−90 (1969).*

(81) Kuzunetsov,V.S., Benbin,S.I.: Agricultural basis of topping in fodder beans, *Izv. timiryazev. se'. −khoz. Akad.*, (1), 100−109 (1965).

(82) Lang Li-Juan : A summary on production of Faba bean in China, *FABIS*, (21), 3−6 (1988)

(83) Lehman,W.E., Lambert,J.W.: Effects of spacing of soybean plants between and within rows on yield and its components, *Agron. Jour.*, 52, 84−86 (1960).

(84) Lian,S., Tanaka,A.: Behavior of photosynthetic products associated with growth and grain production in the rice plant, *Plant and Soil*, 26, 333−347 (1967).

(85) Lovell,P.H.: Translocation of photosynthates in tall and dwarf varieties of pea, *Pisum sativum*, *Physiol. Plant.*, 25, 382−385 (1971).

(86) ………, Oo,H.T., Sagar,G.R.: An investigation into the rate and control of assimilate movement from leaves in *Pisum sativum*, *Jour. exp. Bot.*, 23, 255−266 (1972).

(87) Lucas, E.O., Mlcourn,G.M., Whitford,P.N.: The tarnslocation of ^{14}C photosynthate from leave and pods in *Phaseolus vulgaris*, *Ann. Appl. Biol.*, 83, 285—290 (1976).

(88) Meda, K.,: Pulse caltivation in India —its history and present status, *Res. Rep., Kochi Univ.*, 26, (*Agric, Sci.*, No.12) 105—123 (1977).*

(89) Mcalister, D.F., Krover,O.A.: Response of soybeans to leaf and pod rremoval, *Agron. Jour.*, 50, 674—677 (1958).

(90) McEwen,J.: Effects of defoliating different zones on the plant in field beans (*Vicia fava* L.), *Jour. Agric. Sci.*, 78, 487—490 (1970).

(91) Mohamed,M. El-Fouly: Flower and pod drop, Faba Bean Improvement, Ed. Hawtin, G., Webb, C., 177—184 (1982).

(92) Monsi,M., Saeki,T.: Über den Lichifaktor in den Pflanzengesellshaften und seine Bedeutung fur die Stoffproduktion, *Jap. Jour. Bot.*, 14, 22—52 (1953).

(93) Moriya N., Morimoto,H., Kurata,Y.: Studies on the dual utilization of crops as foods and feeds, V. Broad bean, *Bull. Nat. Inst. Agric. Sci. Japan*, D, (7), 159—163 (1953).*

(94) Murata,Y.: Studies on the photosynthesis of rice plants and its culture significance, *Ibid.*, (9), 1—169 (1961).*

(95) ………, Iyama,J.: Studies on the photosynthesis of forage crops, Ⅱ. Influence of air-temperature upon the photosynthesis of some forage and grain crops, *Proc. Crop Sci. Soc. Japan*, 31, 315—322 (1963).

(96) Muntz,K., Shalldach,I., Mantevffel,R.: The function of the pod for protein storage in seeds of *Vicia faba* L., 4. Seed-dependent reactivation of stored starch from the pods, *Biochem. Physiol. Pflanzen*, 170, 465—477 (1976).

(97) El-Nadi,A.H.: Water relations of beans, Ⅱ. Effects of defferential irrigation on yield and size of broad beans, *Expl. Agric.*, 6, 107—111 (1970).

(98) Nagase,Y., Takemura,S.: Studies on the relationship between the change of growing season and irrigation in upland crops, Ⅱ. The relationships among planting time, plant population and irrigation in soybean culture, *Proc. Crop Sci. Soc. Japan*, 34, 127—132 (1965).*

(99) Naka,J.: Variations of chlorophyll content, transpiration, and respiration of growing process of broad bean plants, *Proc. Meeting Shikoku Branch of Japanese Crop Science Soc.*, (6), 52—53 (1953).*

(100) ………, Tamaki,K. : Physiological and ecological studies on potato plants, Ⅶ. On the physiological role of the stalk during the growing period, *Tech. Bull. Kagawa Agric. Coll.*, 7, 225—230 (1956).*

(101) ………: Changes of osmotic pressure value in various organs of broad bean plants, *Proc. Meeting Shikoku Branch of Japanese Crop Science Soc.*, (8—9), 21—25 (1958).*

(102) Nishimura,M., Nishio,S.: Planting density as affected by the amount of nitrogenous fertilizer application in the culture of Issun Soramame (*Vicia faba*), *Chugoku Agric. Res.*, (36), 62—63 (1967).*

(103) Ojima,M., Fukui.J, Watanabe,I.: Studies of the seed production of soybean, Ⅱ. Effect of three major nutrient elements supply and leaf age on the photosynthetic activity and diurnal changes in

photosynthesis of soybean under constant temperature and light intensity, *Proc. Crop Sci. Soc. Japan*, 33, 437−442 (1965).*

(104) OSAKI,M., HANDA,T., TANAKA,A.: Behavior of carbon- and nitrogen-compounds during ripening in soybean, *Japn. J. Siol. Sci. Plant Nur.*, 59, 190−196 (1988).*

(105) PATE,J.S., ATKINS,C.A., PEOPLES,M.B., HERRIDGE,D.F.: Partitioning of carbon and nitrogen in the nodulated grain legume: principles, process and regulation, Ed. SUMMERFILD, R.J., World Crops: Cool Season Food Legumes, 751−765 (1988).

(106) PEARSON,C.J.: Daily changes in carbon-dioxide exchange and photosynthate translocation of leaves of *Vicia faba*, *Planta*, 119, 59−70 (1974).

(107) PEAT,W.E.: Reproductive losses in the faba bean, *Outlook on Agriculture*, Ⅱ (4), 179−184 (1982).

