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GROWTH, PHOTOSYNTHESIS AND YIELD COMPONENTS IN RELATION TO GRAIN YIELD OF THE FIELD BEAN

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I. INTRODUCTION

The field bean (*Phaseolus vulgaris*) is the grain legume with the 2nd largest production in the world ranking only below the soybean. Twenty-three percent of the world supply is produced in Latin America. In that part of the world it is produced mostly by small farmers and is a staple food especially for the poor as a source of protein. In Hokkaido, Japan, the field bean is also an important crop. The pattern of production and consumption, however, differs from that in Latin America.

The grain yield per unit field area of this crop has been low and progress in pushing up the yield has been slower than for cereal crops such as rice, wheat and maize, in Hokkaido as elsewhere in the world.

Consumer preference for specific grain qualities and also the agronomic conditions under which this crop is grown have contributed to the diversity of varietal characteristics of *Phaseolus vulgaris*.

The 1000-grain weight for different varieties ranges from less than 150 g to more than 700 g with extremes from 30 g to 1000 g. The shape of the grains also varies considerably as does the color of the grains, from white to red to black; uniformity of color also varies, ranging from unmottled to highly mottled. Such grain characteristics are associated with premium prices based on consumer preference and demand in the market for special grain qualities. The selection of varieties that farmers plant is decided not only by the yielding ability of varieties under given cultural conditions but more frequently by the grain characteristics.

The varieties of Hokkaido and of the tropics used in this series of studies are listed in Tables 1 and 2. The seeds of these varieties were provided by the Tokachi Agricultural Experiment Station and the Centro Internacional de Agricultura Tropical (CIAT) in Colombia.

The varieties in Hokkaido are generally classified into the following groups based on grain characteristics; Kintoki, Shiro-kintoki, Nagauzura, Chūnaga-uzura, Tebō, etc. reflecting brand names in the market (Table 1). As the preference of consumers in Japan has been for larger grains, the 1000-grain weight has increased from old to new varieties within each group. As shown in Table 2, tropical varieties are generally smaller in grain size than Hokkaido varieties except for a few determinate varieties.

Varieties of *Phaseolus vulgaris* can be classified by their growth habit into determinates and indeterminates. Stems of the determinates terminate in a flower cluster and those of the indeterminates in a vegetative bud cluster. The determinate habit seems to be evolved from the indeterminate habit²⁰.

Varieties in Hokkaido are generally classified into dwarfs, semi-vines

TABLE 1. Varieties of Hokkaido included in these studies

No.	Variety	Year of recommendation	Growth habit*	1000-grain weight** (g)	Tested in	
					1973	1974
Kintoki Group (large, red, elliptical grains)						
1	Kintoki	1905	D	565	○	
2	Beni-kintoki	1927	D	471	○	
3	Taishō-kintoki	1957	D	634	○	○
4	Shin-kintoki	1964	D	669	○	
5	Showa-kintoki	1966	D	728	○	○
Shirokintoki Group (large, white, elliptical grains)						
6	Shirokintoki	1958	D	435	○	
7	Taishō-shirokintoki	1960	D	611	○	○
8	Tokachi-shirokintoki	1970	S	701	○	○
Nagauzura Group (light brown with purple patches, kidney-shaped grains)						
9	Maru-nagauzura	1939	D	494	○	
10	Kikuchi-nagauzura	1939	D	542	○	
11	Tsunetomi-nagauzura	1939	D	628	○	
Chūnagauzura Group (light brown with purple patches, cylindrical grains)						
12	Chūnagauzura	1924	S	463	○	
13	Tenashi-chūnagauzura	1939	D	481	○	
14	Kairyō-chūnaga	1961	S	513	○	
15	Fukuryū-chūnaga	1972	S	723	○	○
Tebō Group (small, white, elliptical grains)						
16	Ō-tebō	1927	S	298	○	○
17	Kairyō-Ō-tebō	1961	S	326	○	
18	Taishō-Ō-tebō	1969	S	315	○	
19	Gin-tebō	1971	S	387	○	○
High Quality Bean Group (large grains of various colors and shapes)						
20	Ō-fuku	1905	I	714		○
21	Toramame	1939	I	619		○
Others						
22	Kitahara-beninaga	1966	D	633	○	

* D: Determinate. S: Semi-indeterminate. I: Indeterminate.

** From Reports of Tokachi Agr. Expt. Stat.

TABLE 2. Tropical varieties included in these studies

No.	Variety	Country of origin	Growth habit*	1000-grain weight** (g)	Color
23	ICA Guali	Colombia	I	504	Red with brown patches
24	ICA DUVA	Colombia	I	551	Dark red
25	Black Marvel	Venezuela	I	302	Black with gray mottle
26	Argentina 2	Venezuela	I	174	Black
27	PI 172.017	South Africa	II***	347	Light amber
28	Porrillo No. 1	El Salvador	II	261	Black
29	Porrillo Sintetico	Honduras	II	230	Black
30	Jamapa	Venezuela	II	208	Black
31	ICA Pijao	Colombia	II	178	Black
32	PI 307.824	El Salvador	II	178	Black
33	Nep-2	Costa Rica	II	146	White
34	PI 175.277	India	III	225	Light brown
35	PI 310.740	Guatemala	III	219	Black
36	PI 175.278	India	III	199	White
37	PI 310.739	Guatemala	IV	231	Black
38	Trujillo 3	Venezuela	IV	216	Black
39	Trujillo 2	Venezuela	IV	304	Black

* I: Determinate bush. II: Indeterminate bush. III: Indeterminate semi-climbing. IV: Indeterminate climbing.

** Data collected on the seeds sown.

*** Behaved as Type I in Sapporo.

and vines. Dwarfs and semi-vines are grown commercially as bush beans while vines are grown with 2-2.5 meter bamboo-sticks to support the plant. Bush beans are commonly grown. Special varieties of vine-type beans are grown when market demand and prices are high and justify inputs of added labor and money.

At CIAT the following classification is used:

Type I: Determinate bush

Type II: Indeterminate bush

Type III: Indeterminate semi-climbing

Type IV: Indeterminate climbing

According to this classification Type I would be comparable to dwarfs of

Hokkaido ; Types II-III, to semi-vines ; and Type IV, to vines ; respectively. For convenience, these three groups are considered as determinates, semi-indeterminates and indeterminates, respectively, in this paper.

In Latin America the field bean is grown in a mono-crop system like wheat, potato, etc., but it is also often grown with maize in a mixed-crop system as well. Types I-III are used in a mono-crop system. When Type IV is used, the bean climbs up the maize plant grown with it. The yield of maize and bean under this mixed-crop system can be 6 t/ha and 1.5 t/ha, respectively⁶⁾. This type of mixed-crop system is common among subsistence farmers.

Some relationships between the growth habit and the grain characteristics are evident among presently available commercial varieties. For example, the Kintoki or Shiro-kintoki groups of the Hokkaido varieties and also ICA Guali and ICA DUVA of the tropical varieties both have large grains and are determinates. However, there are exceptions ; Ō-fuku and Toramame have a large grain size but are indeterminates.

Growth duration varies with the variety, but it is short compared with other crops. For example, farmers in Hokkaido can sow field beans later in the spring and harvest earlier in the autumn than other crops. Sowing of winter wheat is thus possible in September after the field bean is harvested. Thus, farmers prefer varieties with a short growth duration over some that may yield more with a long growth duration. In the tropics it is possible to harvest a bean crop within two months after sowing³⁹⁾. This permits the inclusion of beans in various cropping systems.

Varieties of *Phaseolus vulgaris* may be short-day or day-neutral plants and may be either determinates or indeterminates¹⁰⁾ although indeterminates are frequently more sensitive to photoperiod than determinates⁶⁾. Growth duration is generally much shorter at higher than at lower temperatures. Some tropical varieties not listed in Table 2 such as Michoacan and PI 312.064 in 1973, and PI 176.693, PI 175.845, PI 175.850 and PI 177.052 in 1975 were tested at Hokkaido University. These did not mature before the autumn frost because they bloomed in late August or September because of low temperatures or long-day conditions.

Many possible combinations of grain characteristics, growth habit, growth duration, etc. result in many varieties. Such a diversity of varieties make studies of the field bean more difficult than for other crops. Because determinates and indeterminates differ widely, it may be more convenient to consider them as two different crops.

To improve the productivity of rice, intensive studies were made into the

relationship between photosynthesis, respiration, dry matter production and grain yield among varieties. The concept of an ideo-type was developed³⁶⁾. The rice plant will produce the maximum yield under an optimum cultural condition, if a variety possesses the morphological traits coincident with the ideo-type. Application of this concept has helped in breeding high yielding rice varieties.

Similar studies on presently available varieties of maize have been conducted. The sink capacity, which is the capacity of grains to accept photosynthates, was found to be the yield limiting factor, rather than the source, which is controlled by the photosynthetic facility of the plant. Increased grain yield thus appears to be more dependent on characteristics that increase the number of grains and less so on characteristics that increase the photosynthetic capacity of the plant³⁷⁾.

The purpose of this paper is to identify the yield limiting factors of presently available varieties of *Phaseolus vulgaris*, and to identify plant traits which are associated with high yielding ability in this crop. The extreme diversity in varietal characteristics was taken into consideration. For this purpose data presented in separate reports published in Japanese by the authors with others²⁹⁻³⁵⁾ are mostly used. Detailed description of experimental methods are thus omitted in this paper because they are available in previous reports.

II. GROWTH, PHOTOSYNTHESIS AND TRANSLOCATION OF PHOTOSYNTHATES UNDER NORMAL CONDITIONS

1. Growth Pattern of a Determinate and a Semi-indeterminate

Observations were made on Taishō-kintoki and Gin-tebō to illustrate the growth pattern of field beans³²⁾. These varieties are the standard commercial determinate and semi-indeterminate in Hokkaido, respectively.

Seeds of these varieties were sown in a field of Hokkaido University after treating with inoculant on May 23, 1973 at a hill spacing of 25 cm × 25 cm, one plant to a hill, with 40 kg N/ha, 75 kg P₂O₅/ha, and 50 kg K₂O/ha applied at sowing (almost equivalent to standard farmers' practices). Another 20 kg N/ha was top-dressed 35 days after sowing. Gin-tebō was supported with bamboo-sticks although this is not the farmers practice. Standard protection measures were taken against weeds, pests and diseases. Rainfall was low from early June to the end of July. Therefore, the field was adequately irrigated during this period. The crops were observed regularly at 10- to 14-day intervals during growth.

Leafing and Branching: The arrangement of the various organs is illustrated for each variety in Fig. 1 and Fig. 2.

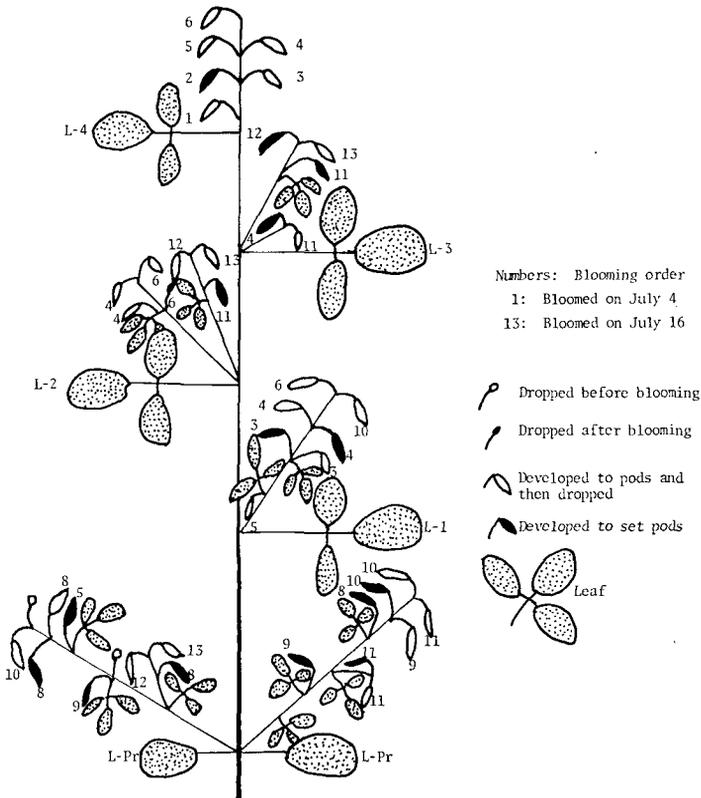


Fig. 1. Diagram of arrangement of leaves and flowers of Taishō-kintoki.

In Taishō-kintoki the main stem terminated above L-4 (the 4th trifoliated leaf) with a length of 35 cm (Fig. 3). The leaf size became larger from L-1 to L-3, and L-4 was the smallest (Fig. 5). After blooming, L-Pr (the primary leaves) started to defoliate, but by the end of growth most leaves were still alive except for L-Pr and some of the leaflets of L-1. Branches come out from the nodes of L-Pr, L-1, L-2 and L-3 (Fig. 1), and branching continued until about full blooming (Fig. 3). The leaf area index (LAI) increased with growth due to development of the leaves on the main stem as well as on branches, reached a maximum value of 3.7 at about full blooming, and was maintained at this state for a long period although there was a slight decrease by the end of growth (Fig. 6). The leaf area ratio (LAR)

increased with growth, reached a peak at about full blooming, and then decreased.

In Gin-tebō the main stem terminated above L-19 with a length of

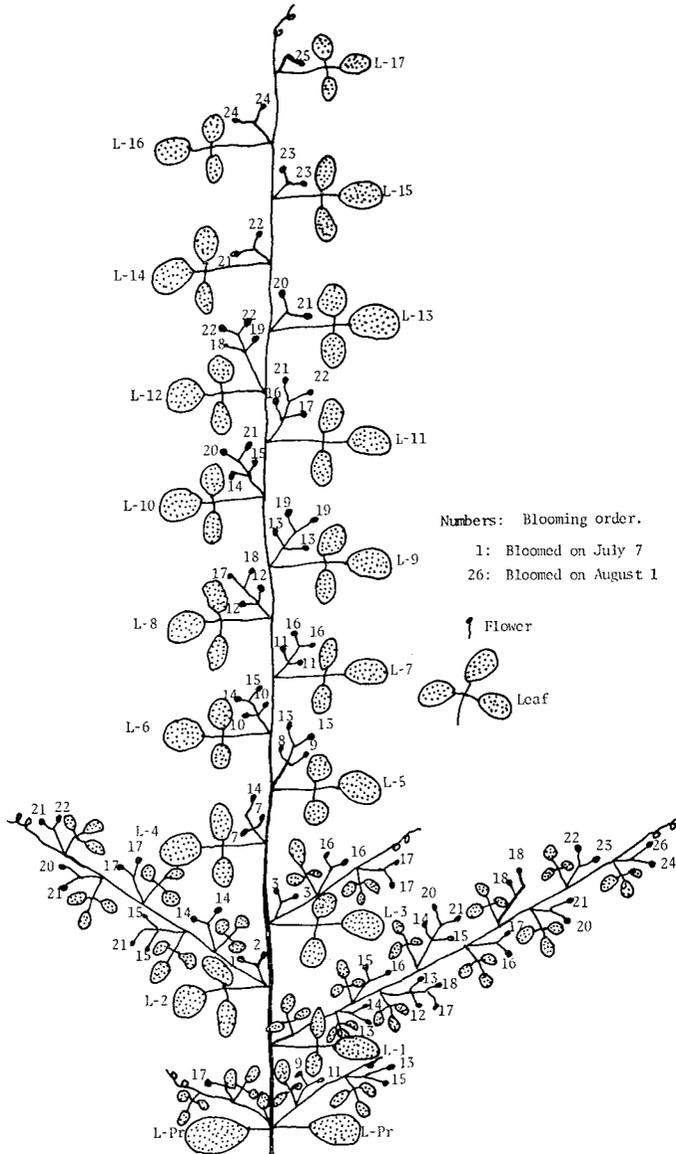


Fig. 2. Diagram of arrangement of leaves and flowers of Gin-tebō.

205 cm, and two internodes at the tip dropped during late growth stages (Fig. 4). L-1 and L-2 were small, L-3 was the largest, and the upper leaves gradually became smaller until L-14 and then more rapidly above L-14 (Fig. 5). L-Pr had defoliated completely by the beginning of blooming, the leaflets defoliated from the lower to the upper leaves, and by the end of growth almost all leaflets had dropped off. Branches came out from L-Pr-L-3, reached a maximum number by the start of blooming, and then many

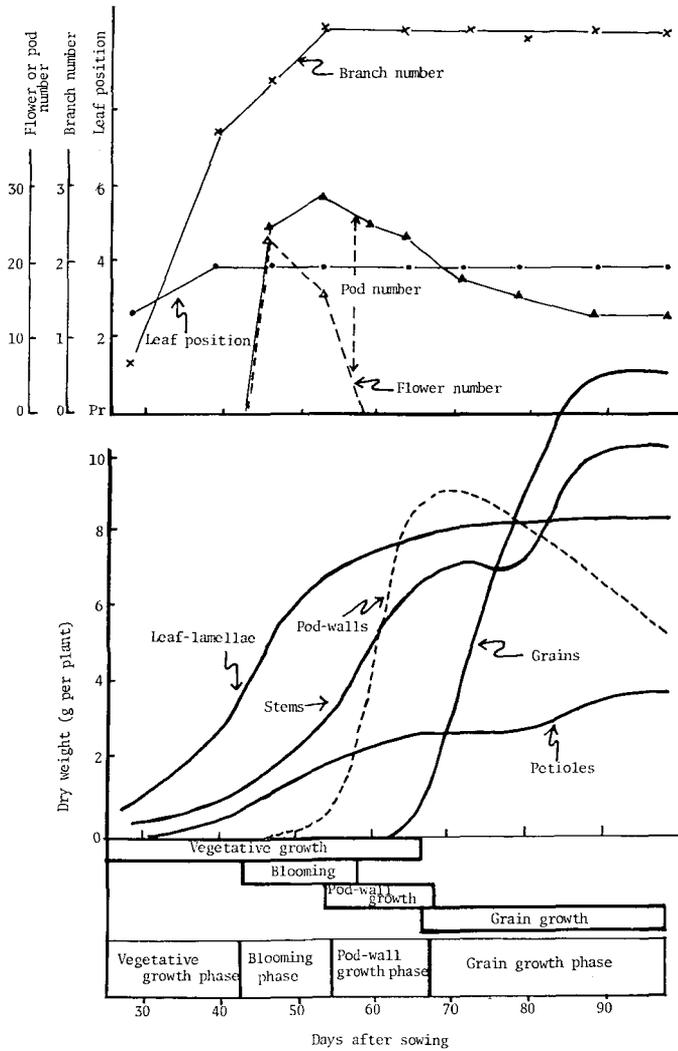


Fig. 3. Growth pattern of Taishō-kintoki.

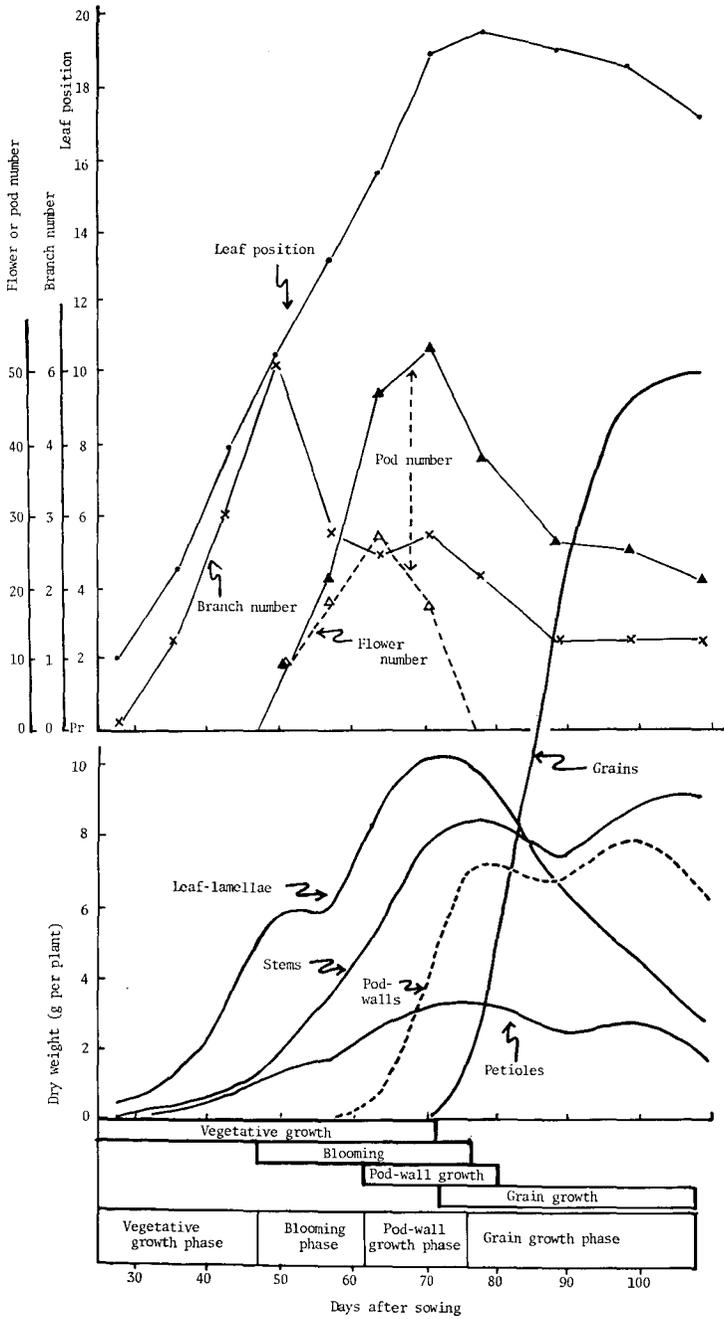


Fig. 4. Growth pattern of Gin-tebō.