(108) ··········: Developmental physiology, The Faba Bean, Ed. HEBBELTHWAIT, P.D., 103−132 (1983).

(109) PICARD,J., SIGWALT,C.: Relationship between plant density and grain yield in field beans (*V. faba*), *Ann. Amelior. Pl.*, 10, 169−175 (1960).

(110) PILBEAM,C.J., HEBBELTHWAITE,P.D., RICKETTS,H.E.: The response of determinate and semi-determinate faba bean varieties to different sowing dates in the spring, *Ann. appl. Biol.*, 114, 377−390 (1989).

(111) ··········,··········, CLARK,A.S.: Effect of different inter-row spacings on faba beans of different form, *Field Crops Res.*, 21, 203−214 (1989).

(112) PLITMAN,U.: Biosystematical study in the annual species of *Vicia* in the Middle East, *Ph. D. Thesis*, *Hebrew Univ.*, 1−31 (1967).

(113) POULAIN,D., KELLER,S., LE GUEN,J., BERTHLEM,P.: Influence of climatic factors on phenology of faba bean (*Vicia faba* L.), *Agric. Fores. Meteoro.*, 45, 195−214 (1989).

(114) PRINE,G.M.: Studies on removal of leaves from Florida 200 corn, *Proc. Soil Crop Sci. Soc. Fla.*, 22, 220−227 (1962).

(115) RAWSON,H.M., HOFSTRA,G.: Translocation and remobilization of ^{14}C assimilated at different stages by each leaf of wheat plant, *Aust. Jour. biol. Sci.*, 22, 321−331 (1969).

(116) RIEPMA WZN,P.: Spacing of broad beans grown for seed, *Meded. 5 Proefsts. Akker Weidebouw*, (12), (1957).

(117) ROSS,M.A., HARPER,J.L.: Occupation of biological space during seedling establishment, *Jour. Ecol.*, 60, 77−88 (1972).

(118) SAEKI,T.: Variation of photosynthetic activity with aging of leaves and total photosynthesis in plant community, *Bot. Mag. Tokyo*, 72, 404−408 (1959).

(119) SAXENA,M.C., HAWTIN,G.C.: Faba beans in China, *FABIS*, (9), 14−20 (1984)

(120) SCHRODER,P.: Einfluss von Temperatur und Lichtintensitat auf das Wachstum von Ackerbohnensorten (*Vicia faba* L.), *Z. Acker-und Pflanzenbau*, 153, 136−147 (1984).

(121) SHIMIZU,T., TSUNO,Y.: Studies on yield forecast in main crops, Ⅱ Photosynthesis of wheat and naked barley under field conditions, *Proc. Crop Sci. Soc. Japan*, 26, 100−102 (1957).*

(122) SOPER,M.H.R.: Field beans in Great Britain, *Field Crop Abstr.*, 9, 65−70 (1956).

(123) SPRENT,J.I., BRAFORD,A.M.: Nitrogen fixation in the field beans (*Vicia faba*) as affected by

population density, shading and its relationship with soil moisture, *Jour. Agric. Sci.*, 88, 303−310 (1977).

(124) Stoy,V.: The translocation of ^{14}C-labeled photosynthetic products from the leaf to the ear in wheat, *Physiol. Plant.*, 16, 851−866 (1963).

(125) Sugiyama,T., Nishi,S., Kato,T.: Fruiting habit of broad bean, *Jour. Japan. Soc. Hort. Sci.*, 18, 138−149 (1949).*

(126) Tamaki,K., Naka,J.: Physiological studies of the growing process of broad bean plants Ⅰ. On the variations of chemical components in various organs of the tops during the growing period, *Tech. Bull. Fac. Agr. Kagawa Univ.*, 11, 13−18 (1959).*

(127) ………,………: Ibid., Ⅱ. On the relations between the variations of chemical components in the tops and roots during the growing period, *Proc. Crop Sci. Soc. Japan*, 27, 97−98 (1958).*

(128) ………,………: Ibid., Ⅲ. Effects of soil moisture on the growth and the variations of chemical components in the various organs, *Tech. Bull. Fac. Agr. Kagawa Univ.*, 22, 73−82 (1971).

(129) ………,………: Ibid., Ⅳ. Effects of N, P, and K nutrient element on the growth and the chemical components in the various organs, *Ibid.*, 23, 2−10 (1971).

(130) ………,………: Ibid., Ⅴ. Effects of shading on the growth and the chemical components in the various organs, *Ibid.*, 23, 157−166 (1972).

(131) ………,………: Asanuma,K. : Ibid., Ⅵ. Effects of partial leaf removal in the flowering and maturing stages on the growth and the variations of chemical components, *Ibid.*, 24, 1−9 (1972).

(132) ………, Asanuma,K., Naka,J.: Ibid., Ⅶ. Effects of plant density on the growth and the seed production, *Ibid.*, 25, 1−11 (1973).

(133) ………, Naka,J., Asanuma,K.: Ibid., Ⅷ. Effects of the length of light duration on the growth and the chemical components, *Ibid.*, 25, 157−170 (1974).