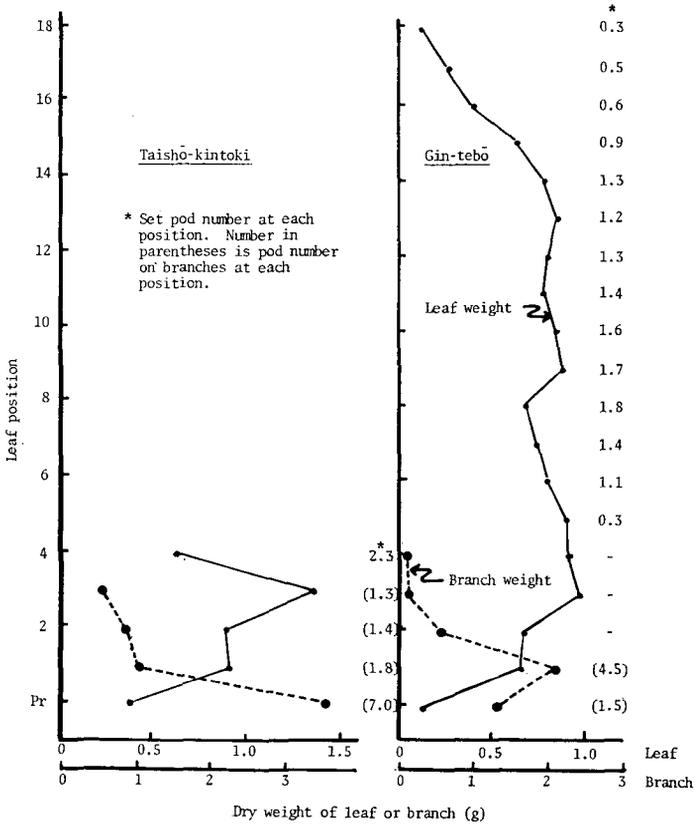


Fig. 5. Dry weight of leaves or branches and number of set-pods at various positions of Taishō-kintoki and Gin-tebō.

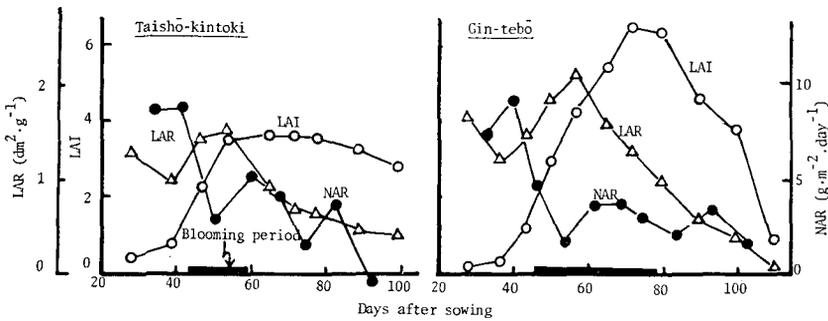


Fig. 6. Changes of LAI, NAR and LAR during growth of Taishō-kintoki and Gin-tebō.

branches dropped off during blooming (Fig. 4). LAI continued to increase until the end of blooming, reached a maximum value of 6.5, and then decreased very rapidly (Fig. 6). LAR increased with growth, reached a peak at about full blooming, and then decreased rapidly. The peak value of LAR was larger in Gin-tebō than in Taishō-kintoki.

Blooming and Pod Setting: In Taishō-kintoki blooming started on the 43rd day after sowing, and the number of blooms increased rapidly with time, reaching a maximum within a one-week period, after which they decreased rapidly. Blooming lasted for about 15 days (Fig. 3). The number of pods increased after blooming, reached a maximum, and then decreased gradually due to abortion until the numbers remained constant.

The order of blooming among flowers was rather complicated: Generally speaking, blooming started from the flowers on R-4*, and then those on R-3; within a branch the flowers of the top raceme bloomed first; and within a raceme the flowers at lower positions bloomed earlier (Fig. 1).

The number of set-pods was largest on B-Pr, followed by R-4 (Fig. 5). The pods on the main stem accounted for less than 20% of the total pod number, and the rest were on the branches. On four selected plants the date when flowers bloomed was recorded and the fate of these flowers was traced to see whether they set pods or not. Flowers which bloomed earlier were not necessarily high in setting percentage, but those which flowered very late failed to set (Table 3). The setting percentage was 42% for the whole plant, and was higher in the branches than in the main stem.

In Gin-tebō blooming started on the 46th day after sowing, and the number of blooming flowers increased gradually, reached a maximum three weeks after the start of blooming and then decreased. Blooming lasted for more than 30 days (Fig. 4). The number of pods increased for 25 days after the start of blooming, decreased gradually due to abortion, and then leveled off. When blooming started, L-7 was developing, and more than 10 leaves came out on the main stem after the start of blooming, but the branch number decreased during this period. The flowers on R-2 bloomed first, then those on R-3, and so on upward. This "lower-to-upper" blooming order is the reverse of that of Taishō-kintoki.

The blooming interval between a raceme at one position and the next raceme on the main stem was about 1.5 days, which was faster than the leafing interval (Fig. 7). Thus, about 70 days from sowing, blooming on

* For convenience the following abbreviations are used to indicate various organs at each position on the main stem; for example L-1, S-1, B-1 and R-1 are the 1st trifoliated leaf, the internode just below L-1, the branch and the raceme at L-1, respectively.

TABLE 3. Number and setting percentage of flowers on main stem and branches which bloomed on successive dates of Taishō-kintoki (Numbers for four plants)

Days after the start of blooming	Main stem	Branches	Total	Setting percentage
0	2/4*	—	2/4	50
1	3/5	—	3/5	60
2	1/5	4/6	5/11	45
3	4/8	6/10	10/18	56
4	0/2	6/10	6/12	50
5	0/1	3/9	3/10	30
6	1/1	4/5	5/6	83
7	—	4/6	4/6	67
8	0/2	6/8	6/10	60
9	0/1	3/8	2/9	33
10	0/1	6/13	6/14	43
11	0/3	4/8	4/11	36
12	0/1	2/12	2/13	15
13		0/5	0/5	0
14		0/4	0/4	0
15		0/1	0/1	0
16		0/1	0/1	0
Total	11/34	48/107	59/141	
Setting percentage	32	45	42	

* Number of set-pods/Number of blooms.

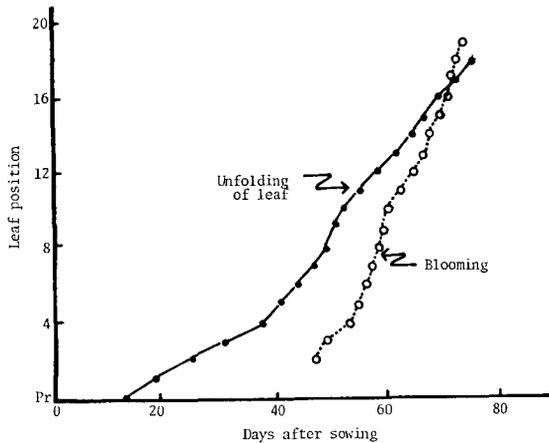


Fig. 7. Date of unfolding of leaves and start of blooming of racemes at various positions on the main stem of Gin-tebō.

R-17 took place ahead of the unfolding of L-17. Although L-18 developed to some extent and the flowers on R-18 and R-19 bloomed, the organs above L-16 dropped off later. These phenomena suggest that when the blooming of a raceme takes place ahead of the unfolding of the leaf at that position, the stem terminates there.

The flowers on a branch started to bloom about two weeks after the flowers on the raceme at the leaf of the main stem from where the branch emerged. Within a branch the flowers on the raceme at a lower position bloomed earlier. Within a raceme the flowers at a lower position bloomed earlier.

The number of set-pods was largest on B-1, one or two on R-6–R-14, less than one on R-15–R-17, and zero on R-2–R-4 (Fig. 5). The pods on the main stem occupied more than 70% of the total pod number. The setting percentage was 25% for the whole plant and was higher in the main stem than in the branches.

Dry Matter Production: In both varieties, dry weight increased actively in the leaf-lamellae first, and then in the stem (Fig. 3 and Fig. 4). As it was difficult to collect all the defoliated leaflets, the weight of leaf-lamellae presented in these figures does not include the weight of this plant part. Nevertheless, in Taishō-kintoki there was no decrease in the weight of leaf-lamellae until the end of growth, whereas in Gin-tebō there was a marked decrease after the rapid grain growth began.

In both varieties the weight of the stems decreased slightly during the initial stage of rapid grain growth, and then increased again during the later growth stages. Changes in the weight of petioles followed a similar pattern to that of the stem.

The weight of pod-walls started to increase rapidly 10 to 15 days after the start of blooming, reached a peak, and then decreased. In Taishō-kintoki this peak occurred about 25 days after the start of blooming, and then the weight decreased considerably. In Gin-tebō, the peak was not prominent because the growth of pod-walls occurred successively from lower to upper positions.

The weight of grains started to increase rapidly about two weeks after the start of rapid pod-wall growth, and continued to increase for about 25 days. The rate of increase of the grain weight was higher, the duration of the period of rapid increase was longer, and the grain yield was higher in Gin-tebō than in Taishō-kintoki (1.89 and 4.00 t/ha, respectively).

The net assimilation rate (NAR) was 8–9 g·m⁻²·day⁻¹ at early growth stages and then decreased rapidly until the start of blooming (Fig. 6).

Although the NAR remained at a rather low level after blooming, there were two small peaks at the rapid growth periods of the pod-walls and of the grains. The decrease of NAR at the end of growth was more significant in Taishō-kintoki than in Gin-tebō.

Carbohydrates: The stems had the highest carbohydrate (sugars plus starch) content of the vegetative organs indicating that the stems are a storage organ for carbohydrates.

The carbohydrate content of the stems decreased gradually during the early growth stages, reached a minimum at full blooming, increased slightly, decreased to give a second minimum at the rapid pod-wall growth, and then

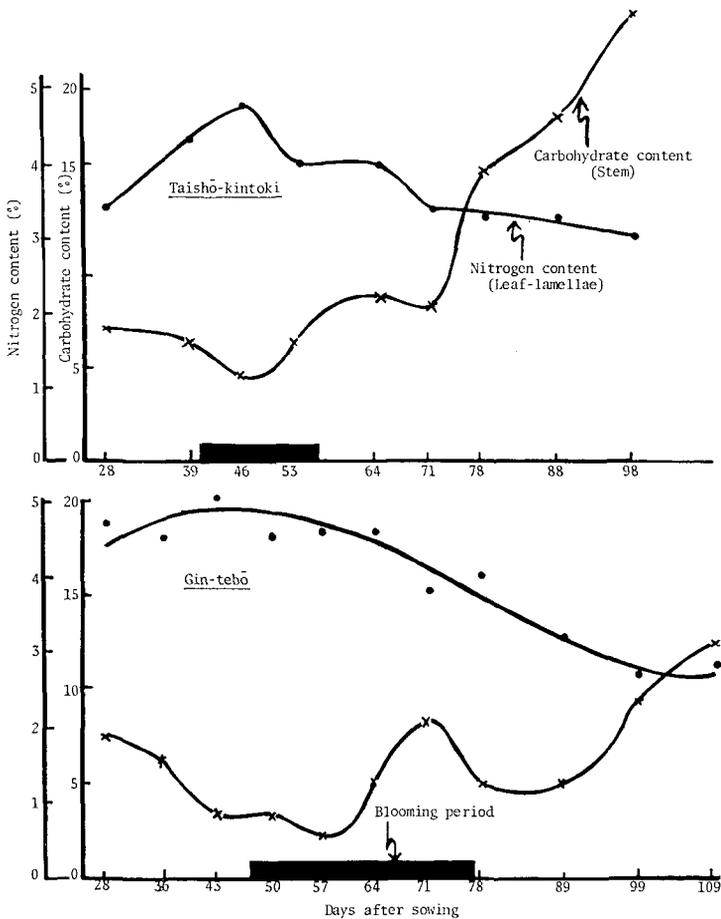


Fig. 8. Changes of nitrogen content of leaf-lamellae and carbohydrate content of main stem during growth of Taishō-kintoki and Gin-tebō.

increased during the later stages of grain growth (Fig. 8). The content was generally higher and the increase during the later growth stages was larger in Taishō-kintoki than in Gin-tebō.

The amount of carbohydrates accumulated in the vegetative organs was negligible before blooming, and increased during grain growth, especially in Taishō-kintoki (Fig. 9).

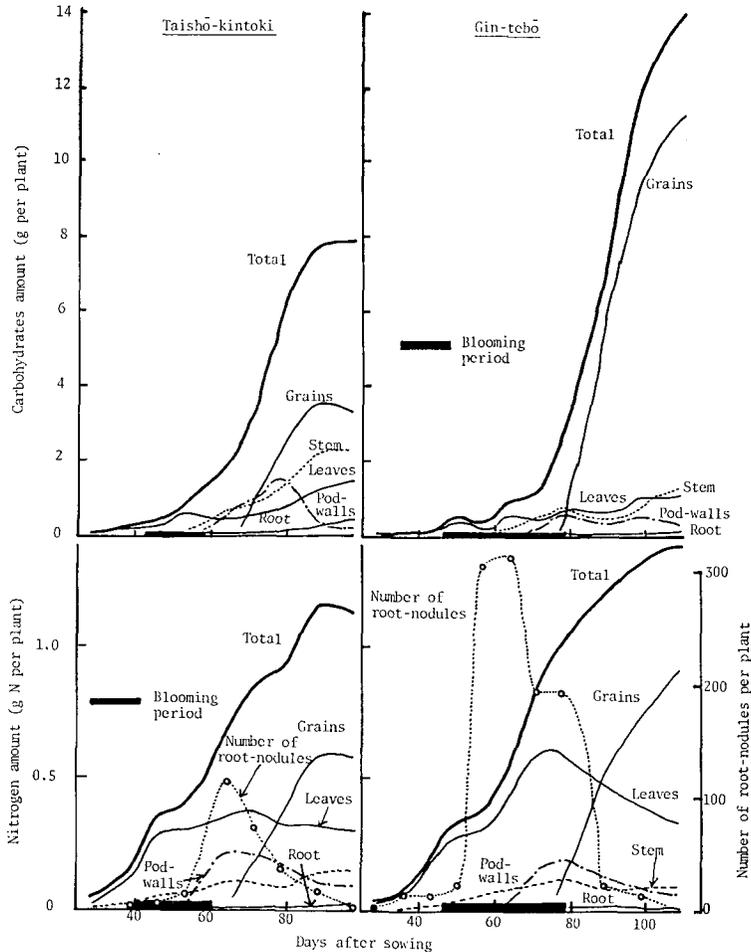


Fig. 9. Accumulation of carbohydrates and nitrogen in various organs, and change of root-nodule number during growth of Taishō-kintoki and Gin-tebō.

Thus, it can be said that at the periods of full blooming and rapid pod-wall growth the source capacity could not catch up with the demands

of the sink, but the source capacity exceeded the sink capacity during the later stages of grain growth. The excess of source capacity was more prominent in Taishō-kintoki than in Gin-tebō.

A considerable amount of carbohydrates accumulated in the pod-walls before the start of rapid grain growth and this accumulation decreased rapidly during grain growth. This observation indicates that the pod-walls serve as a temporary storage organ of carbohydrates that is translocated from the vegetative organ to the grains.

Nitrogen: The leaf-lamellae had the highest nitrogen content indicating that this organ serves as a major storage organ of nitrogen. The nitrogen content of the leaf-lamellae was high at the early growth stages, decreased when the weight of the pod-walls started to increase rapidly, and continued to decrease gradually during grain growth (Fig. 8).

Nitrogen accumulated in the plant continuously throughout growth, although it was slow during the peak of blooming (Fig. 9). The amount of nitrogen accumulated in the plant was far larger after the start of blooming than before. The amount of nitrogen in the leaf-lamellae increased rapidly at the early growth stages, more slowly during blooming, reached a maximum, and then decreased during grain growth, especially in Gin-tebō. The amount in the stems was small. The amount in the pod-walls increased rapidly when growth was rapid, and then decreased considerably when grain growth became rapid. This observation indicates that some nitrogen in the leaf-lamellae and pod-walls is translocated to the grains during grain growth. The amount of nitrogen in the grains increased during grain growth, and was much more than in other organs by the end of growth.

The number of root-nodules was small at the early growth stages, increased rapidly after the start of blooming, reached a maximum at about the period when the pod-walls were growing rapidly, and then decreased (Fig. 9). The maximum number was larger, and the number was kept high for a longer period in Gin-tebō than in Taishō-kintoki. Thus, it can be speculated that root-nodule activity was low until the start of blooming and became higher during the periods of blooming and rapid pod-wall growth, and was higher in Gin-tebō than in Taishō-kintoki.

Composition of Normal and Aborting Pods: The following three samples were collected from Taishō-kintoki: (a) Normally developing pods about 10 days after blooming (grains in them were still extremely small), (b) pod-walls of normally developing pods about 20 days after blooming, and (c) pods about 20 days after blooming, which became yellow, contained no grain, and were considered ready to abort.

These three samples had almost the same weight. The sugar content of the normal young pod-walls (b) was very high, while the aborting pods (c) were apparently lower in sugars and starch content than the other (Table 4). Potassium content was apparently lower in the aborting pods.

TABLE 4. Composition of normal and aborting pods (%)

Condition of pods	N	P	K	Sugars	Starch
(a) Normal young pods	3.11	0.48	2.84	3.36	5.94
(b) Normal pod-walls	2.00	0.28	2.96	13.10	5.13
(c) Aborting pods	2.12	0.28	1.37	1.90	3.62

These data indicate that shortage of carbohydrates during pod-wall growth is one of the causes of abortion, although other causes, such as retarded translocation of mineral elements, can not be excluded completely.

2. Photosynthetic Rate

Photosynthetic Rate of Leaves at Various Positions: The photosynthetic rate per unit leaf area (po) of leaves at various positions on the main stem was measured during the growth of Taishō-kintoki and Gin-tebō³⁴. Measurements were made at 40 klux, because preliminary observations demonstrated that the po increased with an increase of light intensity up to about 40 klux, above which there was almost no increase.

In Taishō-kintoki the po of L-Pr increased at early growth stages, reached a peak, and then decreased (Fig. 10). The po of L-1 and L-3 increased gradually with growth, remained above 30 mg CO₂·dm⁻²·hr⁻¹ for some time and then decreased gradually from about the end of blooming.

In Gin-tebō the po of L-Pr, L-1 and L-3 increased in the early stages, reached a peak, and then decreased rapidly with senescence; the peak moved successively from the lower to the upper leaves. The po of L-6, L-9 and L-12 increased gradually, remained above 30 mg CO₂·dm⁻²·hr⁻¹ for various periods depending upon the position of the leaves, and then decreased gradually almost simultaneously from the later period of blooming. In L-15 the po reached a maximum by the end of blooming and then decreased along with that of L-9 or L-12.

There was no clear difference in the maximum value of po between the two varieties, or among leaves at various positions.

Relation between Photosynthetic Rate and Sugar or Nitrogen Content: With growth of a leaf the leaf area increased, reached a maximum, and

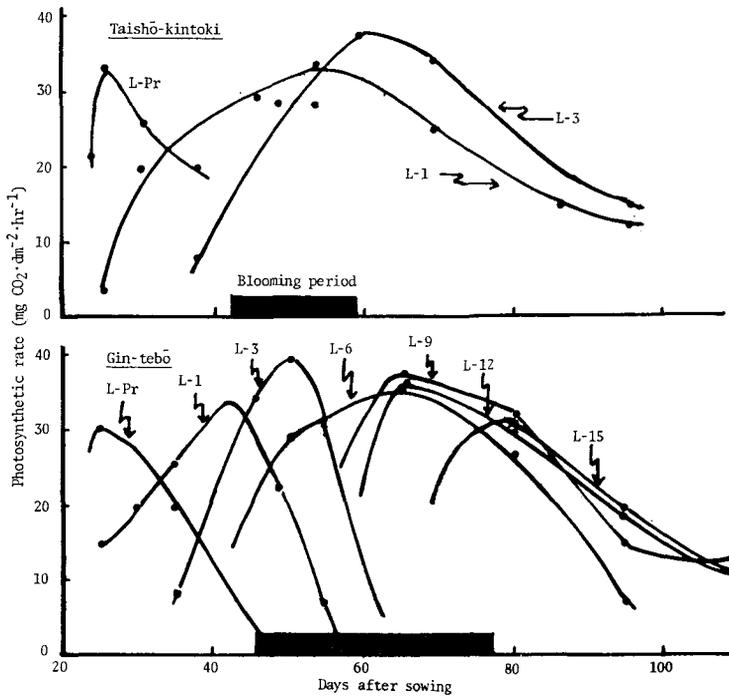


Fig. 10. Changes of photosynthetic rate (at 40 klux) of leaves at various positions on the main stem at successive growth stages of Taishō-kintoki and Gin-tebō.

was kept at this value, and then decreased in some cases (Fig. 11). The dry weight of the leaf-lamella increased with the increase of leaf area, and continued to increase gradually after leaf area expansion ceased. In some cases it decreased at later stages.

The p_o was low in the early stages, increased gradually with growth, reached a peak just after leaf area expansion ceased, and then decreased. The difference of p_o at between 40 klux and 10 klux was larger in young than old leaves.

The respiratory rate per unit area of a leaf was high in the early stages, decreased with growth until leaf area expansion was completed, and then remained almost constant for a long period.

Nitrogen content decreased gradually with age, although a slight increase was evident in some cases at early stages. Chlorophyll content also decreased gradually with age. Sugar content increased slightly or remained constant in the early stages, started to increase about 20 days after the maximum leaf area was reached, and then continued to increase until senescence. Starch

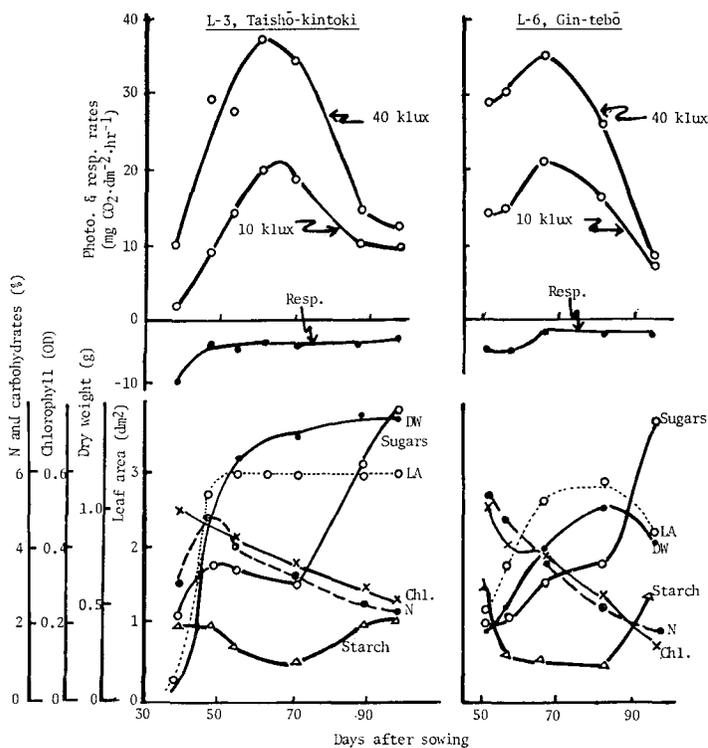


Fig. 11. Changes of photosynthetic and respiratory rates, and content of various constituents during growth of selected leaves.

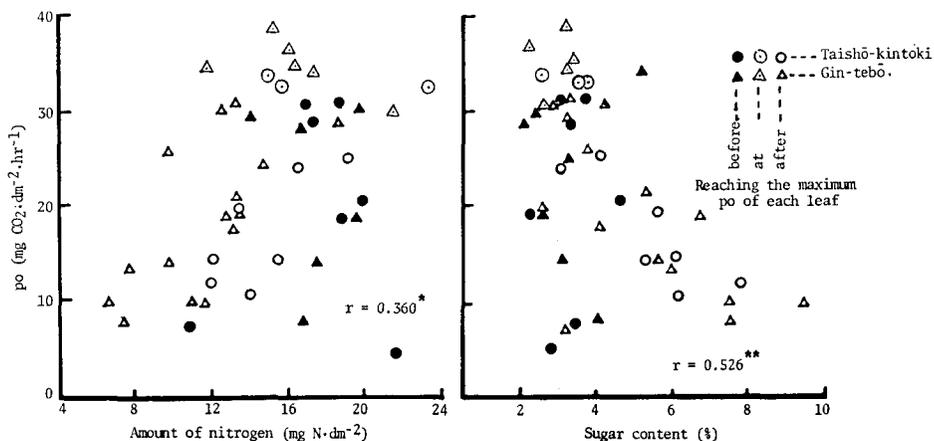


Fig. 12. Relations between p_o and amount of nitrogen per unit leaf area (left), and between p_o and sugar content (right).

content was high at a very early stage, decreased with growth, and increased slightly again in later stages.

Fig. 12 (left) was prepared to assess possible relationships between nitrogen content and p_o when all of the data for leaves at various positions of the two varieties at various growth stages were used. There was a weak correlation between the amount of nitrogen per unit leaf area and p_o . When the p_o was highest for each leaf, these leaves had 12–20 mg N·dm⁻². Leaves whose p_o was increasing with growth generally had a lower p_o value than expected from their nitrogen content. The correlation improves considerably if data are excluded for such leaves. There were, however, some cases of old leaves whose p_o was lower than expected from their nitrogen content.

The result of a similar study to assess the relationship between sugar content and p_o is illustrated in Fig. 12 (right). There was a statistically significant negative correlation between sugar content and p_o . When the p_o was at its highest value for each leaf, sugar content was less than 4%. It appears that when sugar content goes up above 5%, p_o decreases. However, in the cases of young developing leaves, p_o was low even if sugar content was low. There was no relation between starch content and p_o .

The following relationships seem evident: (a) In the case of leaves that have completed their leaf area expansion, p_o is controlled by nitrogen content; and (b) when leaves are aging there are cases when p_o decreases due to an accumulation of sugars caused by interrupted translocation of photosynthates from the leaves.

Photosynthetic and Respiratory Rate of Pods: The respiratory rate of pods (pod-walls and the grains in them) was high at early stages and

TABLE 5. Changes of photosynthetic and respiratory rates of pods during growth (mg CO₂·g⁻¹·hr⁻¹)

Growth stage	Pod length (cm)	Dry weight (g/pod)	Apparent photosynthetic rate at		
			40 klux	10 klux	0 klux
Pods were slender.	6.17	0.09	0.36	0.07	-5.34
Pods fully developed, grains started to grow.	7.08	0.19	0.49	-0.95	-4.40
Pod-walls and grains were juicy and green.	8.40	0.76	-0.22	-0.89	-2.57
Pod-walls started to lose green color, grains were white.	9.60	1.76	-0.50	-0.69	-2.10
Pods-walls were pale yellow, grains were dark red.	—	1.89	-0.92	-0.86	-1.10
Pods were pale brown and grains were dark red and dry	—	1.85	0.00	0.00	0.00

TABLE 6. Specific activity and amount of ^{14}C in various organs after 10 days from ^{14}C feeding at leaves on various positions of Taishō-kintoki at full blooming ($10\ \mu\text{Ci}\ ^{14}\text{C}$ was fed)

Organ		Specific activity (dpm/mg)				^{14}C amount (dpm $\times 10^3$)				
		^{14}C was fed at								
		L-1	L-2	L-3	L-4	L-1	L-2	L-3	L-4	
Leaves	L-4	30	22	29	2646	20	31	26	3017	
	L-3	31	17	1435	6	51	32	2310	11	
	L-2	33	1634	25	6	38	2206	27	6	
	L-1	1549	10	13	7	1750	12	14	9	
	L-Pr	29	13	10	10	24	12	8	10	
Stem	S-4	41	37	297	2050	11	15	101	820	
	S-3	59	76	845	310	19	21	262	124	
	S-2	157	681	439	68	44	252	136	23	
	S-1	336	317	253	59	433	418	306	81	
Roots		219	335	156	42	398	580	315	84	
Racemes	R-4	22	—	146	967	22	—	108	1654	
	R-3	26	18	310	130	5	7	127	30	
Branches	B-3	L & S*	38	22	334	227	29	19	264	170
		Racemes	14	20	125	69	5	1	25	25
	B-2	L & S	21	253	163	11	19	650	182	18
		Racemes	40	89	41	33	22	91	23	16
	B-1	L & S	60	22	31	4	119	62	57	6
		Racemes	30	17	32	4	32	20	35	4
	B-Pr	L & S	33	153	61	23	92	141	218	82
		Racemes	22	98	45	18	27	28	71	29
	Total		—	—	—	—	3160	4598	4615	6219
	Translocation percentage		—	—	—	—	45	52	50	52

* Leaves and stem.

decreased with growth (Table 5). The apparent photosynthetic rate at 10 klux was negative except at very early stages, and at 40 klux it was positive until initiation of the grain growth stage when it became negative.

From these data it seems evident that the pod-walls have the ability to photosynthesize, but the rate is generally less than its respiratory rate, except at very early stages. Consequently pods cannot continue growth on their own photosynthetic products.

3. Translocation of Photosynthates

Using Taishō-kintoki and Gin-tebō, the fate of photosynthates was traced as they were assimilated by the leaves at various positions and at various growth stages³⁰. For this purpose $^{14}\text{CO}_2$ was fed to various leaves, and after about 10 days the plants were sampled, separated into various organs, dried, weighed, ground and assayed for ^{14}C . From the dry weight and the specific activity the amount of ^{14}C in each organ was worked out.

When $^{14}\text{CO}_2$ was fed to L-1, L-2, L-3 and L-4 of Taishō-kintoki at the full blooming stage the following was observed (Table 6): (a) the specific activity was very high in the ^{14}C -fed leaf, especially in L-4; (b) low in all other leaves on the main stem; (c) high in the internode just below the ^{14}C -fed leaf, especially when the feeding was made at higher positions; (d) noticeably high in the branch at the position of the ^{14}C -fed leaf, except for the L-1 feeding; (e) high in the raceme at the position of the ^{14}C -fed leaf

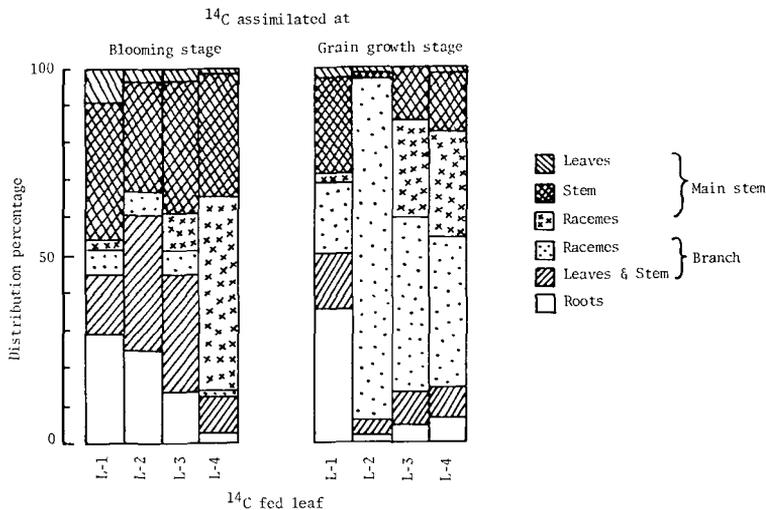


Fig. 13. Distribution of ^{14}C assimilated by leaves at various positions at the blooming and grain growth stages of Taishō-kintoki.

in the cases of L-4 or L-3 feeding; and (f) higher in the roots in the cases of L-2 or L-1 feeding. The total amount of ^{14}C remaining in the plant after 10 days was larger when ^{14}C was fed to the leaves at higher positions. The amount of ^{14}C remaining in the ^{14}C -fed leaf was highest when L-4 was fed and smallest when L-1 was fed. The translocation percentage (percentage of the amount of ^{14}C in organs other than the ^{14}C -fed leaf on the basis of the total amount of ^{14}C remaining in the plant) was slightly lower in the L-1 feeding than in other cases. Fig. 13 (left) shows the distribution of ^{14}C resulting from translocation from the ^{14}C -fed leaf to various organs: (a) Roots received photosynthates more from lower leaves; (b) branches received more from L-2 or L-3; and (c) photosynthates which accumulated in the racemes of the main stem came mostly from L-4.

TABLE 7. Distribution of ^{14}C assimilated at the 1st leaf of B-2 of Taishō-kintoki during grain growth (20 μCi ^{14}C was fed)

Organ		Dry weight (g)	Specific activity (dpm/mg)	^{14}C amount (dpm $\times 10^3$)	
Leaves	Above L-2	3.57	2	6	
	L-2	1.19	3	3	
	Below	1.81	3	5	
Main stem	Above S-2	1.27	74	94	
	S-2	0.45	273	123	
	Below S-2	1.61	205	330	
	Roots	2.55	96	244	
Racemes		4.50	44	198	
Branches	2nd leaf	0.73	21	15	
	B-2	1st leaf	0.72	3143	2263
	Stem	0.53	3083	1428	
	Racemes	0.89	2692	2396	
	B-1	5.75	12	67	
B-Pr		13.22	8	109	
Total		38.79	—	7281	
Translocation percentage		—	—	69	

When ^{14}C was fed at the active grain growth stage of Taishō-kintoki, the tendency of observed specific activities in various organs was almost the same as during the previous growth stage, although the activity was lower in the ^{14}C -fed leaves and higher in the racemes on the branches. A greater amount of ^{14}C remained in the plant when ^{14}C was fed to leaves at upper positions. The translocation percentages at this growth stage were above 68% and were higher than those at the full blooming stage, except for the ^{14}C feeding at L-1 in which it was 41%. The distribution of ^{14}C in various organs (Fig. 13, right) demonstrates that almost all photosynthates at this growth stage accumulate in the racemes (grains), especially those on the branches, except in the case of L-1 feeding when the distribution to the roots was large.

When ^{14}C was fed to the 1st leaf of B-2 of Taishō-kintoki at the start of grain growth, (a) a major portion of ^{14}C was distributed within the branch, especially to the racemes of the branch, and (b) only a small amount was translocated to the main stem, especially the internodes below the L-2 and the roots (Table 7).

When ^{14}C was fed to L-1, L-2, L-3, L-4 or L-6 at the start of blooming of Gin-tebō, the following was observed: (a) The specific activity was high in the ^{14}C -fed leaves, especially when $^{14}\text{CO}_2$ was fed to L-6 which was still in its growing stage; (b) generally low in other leaves on the main stem although noticeably higher values were observed in the growing leaves above

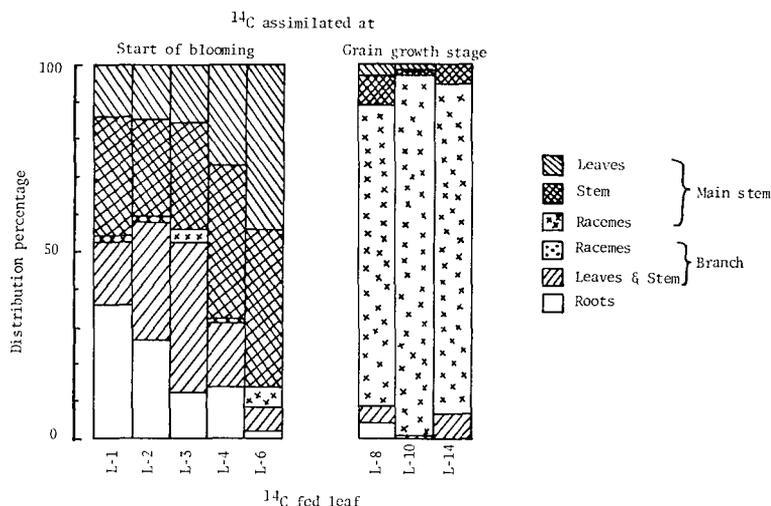


Fig. 14. Distribution of ^{14}C assimilated by leaves at various positions at start of blooming and grain growth stage of Gin-tebō.

TABLE 8. Specific activity and amount of ^{14}C in various organs after 10 days from ^{14}C feeding at leaves on various positions of Gin-tebō during growth stage ($20 \mu\text{Ci } ^{14}\text{C}$ was fed)

Organ		Specific activity (dpm/mg)			^{14}C amount (dpm $\times 10^3$)				
		^{14}C was fed at							
		L-8	L-10	L-14	L-8	L-10	L-14		
Leaves	Above L-15	} 6	} 10	9	} 22	} 29	4		
	L-14			2322			2113		
	L-13			0			0		
	L-12	} 6	} 47	0	} 13	} 70	0		
	L-11			1821			0		
	L-10			2052			2349		
	L-9	} 10	} 5	} 1	} 8	} 5	} 4		
	L-8							1416	46
	L-7							5	46
Below L-6	14	20	1	26	46	4			
Stem	Above S-15	} 11	} 3	345	} 21	} 2	124		
	S-14			715			336		
	S-13			218			10		
	S-12	} 10	} 26	} 22	} 9	} 10	} 19		
	S-11							39	12
	S-10							14	16
	S-9	} 14	} 30	} 6	} 12	} 16	} 15		
	S-8							36	6
	S-7							50	29
	S-5 & 6	} 71	} 5	} 6	} 78	} 6	} 15		
	Below S-4							50	4
Roots	66	1	20	87	2	24			
Racemes	Above R-15	} 9	} 14	1232	} 73	} 133	2230		
	R-14			3382			4532		
	R-13			400			364		
	R-12	} 6	} 301	} 193	} 16	} 1342	} 461		
	R-11							1241	4281
	R-10							11	98
	R-9	} 326	} 98	} 26	} 25	} 347	} 319		
	R-8							153	463
	R-7							134	563
	Below R-6	134	5	26	466	23	319		
Branches	B-3	} 5	} 3	—	} 73	} 7	—		
	B-2			—			—		
	B-1			36			663		
	B-Pr	—	2	—	—	22	—		
Total	—	—	—	3416	9263	11220			
Translocation percentage	—	—	—	59	75	81			

L-5 when ^{14}C was fed to the leaves above L-3; (c) high in organs immediately adjacent to the ^{14}C -fed leaf, *i. e.* the branch and/or the raceme emerging from the node; and (d) higher in the roots when ^{14}C was fed to the lower leaves. The amount of ^{14}C remaining in the plant was smaller in the lower-leaf feedings than the upper-leaf feedings. When ^{14}C was fed to the leaves at lower positions, the ^{14}C was distributed more to the roots and the branches, whereas, when ^{14}C was fed to L-6, most of the ^{14}C was distributed to the leaves and stem of the main stem (Fig. 14, left).

When ^{14}C was fed to L-8, L-10 or L-14 of Gin-tebō during the active grain growth stage, the specific activity was high in the ^{14}C -fed leaves and also in the racemes at the position of the ^{14}C -fed leaf (Table 8). The amount of ^{14}C remaining in the plant was apparently smaller when ^{14}C was fed at L-8 than when it was fed at L-10 or L-14. The translocation percentage was very high (81%) when L-14 was fed, and was lower when the lower leaves were fed. Almost all of the ^{14}C assimilated at this growth stage was distributed to the racemes on the main stem (Fig. 14, right).

From these data the following statements can be made:

(a) The amount of ^{14}C remaining in the plant 10 days after the ^{14}C feeding was less when the ^{14}C was fed to older than to younger leaves. The reason is, most probably, that the loss of photosynthates by respiration is greater in older than younger leaves: As older leaves have more carbohydrates and have more mature sinks, new photosynthates are probably more consumed by respiration than incorporated into constituents.

(b) The translocation percentage is low when a leaf is young because the leaf itself is the major sink. It increases with age and reaches a value of 60-70% when the leaf is fully expanded. It can be as high as 80% when the photosynthates of a leaf are efficiently utilized by the corresponding sink. It decreases to a low value when a leaf becomes old and the sink is no longer active.

(c) A source-sink unit as illustrated in Fig. 15 seems to exist. The unit is composed of a leaf (the source), and an internode just below the leaf; a branch and/or a raceme at the position of the leaf (the sinks). Fig. 16 was prepared by rearranging the data of the ^{14}C feedings at L-10 and L-14 of Gin-tebō (Table 8) and is based on the above-mentioned source-sink unit concept. This figure supports the existence of such a unit in the case of the upper leaves of Gin-tebō during the active grain growth stage: Almost all the photosynthates of L-10 or L-14 are accumulated in the raceme of the unit to which the ^{14}C -fed leaf belongs. A small portion of ^{14}C originating in this unit, however, is translocated to comparable units that occurs

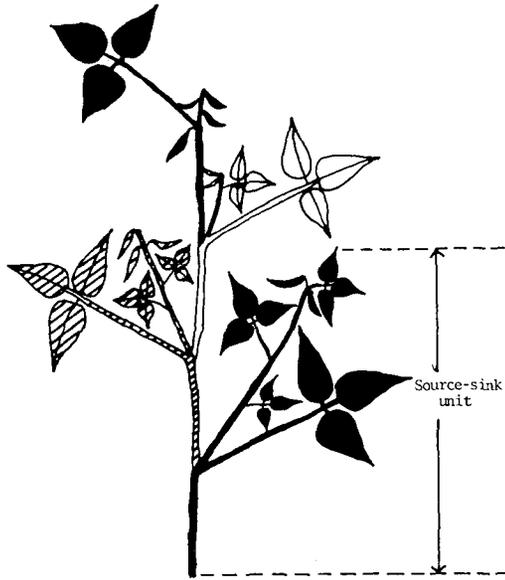


Fig. 15. Diagram of a source-sink unit.

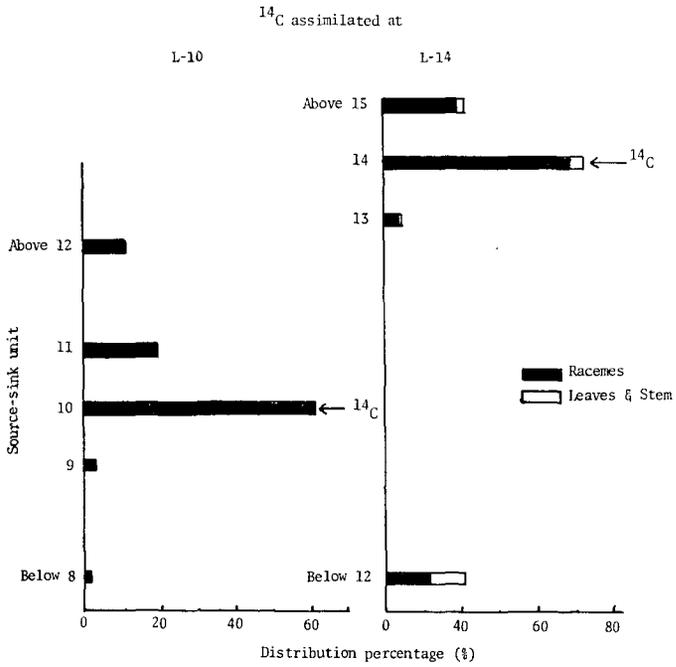


Fig. 16. Distribution of ^{14}C assimilated at L-10 and L-14 at the grain growth stage of Gin-tebō.

above it.

(d) However, this type of source-sink unit is not always prominent. Fig. 17 illustrates that at the start of blooming of Gin-tebō the ^{14}C assimilated by L-6 is translocated actively to the units that occur above this unit and are at their rapid growth stage. The ^{14}C assimilated by L-1, however, is translocated to the lower unit and to the roots. Thus, it can be said that if a very active sink exists nearby, the photosynthates produced by a unit are translocated to the sink by their big demand; and if the source capacity of a unit exceeds the sink capacity within the unit, the excess photosynthates are forced to translocate from the unit.

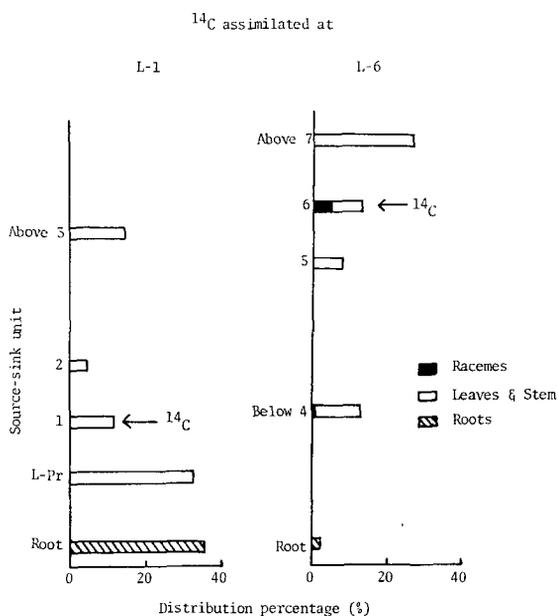


Fig. 17. Distribution of ^{14}C assimilated at L-1 and L-6 at start of blooming of Gin-tebō.

(e) A branch grows with the photosynthates of the leaf at the node of the main stem from which the branch emerges at early stages of its development. Even after blooming, photosynthates of the leaves on the main stem are translocated to the developing grains on branches, especially in the case of Taishō-kintoki. On the other hand, almost no photosynthates are translocated from the leaves of branches to grains produced on the main stem.

4. Discussion

Photosynthetic rate per unit leaf area (p_o) increases with the growth of a leaf, reaches a maximum when the area of the leaf reaches its maximum, maintains the high rate for some time, and then decreases with age due to accumulation of carbohydrates because of slower removal of photosynthates from the leaf by translocation²²⁾ or due to translocation of nitrogen from the leaf.

The maximum photosynthetic rate observed in this study was about $40 \text{ mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{hr}^{-1}$, which is comparable to that of C-3 plants such as rice³⁶⁾, but lower than C-4 plants such as maize³⁷⁾. This value is considerably higher than that reported for the field bean¹⁹⁾.

There was no difference in the maximum p_o value between the two varieties studied, although a varietal difference had been reported¹⁹⁾. Differences in the p_o among leaves at various positions was also small. However, the period during which the p_o remained high differed among varieties or leaf positions.