(134) Tanaka.A, Fujita,K.: Studies on the fruit production of tomato plants on the basis of the source-sink theory (Part 2) Translocation of ^{14}C assimilated by the leaves at various positions, *Jour. Sci. Soil Manure, Japan*, 43, 77−80 (1972).*

(135) ………,………: Nutrio-physiological studies on the field bean (*Phaseolus vulgaris* L.) (Part 1) Translocation of photosynthates in connection with source-sink relationship, *Jour. Sci. Soil Manure Japan*, 45, 157−166 (1975).*

(136) Tanaka,T.N.: Studies on the growth of root systems in leguminous plants, Ⅶ. The growth of adventitious roots from the epicotyl of winter legumes, *Proc. Crop Sci. Soc. Japan* 40, 63−68 (1971).*

(137) Tatemichi,Y.: Studies on the photosynthesis of tobacco plants, 1. An apparatus for the measurement of photosynthesis in plant and changes of photosynthesis and respiration in the course of development, *Proc. Crop Sci. Soc. Japan*, 37, 129−134 (1968).*

(138) Thomas,M.D., Hill,C.R.: The continuous measurement of photosynthesis, respiration, and translocation of alfalfa and wheat growing under field conditions, *Plant Physiol.*, 12, 283−307 (1937).

(139) THOMPSON,R., TAYLOR,H.: Prospects for *Vicia faba* L. in northern Europe, *Outlook on Agriculture* II (3), 127—133 (1982).

(140) THROWER,S.L.: Translocation of labeled assimilates in the soybean, II. The pattern of translocation in intact and defoliated plants, *Aust. Jour. biol. Sci.*, **15**, 629—649 (1962).

(141) TOGARI,Y., KATO,Y., EBATA,M.: Studies on the yield analysis of soybean, I Changes in principal chemical constituents of the soybean plant in relation to its growth, *Proc. Crop Sci. Soc. Japan*, **24**, 103—107 (1955).*

(142) TSUNO,Y., FUJISE,K.: Studies on the dry matter production of sweet potato, *Bull. Nat. Inst. Agr. Sci.*, D (13), 1—131 (1965).*

(143) TUZIMURA,K.: Studies on the nitrogen fixation of leguminous plants with special reference to the stage of growth, *Jour. Sci. Soil Manure Japan*, **21**, 181—184 (1951).*

(144) WADA,Y., WATANABE,S., KURODA,S.: Changes in the photosynthetic activities and chlorophyll contents of growing tobacco leaves, *Bot. Mag. Tokyo*, **80**, 123—129 (1967) *

(145) WATERS,L.Jr., PATRICK,J., BREEN, HARRY,J. MACK, PETER,H., Graham: Translocation of ^{14}C-photosynthate, carbohydrate content, and nitrogen fixation in *Phaseolus vulgaris* L. during reproductive development, *Jour. Amer. Soc. Hort. Sci.*, **105**, 424—427 (1980).

(146) YABUKI,K.: A consideration on the midday depression of photosynthesis, *Jour. Agric. Meteol.*, **19**, 11—14 (1964).*

(147) YAMAGUCHI,J., KAWACHI,K., TANAKA,A.: Studies on the growth of crop plant (part 5) Growth efficiency at successive growth stages and grain productivity of soybean in comparison with rice and maize, *J. Sci. Soil Manure, Japan*, **46**, 120—125 (1975) *

(148) YAMAKI,T., FURUMAYA,T., ISHITSUKA,T.: Studies on the effects of the pod and leaf cutting carried out in the early ripening stages on the growth of soybean plants, *Bull. Ibaraki Agr. Exp. Sta.*, **2**, 70—74 (1959).*

(149) YAMAMOTO,K.: Karyotaxonomical studies on *Vicia*, I On the karyotype and character of some annual species of *Vicia*, *Japan. Jour. Genet.*, **48**, 315—327 (1973).

(150) YAMASAKI,T.: Seasonal changes of the hardiness of common bean plant, *Proc. Crop Sci. Soc., Japan*, **23**, 312 (1955).*

(151) ZHOU XIU-TAO: Faba bean production and research in China, *FABIS*, (3), 24—25 (1981).

(152) ZOHARY,D., HOPF,M.: Domestication of pulses in the Old World, *Sci.*, **182**, 887—894 (1973).

* Japanese with English summary.

和文要旨

蚕豆における秋播型の生育習性とその収量成立機構に関する研究

木暮　秩

蚕豆（*Vicia faba*,L. ）の起源は未確定ながら近東とされているが，ここから西進して地中海沿岸へ，ついで北進して北ヨーロッパ，或は南進して北アフリカへ，また，東進して中国及び日本へ伝播したとされている．この伝播の過程で生態的に異なる秋播型と春播型に分化したものとみられ，前者は中国南部や日本及び地中海沿岸で，後者は高緯度の北ヨーロッパ及び北アフリカや中国の高地において栽培されている世界の６大食用豆類の一つである．

一方，開花・結実習性をみると，秋播型は多数の分枝から成るが伸育が制限され，莢は茎の中央部に集中して着く．これに対して春播型では無限伸育する主茎を主とする少数の茎の全体に莢が散在して着く特性を持っている．また，単位収量は概して秋播型は低いが，収量の安定性は春播型が低い傾向にある．このように生育特性が両者でかなり異なるにも拘らず，本質的には同じ無限伸育性をもつ作物である．

本研究は秋播型が何故に有限伸育的生育を発現するかを，代表的な日本品種について乾物生産と子実収量成立の機構の解析を通して検討した．即ち，孤立個体及び群落について生育並びに各器官の生理的特性，光合成及び呼吸特性，さらに光合成産物の移動特性からみたものである．

第１章　秋播型品種の生育経過と各器官の生理的役割

第１節　生育習性と各器官内成分との関係

秋播型日本品種の生育に伴う地上部及び地下部内炭水化物と窒素成分の消長を検討するとともに，それらの生理的意義を検討した．

(1) 作物の生育経過をみると，初期の越冬中には分枝数の増加と地下部の発達を除けば概して緩慢であった．翌春，気温の上昇に伴い各分枝茎は盛んな伸長と，またこれと並行して開花・結莢がかなり長期間にわたって認められたが，この間の根と根粒の活動は盛んであった．