The translocation percentage of photosynthates from a leaf is low when the leaf is growing or when the leaf becomes old. The maximum value observed was about 80%. This value is lower than that of maize³⁷⁾, but is higher than that of various crops such as tomato²⁹⁾.

A field bean plant is considered to be composed of source-sink units, which are composed of a leaf, an internode, a raceme and/or a branch as illustrated in Fig. 15. When grains in a pod on a raceme of a unit are growing actively, these grains receive photosynthates mostly from the leaf within the unit. In this sense the source-sink unit is prominent in this crop²⁾.

However, as a growing apex does not have a sufficient source within its source-sink unit, it has to receive photosynthates from outside sources. The roots also do not have any source of their own. Thus, these sinks are dependent on the sources of the other units: The roots receive more photosynthates from the lower leaves, while actively growing apexes receive photosynthates from the leaves of a few units below them. On the other hand, when the source capacity exceed the sink capacity within a unit, the photosynthates of the unit are forced to translocate from it. A branch grows by receiving photosynthates mostly from the leaf on the main stem within the unit at early stages; later it grows from the photosynthates of leaves on the branch itself; but still accepts considerable amounts of photosynthates, if there are excess photosynthates produced by the leaf on the main stem. Because of these interactions among the source-sink units, the behavior of

the photosynthates of a leaf is complicated.

When pods grow, a considerable amount of carbohydrate accumulates in the pod-walls, and this accumulated carbohydrate is translocated into the grains during grain growth. Thus, the pod-walls are a temporary storage organ of carbohydrates translocated from the leaves to the grains. The pods perform photosynthesis to some extent, but are not an important photosynthetic source of dry matter for growing grains⁷. Judging from the low sugar content in aborting pods, the supply of photosynthates to growing pods is considered to be one of the key factors which determine the abortion percentage.

Four phases exist during the growth cycle of the field bean, *viz.*, vegetative growth, blooming, pod-wall growth and grain growth phases: (a) During the vegetative growth phase new leaves, branches and the stem differentiate and grow; (b) during the blooming phase the flowers that differentiate before and during this phase bloom, while the growth of leaves and stem also continues; (c) during the pod-wall growth phase the pod-walls grow actively and the growth of vegetative organs, especially the stem, continues; and (d) during the grain growth phase the grains in the developed pod-walls grow actively.

The root-nodules increase their number during the blooming phase, and seem to be most active during the pod-wall growth stage⁹.

In Taishō-kintoki, a determinate, only 4 trifoliated leaves are produced on the main stem, and development of the growth phases is apparent, although the vegetative growth overlaps with the blooming and pod-wall growth phases (Fig. 4).

Blooming proceed from the flowers on the raceme at the top of the main stem to those at lower positions^{15,20}. No new leaf differentiates after the start of blooming on the main stem, but leaves and branches which have already differentiated, and stems, continue to grow. Differentiation of flower primordia takes place at an early growth stage¹⁵. Blooming of flowers is completed within about 15 days. This period is shorter in determinates than indeterminates¹⁹. By the end of blooming the pod-walls of set-pods start to grow actively, and the growth of pod-walls is completed within 15 days. During this phase the stems continue to increase in weight. Then, from a few days before the end of pod-wall growth, the grains start to grow actively, and the active grain growth continues for about 25 days. During this phase the weight of leaves remains at a constant level, while that of the stems and petioles decreases slightly during the most active grain growth, but increases again during later stages.

During the most active periods of blooming and pod-wall growth the carbohydrate content of stems is low. This indicates that the demand of sinks is larger in comparison to the source capacity at these phases: (a) During blooming the sink size is larger because the leaves, branches and stems are actively growing, the root-nodule number is increasing, and blooming flowers also consume considerable amount of photosynthates; and (b) during the active pod-wall growth the stems are still growing and root-nodules consumes considerable amount of carbohydrates⁹ and these nodules may compete for photosynthates with the growing pods. In such a situation the abortion of flowers and young pods may result from an inadequate supply of photosynthates.

It has been estimated that in field beans 20-30% of differentiated flowers bloom, 20-35% of bloomed flowers set, and the setting percentage of differentiated flowers is less than 10%¹⁴. In this study, however, only the flowers which were visible to the naked eye were counted. Thus, the observed setting percentage of Taishō-kintoki was about 40%. Since the pods on the main stem grow ahead of those on the branches, the surplus of photosynthates of the leaves on the main stem is translocated to the branches and is used for the growth of pods. Thus, the setting percentage is higher in branches than in the main stem.

After the number of set-pods is established depending upon the source-sink balance during the blooming and pod-wall growth phases, the grains start to grow by using the carbohydrates and nitrogen stored in the pod-walls and also photosynthates synthesized and nitrogen fixed during the grain growth phase. During this phase the source capacity exceeds the sink capacity. The leaves are kept alive and maintain their weight until the end of growth, carbohydrates continue to accumulate in the vegetative organs¹², and the photosynthetic rate of the leaves decreases.

In this sense the source may be the limiting factor during the blooming and pod-wall growth phases and the source controls the setting percentage. Once the number of set-pods is established, the source may exceed the sink during the grain growth phase.

In Gin-tebō, a semi-indeterminate, about 20 trifoliated leaves are produced on the main stem, and development of the growth phases is not so apparent as in Taishō-kintoki because the growth phases overlap each other (Fig. 5).

Blooming starts from flowers on the raceme at a lower position on the stem, several leaves and racemes have differentiated above the point of blooming, blooming and pod-wall growth occurs successively from lower to upper racemes, and development of new leaves and racemes continues on the stems

acropetally during blooming. Since the activity of the main stem dominates, some weak branches drop off during blooming. Under such circumstances the vegetative growth, the blooming and the pod-wall growth phases overlap each other for a certain period¹⁶⁾.

The carbohydrate content of stems is low during blooming and pod-wall growth. This situation indicates that the sink capacity exceeds the source capacity during these periods. As the competition among sinks for photosynthates during these phases is more critical in this variety than Taishō-kintoki the setting percentage is correspondingly low (25%). However, Gintebō has more set-pods than Taishō-kintoki because it has more flowers due to more nodes on the main stem¹⁶⁾.

The time gap of blooming between the 1st and last flowers is about one month, that of pod-wall growth is shorter, and that of grain growth is still shorter. Thus, grain growth in the many pods is initiated within a short period. Since there are many pods and many grains growing almost at the same time, the demand for nitrogen is considerable. As nitrogen in the leaves is translocated to the grains, the lower leaves defoliate and the photosynthetic rate of the remaining leaves decreases almost concurrently due to shortage of nitrogen.

III. ANALYSIS OF INTERACTIONS AMONG PHOTOSYNTHESIS, TRANSLOCATION AND GROWTH, BY REMOVAL OF VARIOUS ORGANS

1. Compensation within and between the Source-Sink Units

In 1974 one plant of Taishō-kintoki per pot was planted in 10-liter pots each containing 10 kg of a soil mixed with 0.5 g N, 1.0 g P₂O₅ and 1.0 g K₂O, and grown in a glasshouse. At the end of blooming the following three treatments were given to L-4:

- (a) Control.
- (b) Terminal leaflet and one lateral leaflet were removed.
- (c) Terminal leaflet, one lateral leaflet, and pods at the side of the remaining lateral leaflet on R-4 were removed.

Then, ¹⁴CO₂ was fed to the remaining lateral leaflet of L-4, and the distribution of ¹⁴C within the L-4 unit 10 days after ¹⁴C feeding was traced.

The amount of ¹⁴C remaining in the L-4 unit was more in the leaflet-removal treatments than the control (Table 9). When none of the pods were removed, ¹⁴C was distributed more to the pods at the side of the ¹⁴C-fed leaflet on the raceme. However, when preselected pods were removed, distribution of ¹⁴C to the remaining pods increased considerably.

TABLE 9. Effect of removal of leaflets and/or pods on distribution of ^{14}C assimilated at a lateral leaflet of L-4 within the L-4 source-sink unit ($\text{dpm} \times 10^3$)

Organ	Treatment	Control	Leaflets removed	Leaflets and pods removed
L-4	^{14}C fed leaflet	831	1009	1414
	Other leaflets	10	—	—
	Petiole	62	337	230
R-4	Peduncle	92	141	179
	Pods I*	2953	5587	—
	Pods II*	1175	2380	9549
Stem		204	197	361
Total		5327	9651	11733

* I and II: Pods at the same or opposite sides as the ^{14}C fed leaflet, respectively.

Using the Gin-tebo plants which were grown in a field in 1974, the following four treatments were differentiated at the grain growth phase:

- (a) Control.
- (b) R-10 was removed
- (c) Racemes above R-6 were removed.
- (d) All racemes were removed.

Then, ^{14}C was fed to L-10 and traced 7 days after the feeding.

The translocation percentage from L-10 was 76% in the control, decreased slightly when R-10 was removed, and decreased more noticeably when more racemes were removed (Table 10). It is apparent that the translocation percentage is controlled by the sink capacity.

In the control a large amount of ^{14}C was distributed to R-10 and a smaller amount to R-11 and R-9. The removal of R-10 resulted in an increase of ^{14}C distribution to other racemes, particularly to R-11 and R-9. When the racemes above R-6 were removed, the amount of ^{14}C translocated to R-4 and R-5 increased. When all racemes were removed, the amount of ^{14}C translocated to the various remaining vegetative organs increased but the total amount of translocated ^{14}C decreased considerably.

These data demonstrate that each leaflet and some pods within a source-sink unit seem to compose a source-sink sub-unit: The terminal leaflet is the source of all pods within the unit; and a lateral leaflet at one side is the major source of the pods at that side of the raceme. Inter- or intra-

TABLE 10. Effect of removal of racemes on distribution of ^{14}C assimilated at L-10 during grain growth after 7 days from ^{14}C feeding in Gin-tebō ($\text{dpm} \times 10^3$)

Organ	Treatment	Control	Racemes removed		
			R-10	Above R-6	All racemes
Leaves	Above L-12	13	22	42	92
	L-11	18	12	29	56
	L-10	4159	5305	7938	11539
	L-9	7	11	26	55
	L-6~L-8	8	13	77	203
	Below L-5	49	32	28	40
Main stem	Above S-12	8	43	41	95
	S-11	96	112	33	63
	S-10	171	144	343	432
	S-9	43	52	170	265
	S-8~S-5	17	58	440	691
	Below L-5	24	31	588	861
Racemes	R-12	107	794	—	—
	R-11	2386	4156	—	—
	R-10	7294	—	—	—
	R-9	2842	4397	—	—
	R-6~R-8	83	2847	—	—
	Below R-5	105	595	3177	—
Roots		17	398	348	123
Total		17427	18951	13280	15014
Translocation percentage		76	72	40	23

unit compensations appear to operate: If a raceme of a source-sink unit is removed, the racemes just above and below the unit become the major sinks of the leaf of the unit, and if the pods at one side of the raceme of a sub-unit are removed, the remaining pods at the opposite side become the major sink of the leaflet.

2. Effect of Partial Removal of Vegetative or Reproductive Organs on Photosynthetic Rate and Translocation of Photosynthates

Using the potted Taishō-kintoki plants the following three treatments were differentiated at full blooming³⁵⁾.

- (a) Control: No treatment.
 (b) Pod-removal: All pods which existed and developed later were removed.
 (c) Leaf-removal: All leaves, except L-3, which existed and came out later were removed.

After giving these treatments the photosynthetic and respiratory rate of L-3 were measured during the course of growth. Separate plants received one of these three treatments, ^{14}C was fed to L-3 just after and again 20 days after giving treatments, and the distribution of ^{14}C was traced 10 days after the ^{14}C feeding.

When the treatments were differentiated, there were 11 leaves and about 20 young pods (including flowers) per plant. In the control there were 9 mature pods per plant and the leaves became yellow at the end of the experiment. In the pod-removal treatment the leaves became thicker than the control and were kept green, the total plant weight at the end of the experiment was smaller than in the control, but the weight of leaves, stems, branches and roots were more than double that of the respective organs of the control. In the leaf-removal treatment the total plant weight decreased after the treatment was given and became less than one third of the control

TABLE 11. Composition of various vegetative organs as affected by removal of pods or leaves in Taishō-kintoki

Treatment	Organ	L-3		Leaves and stem (Excluding L-3)	Root
		Leaf-lamella	Petiole		
Nitrogen contents (%)					
Control		0.91	0.72	1.11	2.18
Pod-removal		2.66	1.41	2.47	2.12
Leaf-removal		1.01	0.79	1.34	1.93
Sugar contents (%)					
Control		4.76	2.26	2.26	2.38
Pod-removal		8.76	5.96	5.81	3.79
Leaf-removal		2.03	5.86	3.58	1.06
Starch contents (%)					
Control		1.79	3.80	1.79	1.96
Pod-removal		5.18	34.6	13.80	10.90
Leaf-removal		1.64	4.33	3.67	1.49

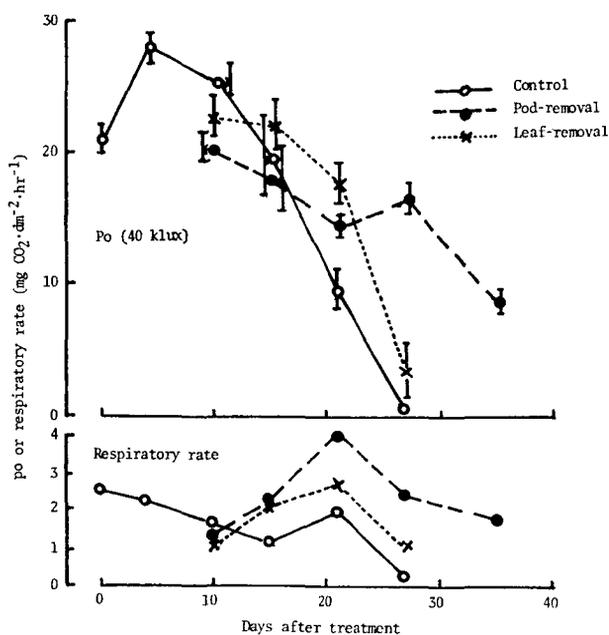


Fig. 18. Changes of po and respiratory rate of L-3 with growth in each treatment.

TABLE 12. Changes of area, dry weight, thickness and composition of L-3 after treatment in Taishō-kintoki

Treatment	Days after treatment	Area (dm ² /leaf)	Dry weight (g/leaf)	Thickness (g/dm ²)	Content (%) of		
					Nitrogen	Sugar	Starch
Control	0	1.785	0.86	0.482	4.63	9.18	1.87
	10	2.427	1.20	0.494	3.59	5.03	1.56
	21	2.069	0.96	0.463	2.07	4.92	1.65
	27	1.856	0.89	0.480	0.91	4.76	1.79
Pod-removal	10	2.468	1.38	0.449	4.00	5.76	1.99
	21	2.161	1.75	0.811	3.11	7.53	3.64
	27	2.109	1.78	0.842	3.05	6.03	4.52
	35	2.035	1.82	0.893	2.66	8.76	5.18
Leaf-removal	10	2.545	1.54	0.605	3.78	7.92	3.26
	21	2.214	1.20	0.542	2.36	6.37	1.54
	27	1.614	0.88	0.543	1.01	2.03	1.64

at harvest, L-3 became yellow and only a few pods developed on R-4, but the grain number per pod and the 1000-grain weight of these developed pods were almost the same as those of the control.

In the pod-removal treatment the contents of nitrogen and carbohydrates, especially that of starch, of the vegetative organs were higher than the control, whereas in the leaf-removal treatment no noticeable change in these contents was observed (Table 11).

In L-3 of the control the *po* reached a maximum value a few days after the start of the experiment when the leaf area expansion ceased, decreased rapidly with age, and was almost zero by the end of the experiment; the respiratory rate decreased with age (Fig. 18); the weight and thickness of the leaf-lamellae decreased slightly; nitrogen content decreased noticeably; and sugar content decreased slightly with age (Table 12). In L-3 of the pod-removal treatment the *po* was slightly lower than the control for about two weeks after giving the treatment, but the decrease with age was slower than the control; the respiratory rate started to increase from 10 days after giving the treatment, and remained high until the end of the experiment; the weight and thickness of lamellae increased; the nitrogen content was far higher than the control; and the content of sugars and starch increased with age. In L-3 of the leaf-removal treatment the *po* was kept slightly higher than the control for some time, but was very low at the end of the experiment; the weight of lamellae decreased considerably; and the contents of nitrogen, sugars and starch decreased noticeably with age.

The translocation percentage was far lower in the pod-removal treatment, and was slightly lower in the leaf-removal treatment than the control (Fig. 19). In the control the ^{14}C assimilated at L-3 at full blooming was distributed uniformly within the plant, except the roots which received only a small amount of ^{14}C , but that assimilated at the grain growth stage accumulated selectively in the grains. In the pod-removal treatment the ^{14}C moved down the stem, and a large portion was translocated to the branches at full blooming, and to the roots at a later growth stage. In the leaf-removal treatment the ^{14}C was distributed uniformly within the plant at full blooming, but only to the grains at the grain growth stage.

Since the plants were grown in pots and only a limited amount of nitrogen was given, the control plants suffered from nitrogen deficiency. The low nitrogen content of leaves due to translocation of nitrogen from the leaves to the grains resulted in a rapid decrease of the *po* during later growth stages. When all pods were removed, the source capacity exceeded the sink capacity although the vegetative organs became alternate sinks,

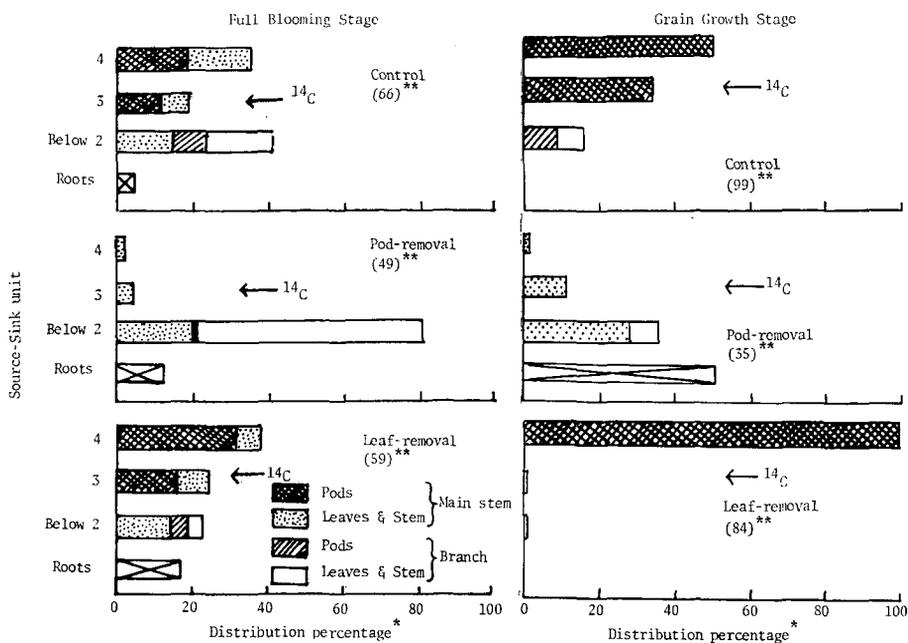


Fig. 19. Distribution of ^{14}C 10 days after ^{14}C feeding at L-3 at full blooming and grain growth in each treatment.

* Percentage of ^{14}C in each organ on the basis of total amount of ^{14}C in plant excluding ^{14}C fed leaf.

** Values in parentheses indicate the translocation percentage.

and the carbohydrate content and weight of the vegetative organs increased, but the total plant weight decreased. Since there was no translocation of nitrogen from the leaves to the grains, the nitrogen content of the leaves remained high, and the pod was kept high. Due to accumulation of carbohydrates in the vegetative organs, however, the rate of respiration which was not geared with growth was accelerated, and this resulted in a decrease of the total dry matter production. When leaves were removed during blooming, flowers and pods aborted due to the insufficient supply of photosynthates and the set-pod number decreased, but the set-pods contained almost the same number of grains with almost the same 1000-grain weight as those of the control. This means that the set-pod number (the sink size) was adjusted to coincide with the source capacity by the abortion of flowers and pods.

3. Effect of Partial Removal of Vegetative and Reproductive Organs on Yield Components

In 1975 Taishō-kintoki was grown in a field by the standard cultural

method, and the following treatments were differentiated^{3D}. All leaves (all-leaf-removal series) or two lateral leaflets of each leaf (leaflet-removal series) were removed 3, 10, 16, 23, 31, 37 and 44 days after the start of blooming. These dates of treatment are named here Nos. 1, 2, 3, 4, 5, 6 and 7, respectively. There was one more treatment (raceme-removal); *i. e.* the racemes at alternate nodes on the main stem and branches were removed 10 days after the start of blooming, and the flowers on each remaining raceme were removed except the one flower which bloomed first in each raceme. Thus, there were 16 treatments in all including the control.

In the control the plant height, branch number and total leaf area increased until the No. 3 stage; the flower number was largest one week after the start of blooming, and became very small within a two-week period; and the pod number was at its maximum at the No. 3 stage, decreased gradually, and then leveled off at the No. 5 stage (Fig. 20, top).

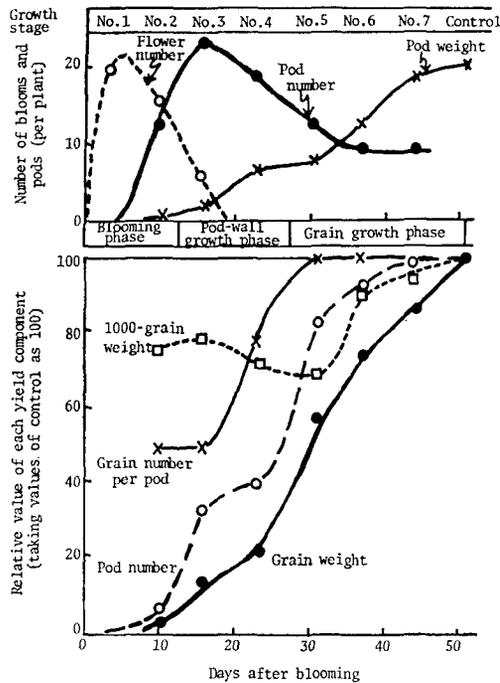


Fig. 20. Changes of flower and pod numbers and pod weight after start of blooming, and relative values of yield components with various treatments in the all-leaf-removal series.

In the all-leaf removal series the earlier the treatment was given, the smaller were the grain weight, pod number and grain number per pod,

while the 1000-grain weight was the smallest with No. 4–No. 5 treatments (Table 13). In the leaflet-removal series the effect on the grain weight and on each yield component was much smaller than in the all-leaf removal series: The grain weight and pod number were decreased slightly by the treatments given at early stages. By the raceme-removal treatment the grain weight and pod number decreased, but the 1000-grain weight was increased slightly.