(2) 地上部における炭水化物・窒素両成分の含有率は越冬中の生育初期に高かったが，開花に伴い一旦低下した後，地上部発達の終期にあたる莢の発育期には顕著に上昇して，これが子実の発達とその充実に深く関与した．

(3) 地下部においては炭水化物含有率の消長は地上部のそれと近似していた．これに対して窒素含有率は根及び根粒の活動と関連し，また，とくに蛋白態窒素は生育期間を通して高く推移して生育並びに子実の充実に深く関与した．

従って，葉は光合成器官として作物体の発達に与り，茎と根及び後期には莢が子実内成分の一時的蓄積器官としての役割を持つことが明らかになった．

第２節　栄養器官と生殖器官の生理的役割

開花始，開花終，緑莢の各期に，開花・結莢の習性を異にする４部位（１：下の６節で無開花，２：その上の５節で開花・結莢多，３：そのうえの５節で開花するが結莢極少，４：最上節で無開花）について，それぞれ摘葉して，生育，乾物生産，及び体内成分に及ぼす影響を検討した．

(1) 作物体の生育並びに茎の伸長・発達にに及ぼす摘葉の影響は，生育に伴って次第に上の部位に移るとともに大きく現れたが，その中で，とくに第２部位における摘葉の影響が最も著しかった．即ち，栄養・生殖両生長が重なって推移する開花始期の摘葉は茎の伸長を遅らし，開花・結莢数を減少させた．開花終期では栄養器官における乾物生産とその蓄積を妨げるとともに，結莢率を低下させ，緑莢期の摘葉は子実の発育を抑制した．

(2) 体内成分への影響を開花終期に摘葉処理した作物体についてみると，栄養器官のうち葉では残された各部位とも澱粉含有率が，茎では糖分，とくに非還元糖含有率が摘葉した部位で低下した．子実に対する影響が大きいのは第２，３部位の摘葉であり，澱粉含有率が低下した．しかし窒素含有率はその変化が小さかった．

従って，生育に伴う栄養器官の役割には部位別に差異があり，とくに多くの莢が集中して着生する第２部位における葉の役割が重要であることが確かめられた．

第３節　草型，乾物生産，及び子実生産に及ぼす栽植密度の影響

栽植密度を疎植（3.8個体/m^2），中植（7.6個体/m^2），密植（15.2個体/m^2），極密植（30.4個体/m^2）として育成し，生育，子実生産への影響を調べ，群落内の競合の様相を物質生産構造面から検討した．

(1) 競合は開花始期からみられ，密植するほど茎長，とくに節間長を伸長させたが，個体当りの茎数・莢数・結莢率・子実数を減少させた．しかし，単位土地面積当り栄養器官の発達と子実収量は疎植＜中植＜密植であって極密植で劣った．

(2) 物質生産構造を10cm毎の垂直分布でみると，葉は当初全層位にみられたが，生育に伴って次第に上の層位に集まる状態になり，密植条件となるほど早く，また顕著に現れた．

(3) 落葉した部位は下層位の相対照度が10％以下であったものと，上の層位で互いに遮蔽し，触れ合ったものにみられたが，これは個体占有土地面積内に生存が制限されたことを示している．

従って，物質生産構造と栄養・生殖両器官の発達からみた正常な生育特性の発現には本実験の密植条件（15個体/m^2）が限界であることが明らかになった．

第２章　光合成及び呼吸特性

第１節　孤立個体の葉と莢の光合成・呼吸作用

開花・結莢習性で分けた４部位の葉と第２部位に着生する莢の光合成・呼吸特性とその乾物生産及び物質分配における意義を検討した．

(1) 葉の光合成は15−30℃の広い範囲で，とくに生育の後期には高温条件にも適応することが分かった．また，光補償点とその飽和点はそれぞれ0.01と0.20−0.30cal, cm^2, min^{-1}であり，光合成速度は20 $mgCO_2$, dm^2, hr^{-1}であるとともに，日中低下現象を示すことが確かめられた．

(2) 葉の光合成はかなり長期間高い値を維持するが，開花期と子実充実初期に高く，これには葉の生理的令とシンクとしての莢・子実の存否が大きく関与した．葉の夜間における呼吸作用は概して低いが，莢の着く第２部位，次いで第３部位で高く，また，日中における光合成の状態を反映した．

(3) 莢の呼吸作用は発育期間及び夜間・日中を通して概して高く，その日変化は特異であって明らかに莢表面においてかなり強い光合成が行なわれることが推察された．しかし葉からの転流物質の受容と莢・子実内における成分への再合成に伴う強い合成物質の消費がそれを打ち消しているものと思われた．

従って，下の部位葉は順次上部位の栄養・生殖器官の発達に関与するが，第２部位葉の働きが子実収量の成立とその安定性とに深く関わるとともに，これが原因となってより上の部位における無限伸育性の発現に体内成分面から制限要因となることが明らかになった．

第２節　光合成・呼吸作用に及ぼす栽植密度の影響

栽植密度を疎植（3.8個体/m^2），密植（15.2個体/m^2），極密植（30.4個体/m^2）にした群落内の競合について，各部位の葉と莢の光合成・呼吸作用面から検討した．

(1) 葉の光合成速度は密植するほど上の部位で下の部位とは反対に促進された．しかし，夜間における葉の呼吸速度は密植条件で下の部位で大となった．また，莢の呼吸作用はとくに極密植した場合に大となった．

(2) 単位土地面積当りの固定されたCO^{2}量は密度が大となるほど大となったが，呼吸量の光合成量に対する割合も大きくなった．このため疎植条件下でみられた第２，３部位葉と莢・子実間の密接なソース・シンク関係は極密植の条件で，とくに第４部位における大きな葉量との間には必ずしも認められず，子実の発達にはつながらなかった．

従って，密植条件が作物体の光合成と呼吸作用の面から好ましい栽植密度であることが確かめられた．

第３章　光合成産物の動態と生育及び子実生産との関係

第１節　開花期以降における^{14}C光合成産物の動態

開花期以後に同化された炭素が，子実収量の成立に果たす役割について，開花始期，開花終期，子実充実期に作物体全体に$^{14}CO_2$を光合成させて検討した．

(1) $^{14}CO_2$供与後の放射能は葉が他器官より優ったが，生育が進むに伴っていずれの器官も大となった．その減衰は供与７日以内に大きな部分がみられたが，生育を通して開花始期の供与では55％，開花終期では50％，子実充実期では45％であった．

(2) 葉によって合成された^{14}C産物の移行先は開花始期では茎と根へ，開花終期から子実充実期には次第に莢から子実へとみられたが，根への移行はいずれの時期においても認められた．

(3) 子実内^{14}C量のうち，茎と根，さらには莢に一旦蓄積された後，移行したものの割合は，開花始期では19％，開花終期では40％，子実充実期では41％を占めた．

従って，開花期から莢の発達期における光合成産物は栄養器官の構成と幼莢の発育に関与し，その後は次第に子実生産に大きく貢献して行くことが明らかになった．

第２節　各部位葉で同化された^{14}C光合成産物の動態

開花期，莢発達期，並びに子実充実期に４部位の葉に$^{14}CO_2$を光合成させて得た産物が，子実の発達に果たす役割を検討した．

(1) 開花期に第１，２部位で合成された^{14}C産物は根及びより上部位器官の発達に向けて移行した．莢発達期では第１部位からは根へ，第２，３部位からは莢と子実へ移行したが，その後は直接子実の充実にあづかった．

(2) 一方，子実充実期においては第４部位の葉における^{14}C合成産物は作物体全体の需要に対する補助的供給者として機能する他，根と根粒の活動を支える役割を果たした。

従って，開花・結莢習性に基づいて分けた各部位の葉で合成した産物が果たす役割は，莢および子実の発達に伴って変化するが，一部は地下部活動の支持を介して正常な生理状態を維持していることが明らかになった。

第３節　分枝間における^{14}C光合成産物の移動

開花後45日目と65日目に摘葉あるいは摘莢し，特定の部位に$^{14}CO_2$を光合成させてそれら産物の茎間相互の移動を検討した。

(1) 光合成産物は栄養器官の発達が止まった開花後45日目では主として莢が，その後20日間を経過した後は子実が受容器官であった。また，それらの受容力は１ａが最大で，ついで２ａ，１ｂの順となり，個体内における開花および着莢の順序を反映していた。

(2) ^{14}C合成産物は各茎内で独立して合成と消費が完結することが認められた。即ち，葉は主に同じ茎にあるシンクに対しソースとしての役割を果たすが，時には個体内の他の茎に対して補足的機能を持つことが認められた。

(3) 莢の呼吸速度は近似していたが，これは同じ茎内或は他の茎から合成物質を受容しても，これに伴う受容力が本質的には変わらないことを示している。

従って，秋播型の日本品種は各茎が本質的には独立して，各茎が一本としてソース・シンク関係をもつことが明らかになった。

本研究の結果を要約すると，秋播型の日本品種の特性は以下のとおりである。

第１章：一般的な生育特性を孤立個体としてみると，春期の開花は栄養器官が最大値の半分程度の頃に始まるために栄養・生殖の両生長が長期間並行し，また，結実にかなりの日数を要する。一方，葉における光合成器官としての役割は作物体の発達状況と深く関連するとともに，茎と根，さらに莢が越冬とそれに続く急速な栄養生長と開花，或は子実内成分に対する一時的貯蔵器官としての役割を果たす。

このような生理的役割は，節位数の増加に伴って開花・結莢習性によって分けた４つの部位のうち，下の部位から順次上へ移動するが，開花・結莢する第２部位の栄養器官の役割が極めて重要であるとともに，これが日本品種の有限的生育を発現する原因となる。

さらに群落内では上述した生育特性の発現は個体占有土地面積によって制限されるが，15個体/m^{2}の栽植密度がその限界である。

第２章：孤立個体の光合成・呼吸特性をみると，生育に伴って下の部位の葉は順次上の部位の各種器官の発達に寄与するとともに，開花始期以降は各部位葉が栄養器官や莢，さらには子実などに果たす役割が変化するが，第２部位葉の合成力とその維持期間が極めて重要である。また，莢の光合成もかなり高い。しかし，個体としては明らかに炭水化物の不足が考えられ，これが生育と子実収量の制限要因となる。

ついで，この光合成・呼吸特性を先に見いだした好ましい栽植密度（15個体/m^2）についてみると，作物体の各器官相互において正常なソース・シンク関係が構成されるなど，子実収量の成立に深く関わる。

第３章：合成産物の移動特性をみると，$^{14}CO_2$を全植物体へ供与して生育の経過と関連させてみると，開花期から30−40日間の光合成産物は栄養器官と莢に，その後は主として子実の生産に関与している。

ついで４つの部位葉に供与して合成産物の行方をみると，生育に伴ってシンクの種類は変わるが，全生育期間

を通して第２部位葉が子実の生産に対して重要であるとともに，後期においては第４部位の葉が根及び根粒の機能の維持を介して重要な役割を持つ．

さらに，葉で合成された産物，主として炭水化物は本質的には各茎で独立してその利用・消費が完結される特性をもつが，茎相互で移動し得る．

以上の諸点から，次に示す結論が得られた。即ち，秋播型の日本品種は，（1)着莢数は多いがその発達及び引き続く子実の発達が物質の合成力によって制約されている．（2)各茎は独立してソース・シンク関係をもっている．（3)しかし，産物の合成とそれらを栄養器官の構成並びに生殖器官の発育の双方へ利用するバランスはかならずしも安定しない．（4)従って，主として炭水化物の不足が有限伸育に似た生育を体内生理面から強制的に発現させられていることが明らかとなった．