TABLE 13. Effect of leaf-removal at various growth stages on grain yield and yield components in Taishō-kintoki

No.	Treatment	Days after start of blooming	Grain weight (g per plant)		Pod number per plant		Grain number per pod		1000-grain weight (g)	
			A	B	A	B	A	B	A	B
			Treatment series*							
1		3	0	11.7	0	7.0	—	3.0	—	559
2		10	0.4	12.1	0.6	7.2	1.6	3.1	415	542
3		16	2.2	12.0	3.2	7.7	1.6	3.0	434	521
4		23	3.8	11.7	3.9	7.4	2.5	3.0	393	528
5		31	9.7	13.7	7.9	9.2	3.2	3.1	384	482
6		37	12.3	13.6	8.8	8.5	2.8	3.1	500	516
7		44	14.8	15.6	9.5	9.7	3.0	3.0	521	538
	Control	—	16.9		9.6		3.2		522	
	Raceme-removal	—	12.5		6.6		3.2		594	
	LSD (0.05)		2.47		1.92		0.66		64.1	

* A: All-leaf-removal series, B: Leaflet-removal series.

In the all-leaf-removal series the total plant weight decreased after treatment in all cases: For example, in the No. 1 treatment the total plant weight at the time when the treatment was given and at harvest were 4.3 g and 2.3 g per plant, respectively. This means that the plants without leaves survived for about 50 days by consuming about 50% of their initial weight mostly by respiration. In the leaflet-removal series the increase of total plant weight after treatment was only slightly less than that of the control: For example, the increase after the No. 1 stage was 15.5 g and 22.0 g in the No. 1 treatment and the control, respectively. This means that the net assimilation rate of the remaining leaflets was about two times of that of the control because the remaining leaf area was about 1/3 of the control. With the raceme-removal treatment the stem-and-root weight was higher, but the total plant weight was lower than for the control.

In the control the carbohydrate content of stems remained at about 10% for about 30 days after the start of blooming, increasing to 15% during the grain growth phase (Fig. 21). It decreased considerably at the end of growth because the plants were almost dead due to a delay in sampling. The carbohydrate content decreased rapidly after the all-leaf-removal treatment, whereas it increased considerably by the raceme-removal treatment. These phenomena suggest that the carbohydrate content is delicately governed by the source-sink relationship.

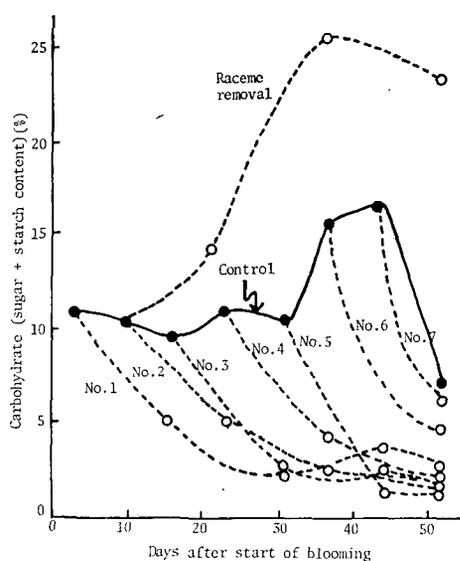


Fig. 21. Carbohydrate content of stem at successive growth stages with various treatments in all-leaf-removal series and raceme-removal treatment.

To illustrate the growth stage when each yield component is established Fig. 20 (bottom) was prepared, in which the relative values of each yield component of the treatments in the all-leaf-removal series, taking the corresponding values of the control as 100, were plotted against the growth stage when each treatment was given. The pod number was influenced strongly by the status of the plant during blooming, and to a smaller extent by that during the pod-wall growth. The grain number per pod was decided by the time when grain growth started. The magnitude of the change of grain number per pod was smaller than that of pod number per plant, and that of 1000-grain weight was still smaller.

The leaflet-removal treatments generally caused only a slight decrease

of the grain yield (Table 13). However, for example, in the No. 1 treatment the grain yield decreased due to a decrease in the pod number, but the stem-and-root weight at harvest was larger than for the control plant. These data suggest that the source capacity generally exceeds the sink capacity, but when a portion of the leaves is removed at a critical stage, the carbohydrate content of the plant decreases suddenly, and the pod number is decided when the content is low. Later, the photosynthetic rate of the remaining leaves may become more active, but the grain yield is bound to be small because the pod number has been decided at the small number.

4. Effect of Topping or Removal of Branches in Varieties with Different Growth Habits

Taishō-kintoki and Gin-tebō were grown in a field by the standard cultural method in 1974, and the following treatments were differentiated: Taishō-kintoki (a determinate)

- (a) Control: No treatment.
- (b) Topping: The main stem was topped above L-2 when L-3 was unfolding.
- (c) Branch-removal: All branches were removed as each branch became visible.
- (d) Leaflet-removal: Two lateral leaflets of all leaves were removed at full blooming.

Gin-tebō (a semi-indeterminate)

- (a) Control: No treatment.
- (b-1) High-topping: The main stem was topped above L-8 when L-9 had unfolded.
- (b-2) Low-topping: The main stem was topped above L-4 when L-5 had unfolded.
- (c) Branch-removal: All branches were removed as each branch became visible.
- (d) Leaflet-removal: Two lateral leaflets of all leaves were removed at full blooming, and the same treatment was also given to the leaves which came out later.

In Taishō-kintoki, no leaf came out after blooming, the node number on the main stem (including the nodes at the cotyledon and L-Pr) was 6 except in the topping treatment, and the branch number was about 5 except in the branch-removal treatment (Table 14). In the control the leaf area of branches was larger than that of the main stem. The leaf area of branches did not increase under the topping treatment while that of the main stem was increased by the branch-removal treatment. In the control of Gin-tebō

TABLE 14. Effect of various treatments on plant height, node number, branch number and LAI of Taishō-kintoki and Gin-tebō

Variety	Treatment	Main stem		Branch number per plant	Leaf area (dm ² /plant)		
		Height (cm)	Node number		Main stem	Branch	Total
Taishō-kintoki	Control	34	6	5.2	6.6	11.2	17.8
	Topping	16	4	4.8	3.5	10.7	14.2
	Branch-removal	31	6	0	10.2	0	10.2
	Leaflet-removal	31	6	5.3	3.5	4.7	7.7
Gin-tebō	Control	109	15.1	1.6	14.7	11.2	25.9
	High-topping	51	10.0	1.8	7.4	10.5	17.9
	Low-topping	15	6.0	4.3	0.6	18.9	19.5
	Branch-removal	134	16.8	0	17.4	0	17.4
	Leaflet-removal	106	14.4	2.0	6.2	7.7	13.9

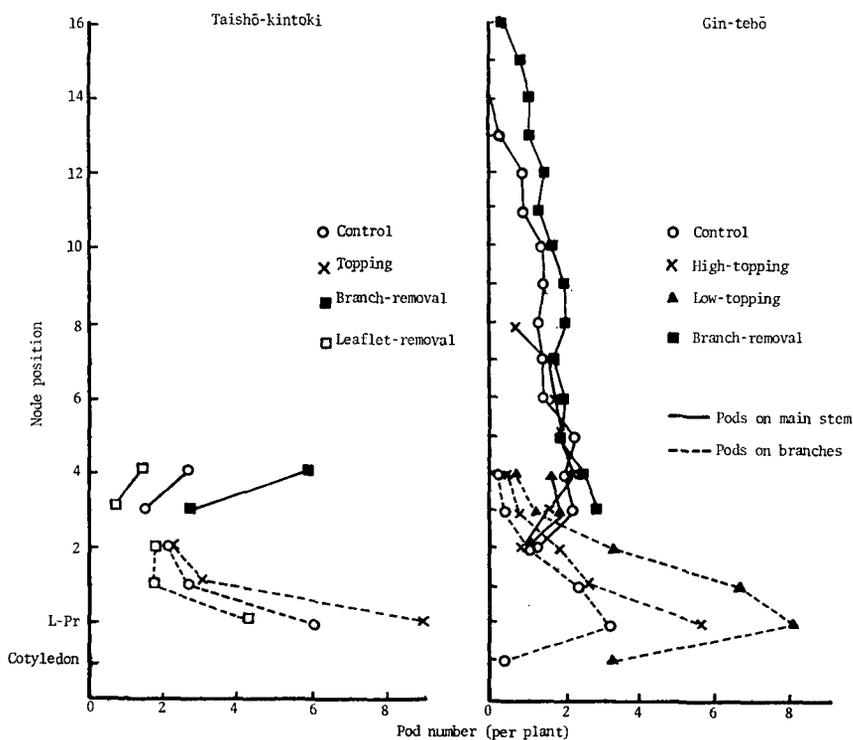


Fig. 22. Pod number on each node of the main stem and each branch at various positions of Taishō-kintoki and Gin-tebō with various treatments.

many new leaves came out on the main stem after blooming, and the leaf area of the main stem was larger than that of the branches. By the low-topping treatment the branch number and the leaf area of the branches were increased, and by the branch-removal treatment the node number and the leaf area of the main stem were increased.

In Taishō-kintoki there were pods on R-4, R-3, B-2, B-1 and B-Pr in the control; by the topping treatment the pod number on the branches was increased; by the branch-removal treatment the pod number on R-4 and R-3 was increased; and by the leaflet-removal treatment the pod number at all positions was decreased (Fig. 22). In Gin-tebō there were pods on R-13-R-2 and B-4-B-Pr in the control; by the topping treatments the pod number on the branches was increased, especially by the low-topping treatment; by the branch-removal treatment the node number on the main stem and the pod number per node were increased; and by the leaflet-removal treatment the pod number at all positions was decreased.

In Taishō-kintoki, by the topping treatment the pod number per plant was decreased slightly; by the branch-removal treatment the pod number per plant was decreased considerably while the 1000-grain weight was increased slightly; and by the leaflet-removal treatment the pod number was

TABLE 15. Effect of various treatments on grain yield, yield components, composition of grains, and amount of nitrogen accumulation in the plant (Taishō-kintoki and Gin-tebō)

Variety	Treatment	Grain weight (g/plant)	Pod number per plant	Grain number per pod	1000-grain weight (g)	Nitrogen content (%)	Starch content (%)	Nitrogen amount (mg/plant)
Taishō-kintoki	Control	18.5	12.4	2.9	515	3.6	38	942
	Topping	16.9	11.2	3.0	502	3.9	40	895
	Branch-removal	10.1	6.6	2.7	566	4.9	36	857
	Leaflet-removal	13.5	9.0	2.9	517	3.4	37	713
Gin-tebō	Control	27.9	19.6	4.4	323	3.4	36	1325
	High-topping	25.5	17.3	4.5	328	—	—	—
	Low-topping	25.9	18.3	4.5	314	3.4	36	1145
	Branch-removal	27.8	17.8	4.8	325	3.5	39	1229
	Leaflet-removal	20.7	14.4	4.5	320	3.4	37	955

decreased slightly (Table 15). In Gin-tebō, by the low-topping treatment the pod number on the main stem was decreased, but that on the branches increased noticeably which almost compensated for the decrease on the main stem; by the branch-removal treatment the pod number per plant was decreased slightly, but this was compensated by an increase in the grain number per pod; and by the leaflet-removal treatment the pod number was decreased. The contents of nitrogen or starch of the grains was not changed

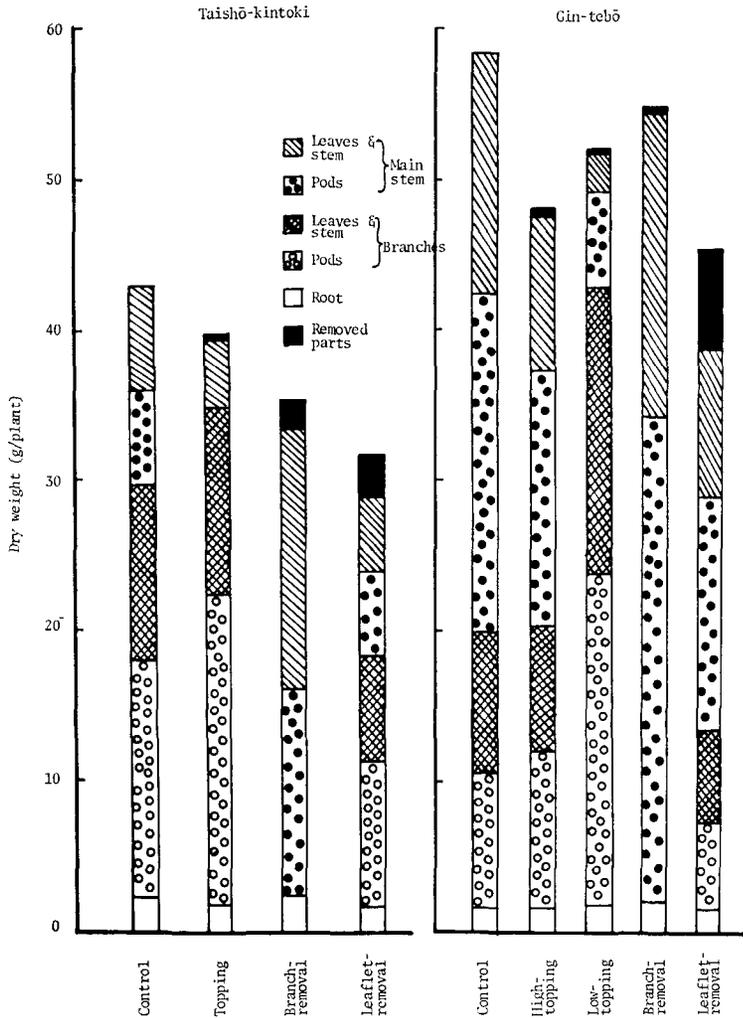


Fig. 23. Effect of various treatments on dry weight of each organ of Taishō-kintoki and Gin-tebō.

by the treatments, except for a slight increase in the nitrogen content by the branch-removal treatment of Taishō-kintoki.

The amount of nitrogen accumulated in the plant was larger in Gin-tebō than in Taishō-kintoki, and was decreased by the leaflet removal treatment (Table 15).

By the topping treatment the weight of the branches was increased, while by the branch-removal the weight of the main stem was increased (Fig. 23). There was a similar trend in the grain weight. Such a compensation between the main stem and branches did not, however, completely nullify the loss of grain yield of the removed portion. The lowest grain yield among the various treatments was 55% and 91% of the grain yield of the control in Taishō-kintoki and Gin-tebō, respectively, indicating that semi-indeterminates are stronger in compensation capacity than determinates.

The change of grain yield caused by the various treatments is mostly due to the change of pod number per plant, and the changes of grain number per pod, 1000-grain weight and composition of grains are small.

The pod number per plant is the product of the node number per plant and the pod number per node. In determinates the change of pod number per plant mostly results from the change of pod number per node because the flexibility of the node number is small. In semi-indeterminates the node number of the main stem or that of the branches is increased considerably by the branch-removal or the topping treatments, respectively, and the pod number per node is also increased by these treatments. This means that the compensation between the main stem and the branches is stronger in semi-indeterminates than in determinates, because the former has a stronger capacity to increase the node number of the main stem as well as on the branches if the other growing points are removed.

5. Effect of Topping at Various Heights on Grain yield in Varieties with Different Growth Habits

Taishō-kintoki and Ō-tebō (Memuro) (determinates), and Fukuryū-chūnaga and Gin-tebō (semi-indeterminates) were planted in a field in 1974 at a wide spacing (50 cm × 25 cm) with support to the semi-indeterminates. These varieties, with no treatment, produced 6, 11, 17 and 22 nodes on the main stem, respectively.

During growth the main stem as well as the branches were topped at various heights (Table 16): For example, Fukuryū-chūnaga-(C) was Fukuryū-chūnaga with no treatment, and Fukuryū-chūnaga-(6) received a treatment to simulate the stature of Taishō-kintoki-(C); the main stem was topped above the 6th-node when L-5 started unfolding, and all branches were also

TABLE 16. Effect of topping at different canopy heights on various plant traits in varieties with different node numbers on the main stem

Varieties and treatments	Plant height (cm)	Stem diameter at the base (cm)	Branch number per plant	Pod number per plant on			Grain weight (g/plant)
				Main stem	Branches	Total	
Taishō-kintoki-(C)*	24	0.73	3.5	2.3	7.1	9.4	13.0
Ō-tebō (Memuro)-(6)	20	0.87	5.7	3.0	26.3	29.3	22.1
” -(C)	57	0.76	6.0	6.9	17.1	24.0	18.1
Fukuryū-chūnaga-(6)	26	0.92	3.6	1.9	13.4	15.3	24.0
” -(11)	76	0.90	3.8	5.1	12.0	17.1	23.6
” -(C)	139	0.68	2.3	9.9	4.5	14.4	18.7
Gin-tebō-(11)	61	0.93	4.0	7.9	18.2	26.1	28.4
” -(C)	203	0.68	1.7	20.0	10.2	30.5	33.6

* See the text.

topped at the canopy height of L-5 when each branch reached that height. With such treatments, Ō-tebō (Memuro)-(6) and Fukuryū-chūnaga-(6) were intended to simulate the stature of Taishō-kintoki-(C); and Fukuryū-chūnaga-(11) and Gin-tebō-(11) the stature of Ō-tebō (Memuro)-(C).

In all varieties under the topping treatments the branch number was increased, the pod number was decreased in the main stem and was increased in the branches, and the total pod number, consequently the grain yield, was kept fairly constant (Table 16). There was, however, a slight decrease of the grain yield in Gin-tebō and slight increases in Fukuryū-chūnaga and Ō-tebō (Memuro) with the topping treatments.

By the topping treatments the weight of roots and the diameter of the stem at the base were increased in all varieties. Such changes are considered to be beneficial for bush beans in lodging resistance.

The grain yield was higher in Gin-tebō and lower in Taishō-kintoki than other varieties regardless of the treatment. Comparisons of the grain yield among Taishō-kintoki-(C), Ō-tebō (Memuro)-(6) and Fukuryū-chūnaga-(6), or among Ō-tebō (Memuro)-(C), Fukuryū-chūnaga-(11) and Gin-tebō-(11) suggest that when topping was made at a given node for the different varieties, the yield was higher for varieties which, without topping, had the greater number of node on the main stem.

Within the limits of the varieties tested and also when plants are widely spaced and supported, (a) the yielding potential of a variety is higher if the

variety possesses more nodes on the main stem; (b) the yielding ability is a varietal character which is not simply related to the node number on the main stem per se, and even if several nodes at the top of the main stem and the branches are cut off, the loss of grain yield of the cut portion is compensated by an increase of yield at the remaining portion depending upon the yielding ability; and (c) with a given variety there seems to exist an optimum node number to produce a maximum grain yield.

In a separate experiment Gin-tebō was grown in a field in 1975 at a 25 cm × 25 cm spacing with support, during growth all branches were removed as each branch became visible, and under this condition 20 nodes were produced on the main stem. The main stem was topped above the 6th-, 8th-, 10th-, 12th- or 14th-nodes when the leaves on the respective nodes started to unfold.

TABLE 17. Effect of topping of main stem at different heights on yield components in Gin-tebō from which all branches were removed

Topped at	Grain weight (g/plant)	Pod number per		Grain number per pod	1000-grain** weight (g)	Leaf-and-stem weight (g/plant)	Leaf-and-stem weight per node (g)
		Plant	Node*				
No topping (20 nodes)	26.5	19.4	1.08	4.8	285	14.7	0.81
14th-node	31.1	22.4	1.86	4.7	295	15.7	1.30
12th-node	25.0	18.3	1.83	4.5	304	14.8	1.48
10th-node	22.6	18.6	2.33	4.4	276	10.8	1.35
8th-node	16.2	14.1	2.35	4.3	268	8.6	1.43
6th-node	15.2	12.7	3.17	4.5	266	6.7	1.68
Normal (with branches)	32.9	29.2	—	4.5	251	30.6	—

* Node at cotyledon and primary leaf were excluded.

** Fully developed grain only.

The grain yield was higher with the 14th-node topping treatment than the no topping treatment, and was decreased progressively by lowering the topping position (Table 17). The pod number per plant showed a similar trend to the grain yield, the pod number per node was increased by lowering the topping position, the grain number per pod did not change appreciably, and the 1000-grain weight was almost constant although it was largest with the 12th node topping treatment.

The weight of leaf-and-stem at harvest was highest with the 14th-node topping treatment, and was decreased by lowering the topping position. The weight of leaf-and-stem per node was apparently smaller in the no topping treatment, and was larger with the 6th-node treatment than other treatments.

A few nodes at the top of stems which grow during the later part of blooming produce almost no pods, but consume photosynthates, and cause a decrease of the pod number per node at lower positions on the stems.

The normal plants with branches had far higher weights of leaf-and-stem and pod number, but were only slightly higher in grain yield than the 14th-node topping treatment because the 1000-grain weight was smaller.

In this experiment in which all branches were removed and plants were supported, 14 nodes on the main stem was the optimum to obtain the maximum grain yield. If branches were allowed to grow and no support was given the optimum node number would be less than 14 due to competition between the main stem and branches and also to lodging.

6. Discussion

A field bean plant is composed of source-sink units, and each unit is further composed of source-sink sub-units. However, these units are not at all rigid, and compensation takes place within or between the units. Thus, the significance of the source-sink unit is not very important in considering methods to improve grain yield.

When all racemes are removed, the photosynthetic rate of leaves decreases for some time due to the inability of the sink. Later, the rate is maintained higher than the control and for a longer period, because the nitrogen content of the leaves is kept higher due to the interrupted translocation of nitrogen from the leaves to the grains; vegetative organs become larger in weight and higher in carbohydrate content because these act as alternate sinks; but as the accumulation of carbohydrates promotes the respiration of these organs, the total dry matter production is less than in the control.

When leaves are partially removed after blooming, the field bean has a unique characteristic by which excess flowers and developing pods abort, and the sink size is adjusted to match the capacity of the remaining source. Thus, the sink capacity is generally matched with or smaller than the source capacity at least during the grain growth phase.

By removing all leaves at successive growth stages after the start of blooming it was demonstrated that (a) abortion of flowers and young pods occurs when the source activity is impaired during the blooming and pod-wall growth phases due to a decrease of the carbohydrate content of the

plant ; (b) the grain number per pod is also decreased when such a condition sets in before the start of grain growth ; (c) the grain number is established by the start of grain growth ; and (d) as the grain number has been adjusted to match with the source capacity, the 1000-grain weight is relatively stable.