従って，将来における蚕豆の子実収量増とその安定性の確保は次の３つの改善策について，育種及び生理面からの手だてに掛かっていると言える指針が得られた．即ち，第１には無駄な栄養器官作りと，それが主たる原因となって引き起こされる倒伏による損失を避けるために，無限伸育性品種よりは有限伸育性品種の栽培が好ましい．この意味から近年作出されつつある完全有限伸育性品種の出現が待たれる．第２には花及び幼莢の脱落及び減少防止策の開発が必要である．そして第３には生育の遅くまで葉の寿命を保持し，また光合成機能の低下を抑制し，併せて根と根粒の機能延長などの技術開発が強く求められる．

香川大学農学部紀要

第１号　幡　克美：アカマツ材の成分並びにパルプ化に関する研究（1955年３月）
第２号　内藤　中人：植物成長ホルモンに関する植物病理学的研究　特に植物病原菌に及ぼす影響について（1957年10月）
第３号　松沢　寛：アオムシコマユバチの生態に関する研究（1958年３月）
第４号　梶　明：和紙原料の醗酵精練に関する研究（1959年３月）
第５号　森　和男：傾斜地蜜柑園経営の構造分析（1960年３月）
第６号　玉置　鷹彦：ガラク並びに池泥の研究（1960年３月）
第７号　上原　勝樹：傾斜地開発利用に関する物理気象的研究（1961年３月）
第８号　桑田　晃：オクラとトロロアオイとの種間交雑およびそれらより育成された種々の雑種ならびに倍数体に関する研究（1961年９月）
第９号　中　潤三郎：甘藷の生育過程に関する作物生理学的研究（1962年３月）
第10号　斉藤　実：香川県及び北愛媛県の地質について（1962年３月）（英文）
第11号　小杉　清：グラジオラスの生産と開花に関する研究（1962年９月）（英文）
第12号　吉良　八郎：貯水池の滞砂に関する水理学的研究（1963年２月）
第13号　野田　愛三：禾穀類の根鞘に関する研究（1963年３月）
第14号　川村　信一郎：豆類のデンプンの研究（1963年３月）（エスペラント文）
第15号　浅野　二郎：種子の耐塩性を中心とした海岸地帯におけるアカマツおよびクロマツ林の成立に関する研究（1963年３月）
第16号　山中　啓：乳酸菌のペントース・イソメラーゼに関する研究（1963年８月）（英文）
第17号　葦沢　正義：香川県における葡萄の旱害に関する研究（1964年３月）
第18号　谷　利一：カキ炭疽病の病態生理学的研究，とくに罹病果実の病徴発現にあずかるペクチン質分解酵素の役割（1965年３月）
第19号　樽谷　隆之：カキ果実の貯蔵に関する研究（1965年３月）
第20号　狩野　邦雄：ラン種子の発芽培地に関する研究（1965年３月）（英文）
第21号　山本　喜良：コモンベッチおよびその近縁種の雑種に関する研究（1965年３月）
第22号　中広　義雄：鶏における飼料の消化率測定法に関する研究（1966年10月）
第23号　井上　宏：ナツダイダイの果実発育に関する研究，とくに水腐病の発生機構を中心として（1967年３月）
第24号　宮辺　豊紀：異常乳の生成と塩類均衡とくにカゼイン燐酸カルシウムに関する研究（1967年８月）（英文）
第25号　十河　村男：樹皮リグニン及び樹皮フェノール類に関する研究（1971年９月）
第26号　大島　光昭：赤クローバーサイレージ中の窒素栄養源に関する研究（1971年11月）（英文）
第27号　辰巳　修三：林木葉部中におけるカルシウムの化合形態とその生理に関する基礎的研究（1974年11月）
第28号　榑谷　勝：ブドウの葉脈黄変による早期落葉の研究（1974年12月）
第29号　倉田　久男：カボチャ・スイカの性の分化におよぼす日長および温度の影響に関する研究（1976年３月）