The 1000-grain weight can be 70% of the control when all leaves are removed after the grain number has been established, and under such a condition all carbohydrate stored in the stem is exhausted. Whereas, it can be 110% of the control when only a few pods are allowed to grow by removing many pods, and under this condition a large amount of carbohydrate is accumulated in the stem.

Treatment to make the leaf area one third of the control at successive growth stages demonstrated that such a treatment caused a slight increase in the abortion of flowers and young pods when it was given during the blooming and pod-wall growth phases, but had almost no effect when it was given after the start of grain growth. This means that the source is the yield limiting factor only during the blooming and pod-wall growth phases, and not during the grain growth phase.

The main stem and branches compensate each other : The growth of branches is accelerated when the apex of the main stem is cut off, and the growth of the main stem becomes more active when branches are removed.

The grain yield is dominantly dictated by the pod number, and the pod number is the product of the node number and the pod number per node. By removing branches the node number and the pod number per node on the main stem are increased. These increases compensate fairly well for the decrease of pod number on the branches in semi-indeterminates, whereas in determinates the node number of the main stem does not increase because it is fixed at a small number, and the increase of pod number per node alone can not fully compensate for the decrease in pod number of the branches. By *topping* the main stem, the branches become more active and produce more nodes, consequently more pods. As the potential to increase the node number on the branches is larger, the compensation ability is far larger in semi-indeterminates than in determinates. Because of these reasons the grain yield of semi-indeterminates is more stable than determinates against the various treatments.

At wide spacings and with support, varieties which produce more nodes on the main stem appear to have a higher yielding potential and a stronger compensation capacity than those which produce fewer nodes. At close spacings under which branching is restricted, however, there seems to exist

an optimum node number on the main stem to obtain a maximum yield. The optimum node number on the main stem for bush beans planted at close spacing appears to be slightly less than 14.

IV. RESPONSE TO CULTURAL CONDITIONS

1. Response to Nitrogen

Nitrogen Response under Water Culture Conditions: One seedling of Taishō-kintoki was transplanted to each pot each containing 4 liters of culture solution, and these plants were grown in a greenhouse with culture solutions containing graded levels of added nitrogen; *i. e.* 0, 10, 30, 60 and 100 ppm N as NH_4NO_3 . The culture solution was prepared by adding 20 ppm P as $\text{NaH}_2\text{PO}_4 \cdot 2\text{H}_2\text{O}$, 50 ppm K as K_2SO_4 , 50 ppm Ca as $\text{CaCl}_2 \cdot 2\text{H}_2\text{O}$, 30 ppm Mg as $\text{MgSO}_4 \cdot 2\text{H}_2\text{O}$, 1 ppm Fe as $\text{FeSO}_4 \cdot 7\text{H}_2\text{O}$, and 0.3 ppm Mn as $\text{MnSO}_4 \cdot 4\text{H}_2\text{O}$ to tap-water which contained about 5 ppm N (mostly as NO_3^-), and was adjusted to pH 6. Thus, the 0 ppm N treatment contained about 5 ppm N. The culture solutions were aerated for 30 minutes at an interval of 2 hours, and were renewed once a week.

The start of blooming and harvesting were 35 days and 69 days after sowing, respectively. At higher nitrogen levels flowers were more and blooming lasted longer. At 0 and 10 ppm N leaves became yellow and L-1 and L-2 defoliated during blooming, but at above 30 ppm N all leaves were kept green until harvest.

The higher the nitrogen level in the culture solution, the higher was the yield of vegetative organs and grains, and the larger the harvest index

TABLE 18. Grain yield and yield components as affected by nitrogen level in culture solution in Taishō-kintoki

N level in culture solution (ppm)		0	10	30	60	100
Dry weight (g per plant)	Grains	1.8	5.7	10.4	17.2	18.9
	Total plant	10.8	22.8	33.2	49.9	53.9
	Harvest index (%)	16.7	25.0	31.1	34.5	35.0
Pod number per plant		3.5	7.5	11.5	13.5	15.0
Complete grain number per pod		1.45	1.36	2.01	2.89	2.93
Incomplete grain number per pod		1.12	1.24	0.86	0.48	0.38
1000-grain weight (g)		294	417	420	435	432
Nitrogen content of grains (%)		3.12	3.53	4.15	4.49	4.34

(Table 18). The nitrogen response was apparent until 60 ppm N, above which it was small.

The pod number per plant, grain number per pod, and 1000-grain weight increased with an increase of nitrogen level. The increase was far larger in the pod number than in other yield components. The incomplete grain number per pod was more at lower than at higher nitrogen levels. The nitrogen content of grains increased with an increase of nitrogen level.

An increase of nitrogen level caused increases of the area, thickness, weight, nitrogen content, and chlorophyll content of leaves (Table 19). Carbohydrate content was highest at 30-60 ppm N, but this tendency was not consistent among leaves at different positions.

TABLE 19. Size and composition of L-1 of Taishō-kintoki at the 41st day from sowing as affected by nitrogen level in culture solution

N level in culture solution (ppm)	0	10	30	60	100
Leaf-area (dm ²)	0.94	1.72	1.73	1.89	2.02
Leaf-thickness (g·dm ⁻²)	0.30	0.31	0.33	0.39	0.46
Leaf-weight (g)	0.28	0.53	0.57	0.74	0.92
Nitrogen content (%)	1.15	1.87	1.91	3.08	3.29
Chlorophyll content (O.D.)	0.09	0.12	0.23	0.44	0.46
Carbohydrate content (%)	7.4	14.0	19.8	19.7	13.5

The photosynthetic rate per unit leaf area at 40 klux, po (40 klux), of a leaf at a certain position was higher at higher nitrogen levels at a given growth stage, and decreased with age (Fig. 24).

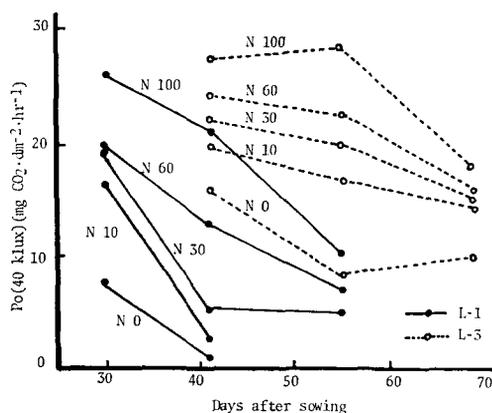


Fig. 24. Photosynthetic rate (po) of L-1 and L-3 at successive leaf ages as affected by nitrogen level in culture solution.

With all the data collected on L-1 and L-3 at various growth stages, there was a statistically significant positive correlation between the p_o and the nitrogen content of leaves (Fig. 25): The p_o was maximal (about 30 $\text{mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{hr}^{-1}$) when the nitrogen content was about 16 $\text{mg N} \cdot \text{dm}^{-2}$ or 4.5% on a dry matter basis. There was no decrease of p_o due to a too high nitrogen content at least within the limits of this experiment. There was also a positive correlation between the chlorophyll content and the p_o ($r=0.814^{xx}$).

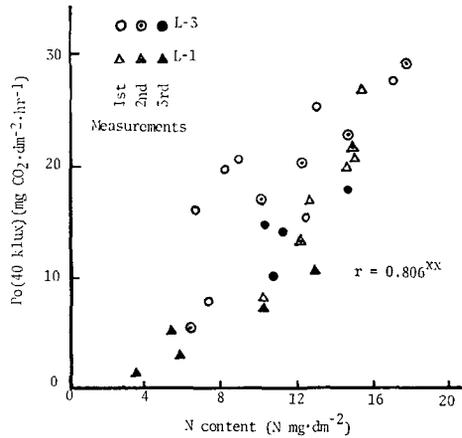


Fig. 25. Relation between nitrogen content of leaves and photosynthetic rate.

The p_o (10 klux)/ p_o (40 klux) ratio was higher at lower than at higher nitrogen levels, and in older than in younger leaves, indicating that a high-nitrogen young leaf responds to strong light better than a low-nitrogen old leaf.

Nitrogen Response under Field Conditions: In 1974 Shōwa-kintoki (a determinate) and Gin-tebō (a semi-indeterminate) were grown in a field with graded levels of nitrogen application; namely, 0, 60, 120 and 180 kg N/ha. In addition to these two field bean varieties two lines of soybean (*Glycine max*), namely A62-1 and A62-2 (medium-duration isogenic lines with and without nodulating habits, respectively), were included in this experiment to compare the nitrogen response between the field bean and the soybean. At planting, both field beans and soybeans were treated with respective inoculants to secure nodulation. Plant density was a hill spacing of 25 cm \times 25 cm, one plant to a hill. 150 kg P_2O_5 /ha as superphosphate and 80 kg K_2O /ha as potassium sulfate were applied uniformly, and nitrogen was applied at graded

levels as ammonium sulfate. Gin-tebō was supported. Each treatment was duplicated, and nitrogen levels and varieties were the main and the sub-plots, respectively. The size of each sub-plot was 3 m × 3 m.

In 1975 Shōwa-kintoki, A62-1 and A62-2 were grown again with graded nitrogen levels; namely 0, 60, 120 and 240 kg N/ha. In this year the soil of the experimental field was more fertile than in 1974, but the other experimental conditions were the same as in 1974.

In 1974 the nitrogen response in the grain yield was slightly higher in Gin-tebō than in Shōwa-kintoki, and that of A62-2 (a root-nodule free soybean line) was similar to the field beans (Fig. 26). The grain yield of A62-1 (a nodulating soybean line) was far higher than field beans: Very high at 0 kg N/ha, slightly decreased with an increase of nitrogen application until 120 kg N/ha, and increased again at 180 kg N/ha. In 1975 the grain yields

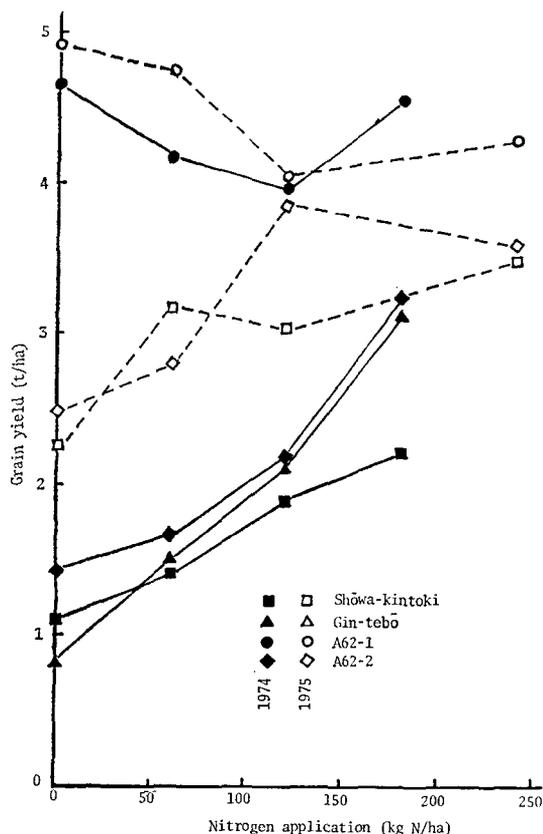


Fig. 26. Effect of nitrogen application to grain yield of field beans and soybeans (1974, 1975).

were generally higher than in 1974 although the trends of nitrogen response of the various lines were similar to those observed in 1974. The yield of Shōwakintoki was increased by nitrogen application from 0 to 60 kg N/ha, but above this level it was maintained at slightly above 3 t/ha until 240 kg N/ha. This suggests that the yield limiting factor above 60 kg N/ha is not nitrogen when the soil fertility is high, and that a heavy nitrogen application until 240 kg N/ha does not have an adverse effect on the grain yield.

The 1000-grain weight and the nitrogen content of grains increased with an increase of nitrogen application except in the case of A62-1 in both experiments (Table 20). The field beans were larger in 1000-grain weight and lower in nitrogen content than the soybeans.

In 1974 the amount of nitrogen accumulated in the plant at harvest was far larger in A62-1 than in other lines (Fig. 27); in A62-1 it decreased

TABLE 20. Effect of nitrogen application on 1000-grain weight and nitrogen content of grains of field beans and soybeans

Year	Variety	Nitrogen level (kg N/ha)			
		0	60	120	180 or 240*
1000-grain weight (g)					
1974	Shōwa-kintoki	554	562	563	571
	Gin-tebō	250	264	296	314
	A 62-1	185	180	178	187
	A 62-2	115	116	117	153
1975	Shōwa-kintoki	611	646	685	708
	A 62-1	198	195	198	190
	A 62-2	138	133	178	179
Nitrogen content of grains (%)					
1974	Shōwa-kintoki	3.38	3.37	3.52	3.67
	Gin-tebō	3.49	3.65	3.76	4.13
	A 62-1	5.98	6.17	5.99	6.18
	A 62-2	4.85	4.78	5.15	5.45
1975	Shōwa-kintoki	2.26	2.71	2.88	3.05
	A 62-1	6.07	5.87	5.89	5.86
	A 62-2	5.22	5.54	5.64	5.44

* 1974: 180 kg N/ha, 1975: 240 kg N/ha.

with an increase of nitrogen application until 120 kg N/ha, above which it increased; and in other lines it was about 70 kg N/ha at no applied nitrogen, increased with an increase of nitrogen application, and at 180 kg N/ha it was smaller in Shōwa-kintoki than in Gin-tebō or A62-2. In 1975 the trends of the amount of nitrogen accumulated in the plant at harvest were similar to those observed in 1974, but the nitrogen amount in A62-2 was more than double that in Shōwa-kintoki with and without applied nitrogen.

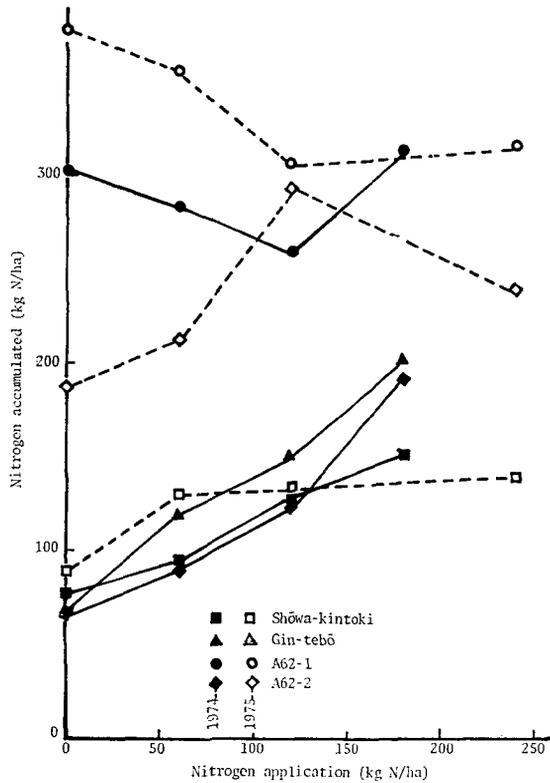


Fig. 27. Effect of nitrogen application on amount of nitrogen accumulated in plants.

In 1974 at the start of blooming, the root-nodule number was more in A62-1 than in the field beans, it decreased with an increase of nitrogen application in all lines, and no root-nodule was observed in A62-2 (Table 21). In the field beans the average root-nodule weight decreased with an increase of nitrogen application, while in A62-1 there was no such trend.

It appears that the field bean is weaker in the power to absorb soil nitrogen and also to fix nitrogen than the soybean. However, many root-

TABLE 21. Effect of nitrogen application on number and average weight of root-nodules at start of blooming in field beans and soybeans (1974)

Variety	Nitrogen level (kg N/ha)			
	0	60	120	180
Root-nodule number per plant				
Shōwa-kintoki	47.7	26.4	8.5	3.9
Gin-tebō	21.7	8.4	7.9	1.9
A 62-1	56.7	35.3	22.7	9.7
Average root-nodule weight (mg per nodule)				
Shōwa-kintoki	2.05	1.25	1.11	1.23
Gin-tebō	5.15	6.38	1.85	1.37
A 62-1	2.77	3.82	2.04	2.57

nodules develop on field bean roots at low nitrogen levels. Thus, it can be speculated that the ability of root-nodules to fix nitrogen is weaker in the field bean than in the soybean. Of course this statement is subject to re-examination under different soil conditions with different rhizobium strains, etc.

In the field bean the amount of nitrogen accumulated in the plant increases with an increase of nitrogen application, and the more the nitrogen accumulates in the plant, the higher the grain yield, 1000-grain weight, and nitrogen content of grains. The yield response to applied nitrogen appears to be higher in semi-indeterminates than in determinates. There is a ceiling of grain yield at a rather low level in field beans, especially in determinates; the yield response is observed only to a certain nitrogen level, which is not nearly as high as in cereal crops; and above which the yield is maintained at the ceiling level until a rather high nitrogen level.

2. Response to Spacing and Support

Response to Spacing: Taishō-kintoki and Gin-tebō were planted in a field in 1973 with six treatments; namely combinations of three spacings (50 cm × 50 cm, 25 cm × 25 cm and 12.5 cm × 12.5 cm [4, 16 and 64 plants/m², respectively]) and two nitrogen levels (0 and 60 kg N/ha). Each treatment was duplicated, and the size of each plot was 3 m × 3 m. All plots received uniform applications of 150 kg P₂O₅/ha and 80 kg K₂O/ha, and the 60 kg N/ha plot received 40 kg N/ha at planting and 20 kg N/ha one month after planting. Gin-tebō was supported.

The plant height was greater in Gin-tebō than in Taishō-kintoki, at wider than at closer spacings (except Taishō-kintoki at 60 kg N/ha), and at 60 kg N/ha than at 0 kg N/ha (Table 22). The node number on the main stem was more in Gin-tebō than in Taishō-kintoki, at wider than at closer spacings, and at 60 kg N/ha than at 0 kg N/ha. The branch number per plant was more at wider than at closer spacings. Taishō-kintoki had more branches at 60 plants/m², but less at 4 plants/m² than Gin-tebō. The changes in these traits, which were caused by the changes of spacing or nitrogen level, were generally smaller in Taishō-kintoki than in Gin-tebō.

TABLE 22. Effect of spacing and nitrogen application on various plant traits, yield components and amount of nitrogen accumulated in the plant in Taishō-kintoki and Gin-tebō

	N level (kg/ha)	Taishō-kintoki			Gin-tebō		
		Plants/m ²					
		64	16	4	64	16	4
Plant height (cm)	0	27	28	28	99	150	170
	60	31	30	29	139	149	152
Node number on main stem	0	5.4	5.8	5.8	14.3	19.9	24.6
	60	5.4	5.0	5.5	17.7	22.2	23.1
Branch number per plant	0	1.6	3.9	4.1	0.2	1.8	9.0
	60	1.5	4.4	5.4	0.3	2.5	9.8
Pod number per plant	0	4.4	10.1	17.2	8.0	28.1	70.4
	60	4.9	12.3	20.2	9.9	28.4	87.3
$\frac{\text{Pod number on main stem}}{\text{Total pod number}}$ (%)	0	70	36	28	96	64	26
	60	61	21	23	94	63	15
Grain number per pod	0	3.0	3.3	3.6	3.7	4.3	5.4
	60	3.0	3.4	3.7	4.0	4.5	4.5
1000-grain weight (g)	0	376	345	334	214	208	210
	60	364	336	348	249	210	212
Nitrogen amount (kg N/ha)	0	158	115	43	249	217	135
	60	209	158	64	349	233	181

TABLE 23. Leaf area index and carbohydrate content of stem as affected by spacing and nitrogen application in Taishō-kintoki and Gin-tebō

Growth stage	N level (kg/ha)	Taishō-kintoki			Gin-tebō		
		Plants/m ²					
		64	16	4	64	16	4
LAI							
Start of blooming	0	1.62	1.01	0.32	2.53	1.40	0.40
	60	3.48	1.55	0.54	3.65	2.74	0.62
Pod growing stage	0	1.74	1.34	0.45	5.32	3.85	2.52
	60	2.82	2.11	0.77	5.61	3.86	2.42
Carbohydrate content of stem (%)							
Start of blooming	0	14.8	8.6	1.3	6.8	5.3	4.6
	60	8.2	4.1	5.3	3.3	3.5	4.4
Pod growing stage	0	12.7	15.3	9.4	5.9	5.6	3.8
	60	9.3	13.5	10.0	6.7	6.7	6.3

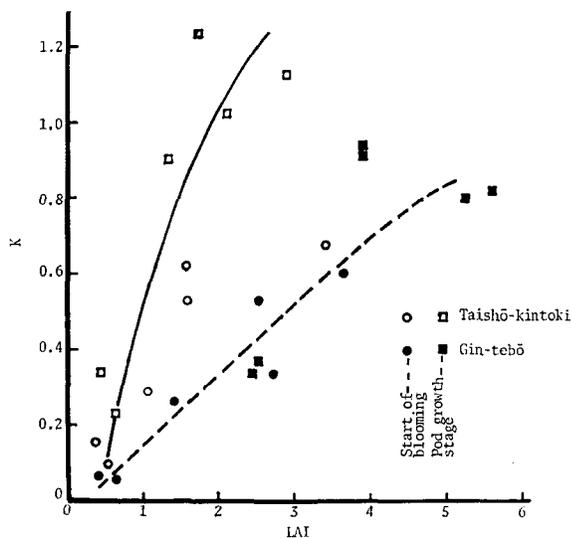


Fig. 28. Relation between LAI and K.

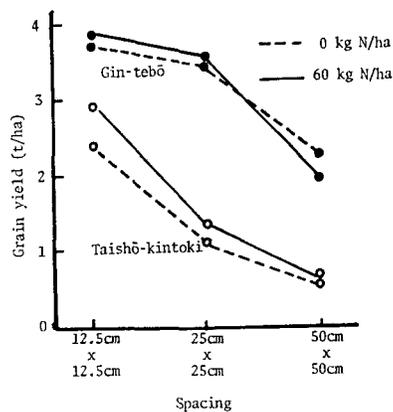


Fig. 29. Response of grain yield to spacing and nitrogen level in Taishō-kintoki and Gin-tebō.

The LAI increased with growth, reached a maximum during the period between the start of blooming and the pod-wall growth stage, and then decreased in all plots. The maximum LAI was reached earlier in Taishō-kintoki than in Gin-tebō, at closer than at wider spacings, and at higher than at lower nitrogen levels. The maximum LAI during growth was greater in Gin-tebō than in Taishō-kintoki, at closer than at wider spacings, and at 60 kg N/ha than at 0 kg N/ha (Table 23). The response of the maximum LAI to spacing was more apparent in Taishō-kintoki than in Gin-tebō. The extinction coefficient was greater at higher LAIs, and at a given LAI it was lower in Gin-tebō than in Taishō-kintoki (Fig. 28).