第30号　鎌田萬：中小河川治水計画に適用する計画降雨の合理的算定法に関する研究（1976年６月）

第31号　山本弘幸：エンバク冠さび病の抵抗性発現機構に関する研究（1978年３月）

第32号　岡本秀俊：テントウムシの摂食の生態に関する実験的研究（1978年３月）

第33号　山崎徹：*p*-ヒドロキシフェニル並びにシリンギルリグニンに関する研究（1978年９月）（英文）

第34号　市川俊英：イネを加害する４種の同翅亜目頸吻群昆虫の配偶行動に関する研究（1979年２月）（英文）

第35号　吉田博：農業生産共同組織の展開・構造・運営に関する研究（1980年３月）

第36号　一色泰：鶏盲腸の栄養生理学的研究（1980年３月）

第37号　中條利明：富有カキ果実の発育ならびに品質に及ぼす温度条件に関する研究（1982年２月）

第38号　五井正憲：温帯花木の花芽形成ならびに開花調節に関する研究（1982年２月）

第39号　松井年行：和三盆糖の食品学的研究（1982年２月）

第40号　藤目幸擴：ハナヤサイ類の花らい形成並びに発育の温度条件に関する研究
— 特に異常花らいについて —（1983年２月）

第41号　西山壮一：カンガイ用管水路における空気混入流の水撃作用に関する研究（1983年２月）

第42号　真山滋志：エンバク冠さび病の抵抗性発現におけるアベナルミンの役割（1983年10月）（英文）

第43号　門谷茂：海洋堆積物中のアミノ酸の初期続成過程に関する研究（1983年10月）

第44号　一井真比古：水稲育種における再生茎形質の選抜指標としての効用に関する研究（1984年11月）（英文）

第45号　片岡郁雄：ブドウ果実の着色に関する研究
— とくにアブシジン酸による着色の制御について —（1986年10月）

第46号　鈴木晴雄：畑地栽培におけるフィルムマルチと植被が地温に及ぼす影響に関する農業気象学的研究（1986年10月）

第47号　蓑輪雅好：開放型畜舎内の放射熱環境に関する研究（1986年10月）

第48号　藤田政之：サツマイモ塊根組織のチトクロムＰ-450系酵素に関する研究（1986年10月）

第49号　田中道男：組織培養によるファレノプシスの栄養繁殖に関する研究（1987年２月）

第50号　長谷川曠：東洋系シンビジウムの繁殖に関する研究（1987年12月）

第51号　笠井忠：大豆の少糖類の加水分解に関する研究（1987年12月）

第52号　青柳省吾：四国北部の瀬戸内沿岸における花崗岩風化残積土（マサ土）および安山岩風化残積土の土壌特性に関する研究（1987年12月）

第53号　片山健至：*Fusarium solani* M-13-1によるリグニンサブストラクチャーモデル化合物の分解（1989年11月）（英文）

第54号　増田拓朗：植栽基盤としてのマサ土の問題点とその改良法に関する研究（1990年10月）

第55号　多田邦尚：海水中の溶存タンパク様物質およびアミノ酸の動態に関する研究（1990年10月）

第56号　深井誠一：ダイアンサスおよびキク属植物における茎頂の凍結保存に関する研究（1992年10月）

第57号　吉田裕一：イチゴの花器および果実の発育に関する研究
— ‘愛ベリー’ の奇形果発生を中心として —（1992年10月）

第58号　越智正：燧灘の化学環境特性と物質循環に関する研究（1992年10月）

第59号　木暮秩：蚕豆における秋播型の生育習性とその収量成立機構に関する研究（1992年12月）（英文）

Memoirs of Faculty of Agriculture, Kagawa University

No. 1 Katsumi HATA : Studies on the Constituents and Pulping of "Akamatsu"(*Pinus densiflora* SEB et ZUCC) Wood (March, 1955)

No. 2 Nakato NAITO : Phytopathological Studies Concerning Phytohormones with Special Reference to Their Effect on Phytopathogenic Fungi (October, 1957)

No. 3 Hiroshi MATSUZAWA : Ecological Studies on the Branconid Wasp, *Apanteles glomeratus* (March, 1958)

No. 4 Akira KAJI : Studies on the Retting of Plant Fiber Materials for Japanese Paper Manufacture (March, 1959)

No. 5 Kazuo MORI : An Analytical Study on the Structure of the Mandarin Orange Growing Orchard Farm in a Sloping Land Region (March, 1960)

No. 6 Takahiko TAMAKI : Studies of Garaku Paddy Soil and Reservoir Deposits (March, 1960)

No. 7 Masaki UEHARA : Physical and Meteorological Studies on the Cultivation and Utilization of Slope Land (March, 1961)

No. 8 Hikaru KUWADA : Studies on the Interspecific Crossing between *Abelmoschus esculentus* MOENCH and *A. Manihot* MEDIC and the Various Hybrids and Polyploids Derived from the Above Two Species (September, 1961)

No. 9 Junzaburo NAKA : Physiological Studies on the Growing Process of Sweet Potato Plants (March, 1962)

No.10 Minoru SAITO : The Geology of Kagawa and Northern Ehime Prefectures, Shikoku, Japan (March, 1962) (in English)

No.11 Kiyoshi KOSUGI : Studies on Production and Flowering in Gladiolus (September, 1962) (in English)

No.12 Hachiro KIRA : Hydraulical Studies on the Sedimentation in Rerservoirs (February, 1963)

No.13 Aizo NODA : Studies on the Coleorhiza of Cereals (March, 1963)

No.14 Sin'itiro KAWAMURA : Studoj pri Ameloj de Legumenoj (March, 1963) (in Esperanto)

No.15 Jiro ASANO : A Study on the Formation of Pine Forests on Seaside Areas, giving due Consideration to the Salt Resistance of the Seeds (March, 1963)

No.16 Kei YAMANAKA : Studies on the Pentose Isomerases of Lactic Acid Bacteria (August, 1963) (in English)

No.17 Masayoshi ASHIZAWA : Studies on the Drough Damage of Grape Trees in the Region of Kagawa Prefecture (March, 1964)

No.18 Toshikazu TANI : Studies on the Phytopathological Physiology of Kaki Anthracnose, with Special Reference to the Role of Pectic Enzymes in the Symptom Development on Kaki Fruit (March, 1965)

No.19 Takayuki TARUTANI : Studies on the Storage of Persimmom Fruits (March, 1965)

No.20 Kunio KANO : Studies on the Media for Orchid Seed Germination (March, 1965) (in English)

No.21 Kiyoshi YAMAMOTO : Studies on the Hybrids among the *Vicia sativa* L. and its Related Species (March, 1966)

No.22 Yoshio NAKAHIRO : Studies on the Method of Measuring the Digestibility of Poultry Feed (October, 1966)

No.23 Hiroshi INOUE : Studies on the Fruit Development of Natsudaidai (*Citrus Natsudaidai* HAYATA), with Special Reference to Water Spot Injury (March, 1967)