The grain yield per unit field area was higher in Gin-tebō than in Taishō-kintoki, at closer than at wider spacings, and at 60 kg N/ha than at 0 kg N/ha (Fig. 29). The response to spacing was greater in Taishō-kintoki than in Gin-tebō, but the yield even at 64 plants/m² was higher in Gin-tebō than in Taishō-kintoki. The nitrogen response in the grain yield was generally small, although it was slightly larger at closer spacings, especially in Taishō-kintoki. The maximum yield obtained was 3.9 and 3.0 t/ha in Gin-tebō

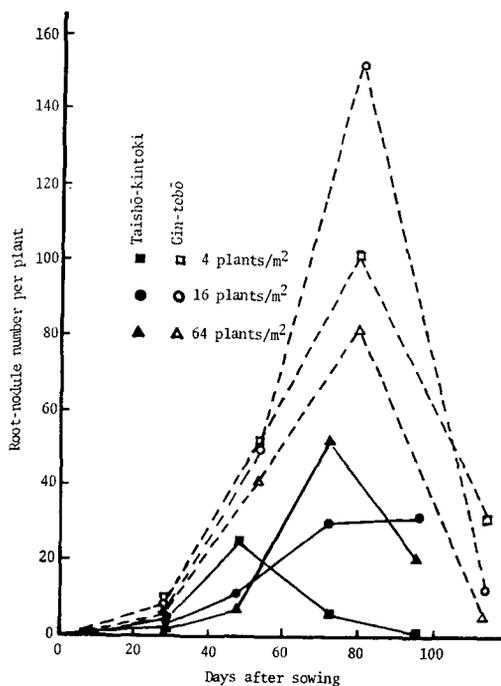


Fig. 30. Changes of root-nodule number during growth with no nitrogen application at various spacings in two varieties.

and Taishō-kintoki, respectively.

The total plant weight at harvest followed a similar trend to the grain yield. However, the harvest index was higher at closer than at wider spacings; its range was 0.51–0.35 in Taishō-kintoki and 0.49–0.38 in Gin-tebō.

The pod number per plant was more in Gin-tebō than in Taishō-kintoki, and at wider than at closer spacings (Table 22). The proportion of pods on the main stem to all pods was higher at closer than at wider spacings, and it was as high as 95% in Gin-tebō at the closest spacing. The grain number per pod was more in Gin-tebō than in Taishō-kintoki, and was slightly more at wider than at closer spacings. The 1000-grain weight was larger in Taishō-kintoki than in Gin-tebō, and it changed only slightly with the change of spacing. The effect of nitrogen application on the yield components was generally small.

The amount of nitrogen accumulated in the plant at harvest was more in Gin-tebō than in Taishō-kintoki, at closer than at wider spacings, and at 60 kg N/ha than at 0 kg N/ha, especially at 64 plants/m² (Table 22).

The root-nodule number per plant was apparently more in Gin-tebō than in Taishō-kintoki (Fig. 30). Generally, it increased with growth, reached a peak, and then decreased. However, the pattern of fluctuation with growth

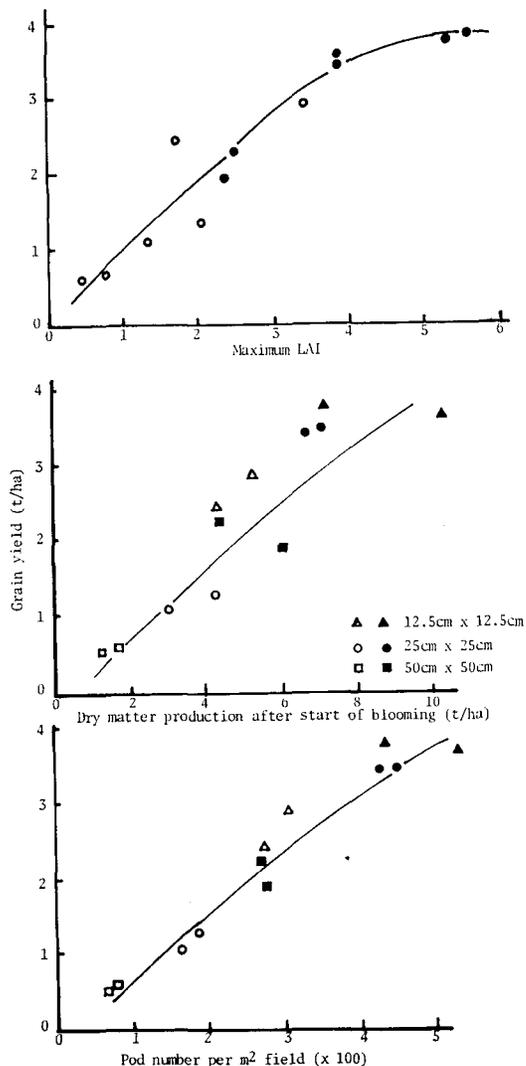


Fig. 31. Relations between grain yield and maximum LAI during growth (top), dry matter production after start of blooming (middle), and pod number per unit field area (bottom).

was different among varieties and spacings. In Taishō-kintoki at wider spacings the root-nodule number was more than at closer spacings at early growth stages, and decreased more rapidly probably because of the high nitrogen content of the plant until late growth stages. At closer spacings it increased significantly to a high value during the grain growth phase probably because of the low nitrogen content of the plant. In Gin-tebō there was a noticeable peak at the grain growth phase at all spacings, and the peak was highest at 16 plants/m². The average weight of root-nodules was larger in Taishō-kintoki than in Gin-tebō at least at the start of blooming.

The carbohydrate content of the stem was higher in Taishō-kintoki than in Gin-tebō, at closer than at wider spacings, and with no nitrogen than with 60 kg N/ha (Table 23).

The grain yield was positively correlated with the maximum LAI during growth (Fig. 31): It increased noticeably until the LAI reached 4, above which there was almost no increase. The grain yield was also positively correlated with the dry matter production after the start of blooming, and also with the pod number per unit field area.

Response to Spacing and Support: In 1974 Taishō-kintoki and Gin-tebō were grown in a field at plant spacings of 12.5 cm × 6.25 cm, 12.5 cm × 12.5 cm, 25 cm × 25 cm, and 50 cm × 50 cm (128, 64, 16 and 4 plants per m², respectively),

TABLE 24. Effect of plant spacing and support on various traits of Taishō-kintoki and Gin-tebō (1974 and 1976)

Variety	Taishō-kintoki				Gin-tebō							
	128	64	16	4	128		64		16		4	
Support	—	—	—	—	+	—	+	—	+	—	+	—
1974												
Plant height (cm)	29	28	25	23	—	—	50	52	64	63	90	71
Node number on main stem	5.9	6.0	6.1	6.2	—	—	12.6	10.8	14.8	14.4	16.7	14.7
Branch number per plant	0.7	2.0	3.5	4.1	—	—	0.6	0.7	2.9	4.1	6.9	7.1
Maximum LAI	3.02	2.16	1.02	0.44	—	—	3.41	3.83	2.82	2.55	0.97	0.98
1976												
Plant height (cm)	44	38	25	25	90	66	95	75	104	100	119	103
Node number on main stem	6.3	6.4	6.3	6.2	11.9	10.2	13.2	11.5	16.9	14.4	22.2	17.2
Branch number per plant	0.3	1.6	4.2	6.2	0	0	0	0	3.2	3.1	9.5	10.7
Maximum LAI	6.56	5.37	2.81	0.92	7.48	7.97	5.99	5.39	4.36	4.03	2.74	4.08

and in the case of Gin-tebō each plot was sub-divided into with and without support plots. Each plot received uniform applications of 40 kg N/ha, 150 kg P₂O₅/ha and 80 kg K₂O/ha, and the soil of the experimental field was poor in nitrogen. Thus, nitrogen deficiency symptoms developed during growth, especially at close spacings. In 1976 an experiment with almost the same design as in 1974 was carried out. In this case, however, the soil of experimental plot was better than in 1974, 100 kg N/ha was applied basally, and nitrogen top-dressing was made whenever nitrogen deficiency symptoms became visible. Thus, it can be considered that the two experiments were conducted at low (1974) and high (1976) nitrogen levels although these experiments were conducted in different years.

The plant height was larger in 1976 than in 1974 (Table 24). It was larger at closer than at wider spacings in Taishō-kintoki, but the trend was reverse in Gin-tebō. The node number on the main stem was constant at 6 in Taishō-kintoki, but it changed considerably from 10 to 22 in Gin-tebō;

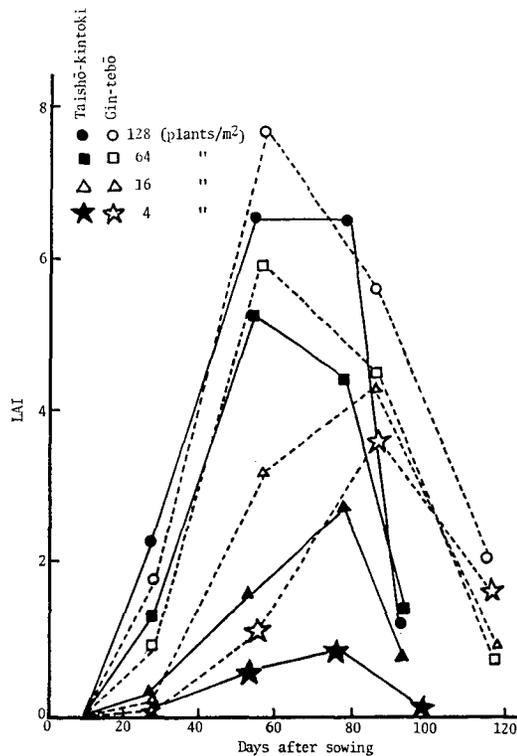


Fig. 32. Changes of LAI during growth at various spacings of Taishō-kintoki and Gin-tebō (1976).

more in 1976 than in 1974, and also more at wider than at closer spacings. The branch number per plant increased with an increase of spacing. It was slightly more in Taishō-kintoki at close spacings, but more in Gin-tebō at wide spacings.

The LAI increased with growth, reached a maximum, and then decreased (Fig. 32). The maximum LAI came earlier at closer than at wider spacings. The LAI at wider spacings especially in Gin-tebō, continued to increase until a late growth stage. Thus, the difference in the LAI at later growth stages among spacings became smaller. The maximum LAI during growth was larger in 1976 than in 1974, and in Gin-tebō than in Taishō-kintoki (Table 24). It decreased from closer to wider spacings, and this decrease was more noticeable in Taishō-kintoki than in Gin-tebō.

The grain yield per unit field area was higher in 1976 than in 1974, it increased from wider to closer spacings, and this increase was more

TABLE 25. Effect of spacing and support on grain yield and yield components of Taishō-kintoki and Gin-tebō (1974 and 1976)

Variety	Taishō-kintoki				Gin-tebō											
	128		64		16		4		128		64		16		4	
Plant number per m ²	128	64	16	4	128	64	16	4	128	64	16	4	128	64	16	4
Support	-	-	-	-	+	-	+	-	+	-	+	-	+	-	+	-
1974																
Grain yield (t/ha)	2.44	2.19	1.52	0.78	—	—	2.96	3.20	2.07	2.22	1.56	2.04				
Pod number per m ²	196	156	93	42	—	—	248	261	150	167	103	128				
Grain number per pod	2.16	2.33	2.79	2.96	—	—	3.62	3.56	4.12	4.05	4.33	4.44				
1000-grain weight (g)	569	569	562	582	—	—	316	332	319	315	315	347				
1976																
Grain yield (t/ha)	3.56	2.72	2.86	1.57	3.33	3.46	3.08	3.20	2.99	2.94	3.20	3.09				
Pod number per m ²	308	217	181	104	318	321	263	259	251	274	283	303				
Grain number per pod	2.43	2.70	3.36	3.15	3.35	3.47	3.83	4.01	4.17	3.98	4.22	3.85				
1000-grain weight (g)	477	466	470	480	314	310	309	309	286	270	268	265				

noticeable in 1974 than in 1976, and in Taishō-kintoki than in Gin-tebō (Table 25). The maximum yield observed was about 3.5 t/ha for the two varieties in 1976 at the closer spacing. However, the yield was generally higher and the decrease of yield with an increase of spacing was less in Gin-tebō than in Taishō-kintoki. In Gin-tebō the yield was slightly higher without support than with.

The pod number per unit field area was more at closer than at wider spacings, and in 1976 than in 1974 (Table 25). It was more in Gin-tebō than in Taishō-kintoki, and this varietal difference was larger at wider than at closer spacings, and in 1976 than in 1974. In Gin-tebō at wide spacings the pod number was slightly more without support than with. The proportion of the pod number on the branches to the total pod number was larger at wider than at closer spacings, in Taishō-kintoki than in Gin-tebō, and without support than with. The grain number per pod decreased slightly with a decrease of spacing, and the 1000-grain weight was kept almost constant.

Fig. 33 demonstrates the pod number at each node on the main stem and on each branch at various positions in 1976: In Taishō-kintoki the node number on the main stem was 6 at all spacings; the pod number per node on the main stem was largest at the L-3 position at all spacings, and increased with an increase of spacing; at 128 plants/m² there were almost no branches, hence no pods on branches, whereas at 4 plants/m² a considerable number of pods were produced on branches, especially on B-Pr

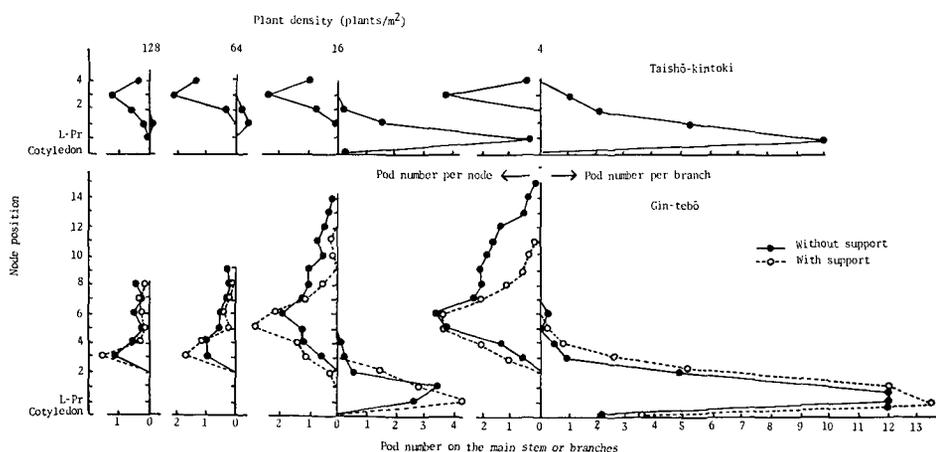


Fig. 33. Effect of spacing and support on pod number on each node of the main stem or on each branch at various positions (1976).

or B-1; and the pods on branches were far more in number than those on the main stem. In Gin-tebō the number of nodes on the main stem which produced pods was 8 at 128 plants/m², and was 15 at 4 plants/m²; the pod number per node on the main stem increased from closer to wider spacings; the position of the node on which the maximum number of pods was produced moved up; and the number of pods produced on branches was nil at 128 or 84 plants/m² and was many at 4 plants/m², especially on B-Pr or B-1.

These data suggest that in Taishō-kintoki, a determinate, the node numbers on the main stem and branches are genetically fixed at a small number, and the potential to increase the pod number on the main stem as well as on the branches is limited, although the pod number per node or per branch increases to a certain extent with increases of spacing and nitrogen application. Whereas, in Gin-tebō, a semi-indeterminate, the potential to increase the node number on the main stem and on branches is high, and the pod number per node or per branch increases considerably with increases of spacing and nitrogen application.

Comparison between treatments with and without support in Gin-tebō reveals that without support the node number and the length of the main stem are less than with support because the stem can not keep standing upright; the number of nodes which produce pods and also the pod number

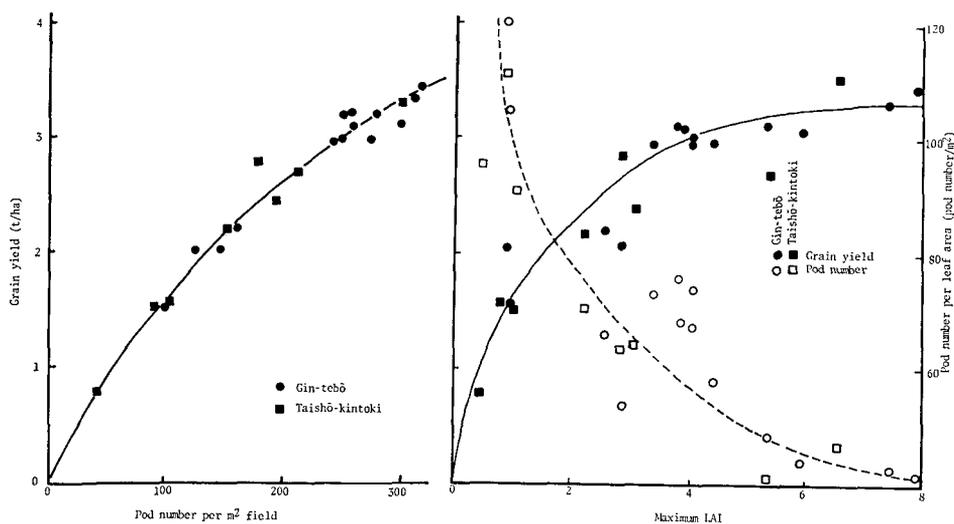


Fig. 34. Relations between pod number and grain yield (left), and between maximum LAI and grain yield, and pod number per leaf area (right).

per node at higher positions on the main stem decrease ; but these decreases are compensated for by an increase in the pod number per node at lower positions on the main stem and on branches ; the total pod number per plant increases slightly.

There is a positive correlation between the pod number and the grain yield (Fig. 34, left). Taishō-kintoki and Gin-tebō followed the same correlation curve because the former had fewer grains per pod and larger grains than the latter. The grain yield increased with an increase of the LAI (Fig. 34, right). The increase was apparent until the LAI reached about 4, above which there was no further increase. The grain number per unit leaf area decreased noticeably with an increase of the LAI. Thus, it can be said that a limitation in the grain number makes the efficiency of leaves lower at large LAI's.

3. Discussion

An increase of nitrogen accumulation in the plant makes the area of individual leaves larger, the leaf number more by increasing the node number on the main stem (only in semi-indeterminates) and the branches, the contents of nitrogen and chlorophyll of leaves higher, the photosynthetic rate per unit leaf area higher, and the longevity of leaves greater. Thus, the source capacity increases with an increase of nitrogen supply. When more nitrogen is accumulated in the plant, more pods are produced, and each pod produces more grains. Such an increase in the sink size permits the expression of source capacity, and these result in increases in the total dry matter production and the grain yield. The 1000-grain weight and the nitrogen content of grains increase with an increase in the amount of nitrogen accumulated in the plant. In these respects, the field bean is similar to cereal crops.

Since the field bean is a leguminous crop, it is expected to fix nitrogen by its root-nodules. However, so far as the results of the experiments described above are concerned, the ability to fix nitrogen is weaker in the field bean than in the soybean²⁴. By the acetylene reduction technique, the maximum amount of nitrogen fixed of the field bean was estimated to be 25-30 kg/ha/growth cycle²⁹. This value is more than the amount estimated for the field bean but less than that for the soybean in this paper.

Many root-nodules are produced on the roots of field beans growing in soils low in nitrogen supply. But, the ability of these root-nodules to fix nitrogen seems to be weaker than in other legumes¹³.

The root-nodule number increases with growth especially after the start of blooming, reaches a maximum at about full blooming, and then decreases. The nodulation is adversely affected by nitrogen application, and with nitrogen

application at high levels almost no root-nodules are produced^{4,20}. Generally speaking, semi-indeterminates produce more nodules or larger nodules than determinates, which may suggest a relatively strong capacity for semi-indeterminates in nitrogen fixation¹².

The yield response to nitrogen application of the field bean is large²⁴, and there is varietal difference in the nitrogen response: Semi-indeterminates respond better than determinates because the former have a higher potential productivity than the latter.

It has been stated that since nitrogen fixation is adversely affected by nitrogen application, a small amount of nitrogen application causes a decrease in grain yield and only nitrogen application at very high levels results in an increase in the grain yield by counteracting the decrease of nitrogen fixation¹⁷. This phenomenon was observed in the soybean (A62-1) in the experiment described above, but not in the field bean.

Spacing controls the growth considerably. At closer spacings plants compete with each other for nitrogen when the nitrogen supply of the soil is insufficient, and for solar radiation when nutrients in the soil are abundant. At close spacings with a sufficient supply of nitrogen the field bean grows taller, but is smaller in the number of nodes on the main stem and in the number of branches. Thus, the pod number per plant is smaller. However, since there are more plants per unit field area, the grain yield per unit field area is generally higher at closer than at wider spacings. Because of this, the grain yield is generally higher at closer than at wider spacings^{9,25} although the yield is frequently maintained at a fairly constant level within a certain range of spacings^{11,23}, and sometimes it decreases at too close spacings^{23,27}.

At close spacings under which a high grain yield per unit field area can be expected the majority of pods are produced on the main stem because only a small number of branches develop. Thus, in obtaining a very high yield, the productivity of the main stem is more important than that of the branches.

The grain yield is highly correlated with the pod number: An increase in pod number results in an increase of the grain yield. The pod number can be expressed as the product of the node number per plant and the pod number per node, and the node number can further be divided into the node number on the main stem and that on the branches. The grain number per pod and the 1000-grain weight are strongly controlled genetically although these yield components change to some extent with changes in growing conditions.

In determinates the node number of the main stem and of each branch

is genetically fixed at a small number, and is difficult to increase by an improvement in growing conditions. Thus, the potential to expand the plant size is limited although the branch number increases under favorable conditions. On the other hand, in semi-indeterminates, the node number on the main stem increases considerably and also each branch has the potential to produce many nodes when the growing conditions are favorable. Thus, the response of the grain yield per unit field area to nitrogen application is larger, and response to spacing is less in semi-indeterminates than determinates^{3,21}.

The LAI increases with an increase in nitrogen application and also with a decrease in spacing. There is a relation between the LAI and the grain yield: With an increase in the LAI the grain yield increases until it reaches about 4, above which there is no further increase in the grain yield. Thus, it can be considered that with LAIs above 4, mutual shading among the leaves makes the leaf efficiency low. This situation can be predicted from the large extinction coefficient of the leaves.

The extinction coefficient is smaller in semi-indeterminates when these are grown with support than in determinates. This difference may be due to a sparser distribution of the leaves because of the taller stature of semi-indeterminates. In this sense, semi-indeterminates may be better favored than determinates in the efficiency of photosynthesis when the LAI is large. However, this speculation seems to be not true at least as far as the grain yield is concerned: At a given LAI there was no difference in grain yield between these two groups (Fig. 34, right). This may suggest that the grain yield is not directly controlled by the potential photosynthetic capacity of a population.