No.24 Toyoki MIYABE : Studies on the Production and the Salt Balance in Relation to Calcium Phosphocaseinate of Abnormal Milk (August, 1967) (in English)

No.25 Murao SOGO : Studies on the Bark Lignin and Bark Phenolic Compounds (September, 1971)

No.26 Mitsuaki OHSHIMA : Studies on Nutritional Nitrogen from Red Clover Silage (November, 1971) (in English)

No.27 Shuzo TATSUMI : Fundamental Studies of the Chemical Forms of Calcium and Their Metabolisms in the Tree Leaves (November, 1974)

No.28 Masaru KURETANI : Studies on the Early Summer Defoliation of Grape Vines Caused by Veinyellowing (December, 1974)

No.29 Hisao KURATA : Studies on the Sex Expression of Flowers Induced by Day-length and Temperature in Punpkin and Watermelon (March, 1976)

No.30 Takashi KAMADA : Studies on the Rational Estimation of Rainfall for Design Flood (June, 1976)

No.31 Hiroyuki YAMAMOTO : Study on the Mechanism of Resistance Expression in the Crown Rust Disease of Oat (March, 1978)

No.32 Hidetoshi OKAMOTO : Laboratory Studies on the Food Ecology of Aphidophagous Lady Beetles (Coleoptera : Coccinellidae) (March, 1978)

No.33 Toru YAMASAKI : Studies on *p*-Hydroxyphenyl- and Syringyl Lignins (September, 1978) (in English)

No.34 Toshihide ICHIKAWA : Studies on the Mating Behavior of the Four Species of Auchenorrhynchous Homoptera which Attack the Rice Plant (February, 1979) (in English)

No.35 Hiroshi YOSHIDA : A Study of the Development, Structure and Management of Co-operative Groups (March, 1980)

No.36 Yutaka ISSHIKI : Nutritional and Physiological Studies on the Function of Ceca in Chickens (March, 1980)

No.37 Toshiaki CHUJO : Studies on the Effects of Thermal Conditions on the Growth and Quality of Fruits of Fuyu Kaki (February, 1982)

No.38 Masanori GOI : Studies on the Flower Formation and Forcing of Some Ornamental Trees and Shrubs in East Asia (February, 1982)

No.39 Toshiyuki MATSUI : Food Chemical Studies on Wasanbon-to Sugar (Japanese traditionally refined sugar) (February, 1982)

No.40 Yukihiro FUJIME : Studies on Thermal Conditions of Curd Formation and Development in Caulifower and Broccoli, with Special Referene to Abnormal Curd Development (February, 1983)

No.41 Souichi NISHIYAMA : Studies on the Water Hammer of the Air-entrained Flow in Irrigation Pipe Lines (February, 1983)

No.42 Shigeyuki MAYAMA : The Role of Avenalumin in the Resistance of Oats to Crown Rust (October, 1983) (in English)

No.43 Shigeru MONTANI : Early Diagenesis of Amino Acids in Marine Sediments (October, 1983)

No.44 Masahiko ICHII : Studies on the Utillity of Ratoon Traits of Rice as the Indicator of Agronomic Characters in Breebing (November, 1984) (in English)

No.45 Ikuo KATAOKA : Studies on the Coloration of Grape Berries with Special Reference to the Regulation of Color Development by Abscisic Acid (October, 1986)

No.46 Haruo SUZUKI : Agrometeorological Studies on the Effect on Soil Temparature, of Film Mulching and Canopy in the Upland Mulching Culture (October, 1986)

No.47 Masayoshi MINOWA : A Study on Thermal Radiation Environment in an Open-type Livestock Barn (October, 1986)

No.48 Masayuki FUJITA : Studies on Cytochrome P-450-Dependent Mixed Function Oxygenase in Sweet Potato Root Tissue (October, 1986)

No.49 Michio TANAKA : Studies on the Clonal Propagation of *Phalaenopsis* through *in vitro* Culture (February, 1987)

No.50 Atushi HASEGAWA : Studies on the Propagation of Oriental Cymbidium (December, 1987)

No.51 Tadasi KASAI : Studies on the Hydrolysis of Oligosaccharides of Soybeans (December, 1987)

No.52 Shogo AOYANAGI : Studies on the Physical Properties of Residual Granitic and Andesitic Soils in Setouchi Coastal Region, Northern Shikoku (December, 1987)

No.53 Takeshi KATAYAMA : Degradation of Lignin Substructure Model Compounds by *Fusarium solani* M-13-1 (November, 1989) (in English)

No.54 Takuro MASUDA : Studies on the Charactaristics of Masa Soil as a Medium for Tree Growth and Methods for its Improvement (October, 1990)

No.55 Kuninao TADA : Behavior of Dissolved Proteinous Substances and Amino Acids in Seawater (October, 1990)

No.56 Seiichi FUKAI : Studies on the Cryopreservation of Shoot Tips of *Dianthus* and *Chrysanthemum* (October, 1992)

No.57 Yuichi YOSHIDA : Studies on Flower and Fruit Development in Strawberry, with Special Refference to Fruit Malformation in 'Ai-Berry' (October, 1992)

No.58 Tadashi OCHI : Studies on the Characteristics of Chemical Environment and the Recycling of Nutrient in Hiuchi Nada Sea Area (October, 1992)

No.59 Kiyoshi KOGURE : Studies on the Growth Habit and its Relations to the Mechanism of Yielding Process in Winter Type of Faba Bean (*Vicia faba* L.) (December, 1992) (in English)

平成４年12月22日印刷　平成４年12月25日発行

香川県木田郡三木町
香川大学農学部

印刷所　アート印刷株式会社
香川県木田郡三木町池戸1779番地13
電話（0878）９１－０１７０番