An increase of the LAI accompanied a decrease of pod number per unit leaf area. The absence of a yield response to an increase of the LAI above 4 was not due to the mutual shading of the leaves, but to an insufficient sink size. At closer spacings where the mutual shading was more serious, the carbohydrate content of the stem was higher than at wider spacings. This indicates that an excess of source capacity over the sink capacity is larger at closer than at wider spacings.

Semi-indeterminates are generally grown without support by farmers although it has the ability to climb a support. When no support is given the tip portion of the stem bends even if the canopy does not completely fall down, and the arrangement of leaves is disturbed. Thus, by a simple speculation it seems logical to consider that the grain yield is higher with support than without support because of the better light distribution within

the canopy. However, the grain yield is often higher without support than with. The reason is that when support is given, the growth of the main stem is accelerated, and this results in a decrease of the number of pods on the nodes at lower positions on the main stem and also decreased activity of the branches, while few pods are produced at the tip portion of the main stem which grows only with support. Thus, without support more pods are produced at the lower position on the main stem and on the branches, and the grain yield is higher than with support.

V. COMPARISON OF VARIETAL TRAITS AND THEIR RELATION TO YIELD

1. Varietal Difference and Response to Environmental Conditions of Various Traits

The 20 Hokkaido varieties listed in Table 1 plus ICA DUVA and Argentina 2 in 1973, the 9 varieties listed in Table 26 in 1974, and the 10 Hokkaido varieties listed in Table 1 plus Ō-tebō (Memuro) and the 17 tropical varieties listed in Table 2 in 1975 were tested at Hokkaido University³⁹. These varieties include determinates, semi-indeterminates and indeterminates in Hokkaido and in the tropics. The experimental plot was in the same block in 1973 and 1975, and in 1974 it was in another block where the soil fertility was inferior to that of 1973 or 1975. The rate of fertilizer application was 40 kg N/ha, 100 kg P₂O₅/ha and 80 kg K₂O/ha in all years. The date of sowing was May 21, 16 and 28 in 1973, 1974 and 1975, respectively. The hill spacing was 50 cm × 25 cm in 1973, and 25 cm × 25 cm in 1974 and 1975. One plant was planted to a hill. Bamboo-sticks were provided to individual plants of indeterminates and semi-indeterminates. In 1973 and 1975 each variety had duplicate plots, whereas there was no replication in 1974 because of a shortage of seeds.

As the 9 varieties listed in Table 26 were common to the three years, data of various traits of these varieties were subjected to variance analyses. Because there was no replication in 1974, the interaction between variety and year could not be statistically tested.

The duration from sowing to start of blooming varied significantly from year to year due, most probably, to the difference of date of sowing from year to year: The earlier the sowing in spring, the longer the duration. It also varied significantly among varieties.

The F value for variety was much larger than that for year in the plant height, the node number on the main stem and the 1000-grain weight, and was smaller in the grain weight, the total plant weight, the pod number

TABLE 26. Summarized data of various plant traits of nine varieties in three years

Year and variety	Days from sowing to blooming	Plant height (cm)	Node number on main stem	Branch number per plant ^{a)}	Dry weight per plant (g)		Pod number per plant	Grain number per pod	Grain number per plant	1000-grain weight (g)	
					Grain	Total					
1973	48.1	79	12.0	5.8	20.3	60.9	20.4	2.6	83	310	
1974	52.7	45	10.4	5.4	10.5	22.6	7.0	3.0	33	356	
1975	44.2	95	13.9	3.7	16.1	34.1	11.7	3.2	53	363	
Taishō-kintoki	43.7	26	6.3	4.4	11.7	37.3	12.3	2.5	29	409	
Taishō-shirokintoki	44.0	28	6.7	4.3	11.3	39.0	11.3	2.5	28	415	
Shōwa-kintoki	45.3	31	7.3	4.7	11.0	40.3	10.0	2.2	23	492	
Tokachi-shirokintoki	50.0	87	13.3	3.4	14.3	43.7	13.0	2.9	40	337	
Fukuryū-chūnaga	47.0	78	14.7	3.8	14.7	55.3	14.3	2.8	37	406	
Gin-tebō	49.3	161	20.3	4.8	21.7	68.3	23.3	4.2	96	221	
Ō-tebō	51.3	168	23.3	5.3	19.3	68.7	33.0	3.2	100	204	
Argentina 2	53.0	43	7.3	7.0	20.3	84.7	36.0	3.3	111	190	
ICA DUVA	51.0	37	7.7	6.8	16.7	84.7	14.7	2.8	41	415	
F value for	Year	79.05**	6.47**	13.18**	2.87	7.21**	29.56**	11.48**	1.82	7.76**	5.06*
	Variety	17.12**	10.43**	76.24**	1.20	1.64	4.54**	3.45*	2.34	5.09**	25.88**

a) Effective branches.

*, **: Significant at 5 and 1% levels, respectively.

per plant and the grain number per plant. The heritability of the plant height, the node number on the main stem and the 1000-grain weight is large, and other traits are influenced by the environmental condition more strongly.

The total plant weight, the grain weight, the pod number and the grain number per plant were much larger in 1973 than in other years due to the wider spacing, and were smaller in 1974 than in 1975 because the soil fertility was low. The plant height was greater, the number of nodes on the main stem was higher, and the effective branch number was lower in 1975 than in 1974, due, probably, to better soil conditions and to less solar radiation in July.

For convenience, 8 varieties (excluding Shōwa-kintoki in Table 26) were divided into 4 groups by their growth habits, varieties with similar growth habits were considered as replicates, and the data were subjected to variance analyses to examine the interaction between variety group and year (Table 27). The interaction was significant at the 1% level in plant height, effective branch number per plant and grain weight; significant at the 5% level in total plant weight; and not significant in other traits.

TABLE 27. Combined data of plant height, effective branch number and grain weight of four variety groups in three years

Year and variety group	Plant height (cm)	Effective branch number per plant	Grain weight per plant (g)
1973	85	5.8	21.5
1974	48	5.5	11.1
1975	103	3.6	16.1
Hokkaido determinates ^{a)}	27	4.3	11.5
Hokkaido semi-indeterminates ^{b)}	83	3.6	14.5
" " c)	165	5.1	20.5
South American determinates ^{d)}	40	6.9	18.5
Year	67.89**	17.54**	10.00**
F value for Variety	248.83**	17.38**	22.09**
Y×V	22.68**	12.40**	5.88**

a) Taishō-kintoki and Taishō-shirokintoki.

b) Tokachi-shirokintoki and Fukuryū-chūnaga.

c) Gin-tebō and Ō-tebō.

d) Argentina 2 and ICA DUVA.

** Significant at 1% level.

The variation in plant height between years was more noticeable in semi-indeterminates than in determinates. The significant interactions in branch number and grain weight were mostly due to the more active branching character of the tropical varieties (Argentina 2 and ICA DUVA) than the Hokkaido varieties, which was exhibited under the wider spacing in 1973 and also under the inferior soil condition in 1974.

2. Varietal Traits and Yielding Ability

Relations between the grain yield and various traits are discussed in the following pages by using the data collected on 22 varieties in 1973 and on 27 varieties in 1975.

Plant Height, Node Number, Branch Number and Leaf Area Index: The days from sowing to the start of blooming ranged from 45 to 55 days in 1973 and those from sowing to full blooming ranged from 39 to 58 days in 1975 (Fig. 35). Early varieties are more frequent among the Hokkaido

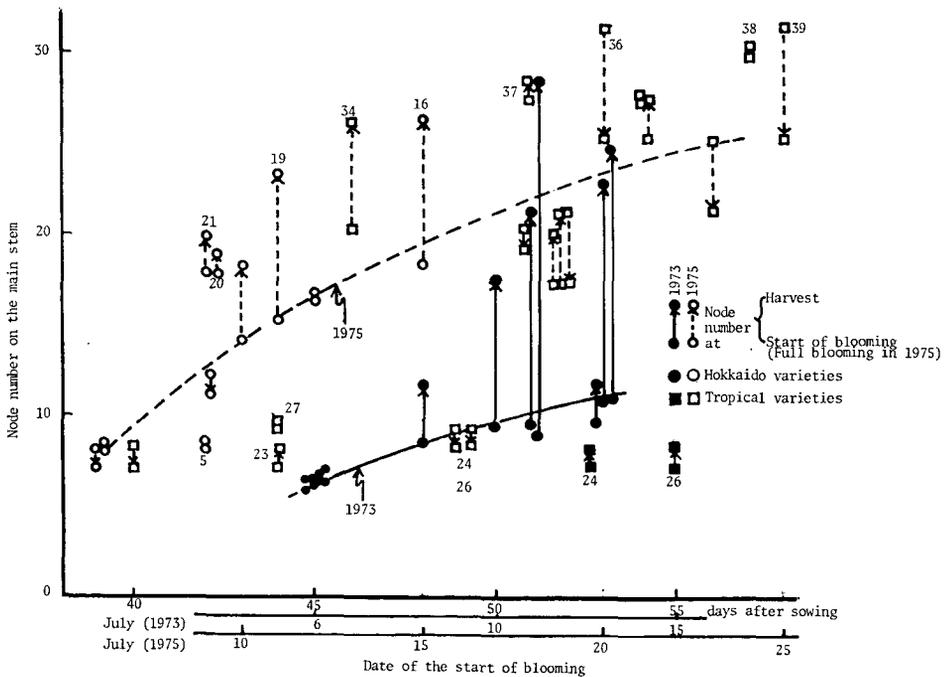


Fig. 35. Relation between days from sowing to start of blooming and node number on the main stem at start of blooming in 1973 and 1975.

Numbers in the above figure and also in the following figures are the number of varieties listed in Table 1 and 2.

varieties than the tropical varieties, and among determinates than others.

In 1973 the node number on the main stem ranged from 6 to 11 at the start of blooming, and from 6 to 28 at harvest. There was a tendency that the later the start of blooming, the more the node number on the main stem at the start of blooming, and also the more the increase in node number after the start of blooming. However, ICA DUVA and Argentina 2, tropical determinates, were exceptions: These varieties were late in the start of blooming, but had a small node number and no new node developed after this growth stage. In 1975 the node number on the main stem was from 6 to 31 at full blooming, and was from 6 to 30 at harvest. Similar trends to 1973 were observed in the relations between the node number and the date of blooming. In some tropical late varieties there was a decrease of the node number on the main stem after full blooming due to the death of a few nodes at the tip.

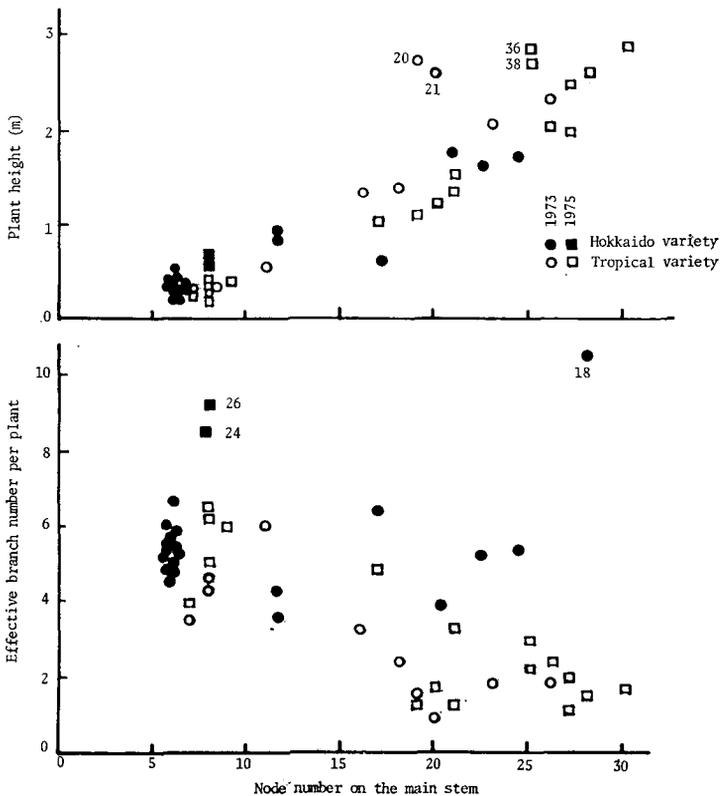


Fig. 36. Relations between node number on the main stem and plant height (top), and between node number and effective branch number (bottom) in 1973 and in 1975.

These data demonstrate that in Hokkaido determinates the growth duration is short, and the node number on the main stem is small at the start of blooming and does not increase after that stage; in tropical determinates the growth duration is long but the node number at the start of blooming is less than expected from the date of blooming; in semi-indeterminates and indeterminates the growth duration is medium or late, the node number at the start of blooming is more and also the increase of node number after that stage is more in longer duration varieties, and several nodes at the tip drop off after reaching a maximum node number on the main stem in varieties with a long growth duration. Thus, there is a trend that the longer the growth duration, the larger the node number on the main stem.

The more the node number on the main stem, the higher the plant (Fig. 36, top). In some indeterminates, however, the plant height was larger than expected from the node number. This means that the internodes are longer in some indeterminates than in other varieties.

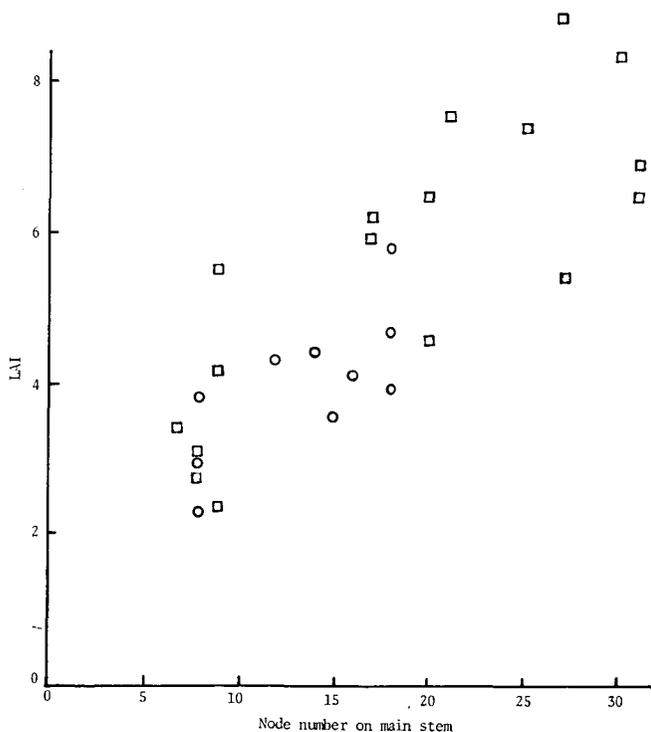


Fig. 37. Relation between node number on the main stem and LAI at full blooming in 1975.

There was no relation between the node number on the main stem and the effective branch number in 1973 when the spacing was wide (Fig. 36, bottom): ICA DUVA and Argentina 2 had 8 nodes and Taishō-Ō-tebō had 28 nodes on the main stem, but all these varieties had far more branches than other varieties. In 1975 when the spacing was close, however, the more the node number on the main stem, the less the branch number. There was also a trend that the more the node number on the main stem, the larger the LAI (Fig. 37).

Thus, it can be said that there is no simple relation between the node number on the main stem and the branching activity. But, at close spacings a variety which produce many nodes on the main stem produces many leaves, consequently a large LAI; the canopy of the population of such a variety becomes over-crowded, and the effective branch number is less.

Yield Components: There was a positive correlation between the pod number per plant and the grain number per plant (Fig. 38, top). This means that the grain number per plant is more strongly controlled by the pod number per plant than by the grain number per pod. In 1973, varietal difference in the pod number per plant was larger and the correlation was better than in 1975. In 1975 some tropical varieties did not mature completely due to a too long growth duration, and data of these varieties did not fit the above-mentioned correlation because some pods produced only a small number of grains.

In 1973 when the plant spacing was wide, the pod number per plant was higher with varieties having more nodes on the main stem, except for Argentina 2 which had many pods with a small node number on the main stem due to the large number of primary and secondary branches (Fig. 38, bottom). Tall varieties were not necessarily low in branch number, and each branch produced as many nodes as the main stem.

In 1975 when the plant spacing was close, there was no simple relation between the node number on the main stem and the pod number per plant because the more the node number on the main stem, the less the branch number. However, among varieties with more than 20 nodes on the main stem, there was more chance of varieties with many pods probably because the pod number on the main stem is larger. Jamapa was an exceptional variety; it had many pods although the node number was 17.

Argentina 2 produced many pods at a wide spacing (in 1973) due to active branching, but at a close spacing (in 1975) this branching ability was not expressed and the pod number was not large.

There was a loose correlation between the grain number per plant and

the 1000-grain weight (Fig. 39, top). Varieties which produced many grains tended to have a small 1000-grain weight. Of course, the varieties which did not mature completely had a smaller 1000-grain weight than expected from the grain number.

The grain yield per plant, however, tended to increase with an increase in the grain number per plant (Fig. 39, bottom), because the decrease in the 1000-grain weight associated with an increase in the grain number was not so large as to keep the grain yield constant. This correlation was apparent in 1973 (depicted by a curve in Fig. 39), but was not so in 1975.

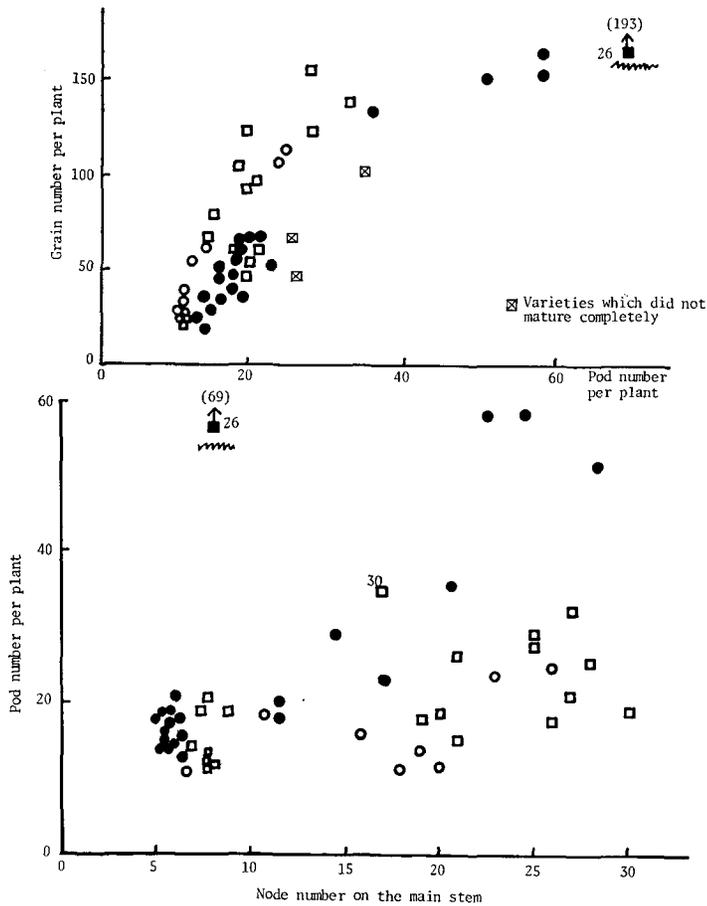


Fig. 38. Relations between pod number per plant and grain number per plant (top), and between node number on the main stem and pod number per plant (bottom). (Symbols and numbers in this and following figures are the same in Fig. 35).

In 1975 varieties with more diverse characteristics were included in the experiment than in 1973. Ōfuku and Toramame, Hokkaido indeterminates, had a larger 1000-grain weight and produced a higher grain yield than expected from the grain number. On the other hand, many tropical varieties had a smaller 1000-grain weight and produced a lower grain yield than expected from the grain number.

The nitrogen content of the grains ranged from 3.6% to 5.0%: It was between 3.8 and 4.2% for Hokkaido varieties; and with tropical varieties

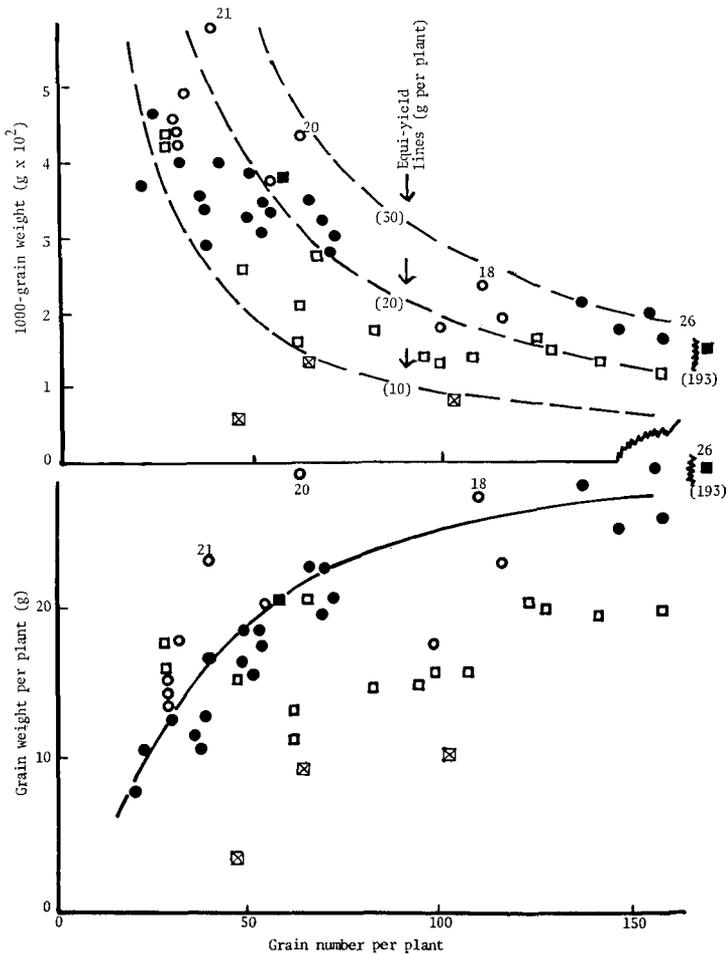


Fig. 39. Relations between grain number per plant and 1000-grain weight (top), and between grain number and grain weight per plant (bottom).

the nitrogen content tended to become lower with an increase of the 1000-grain weight.

Total Plant Weight and Grain Weight: The grain yield (at 15% moisture), calculated from the data collected on the limited number of plants without border effects in 1975 was above 5 t/ha in Ōfuku (an indeterminate with large grains), above 4 t/ha in Toramame (an indeterminate with large grains), Gin-tebō and Ō-tebō (semi-indeterminates with small grains), and below 4 t/ha in other varieties. It was generally lower in 1973 than in 1975 because of the wide spacing.

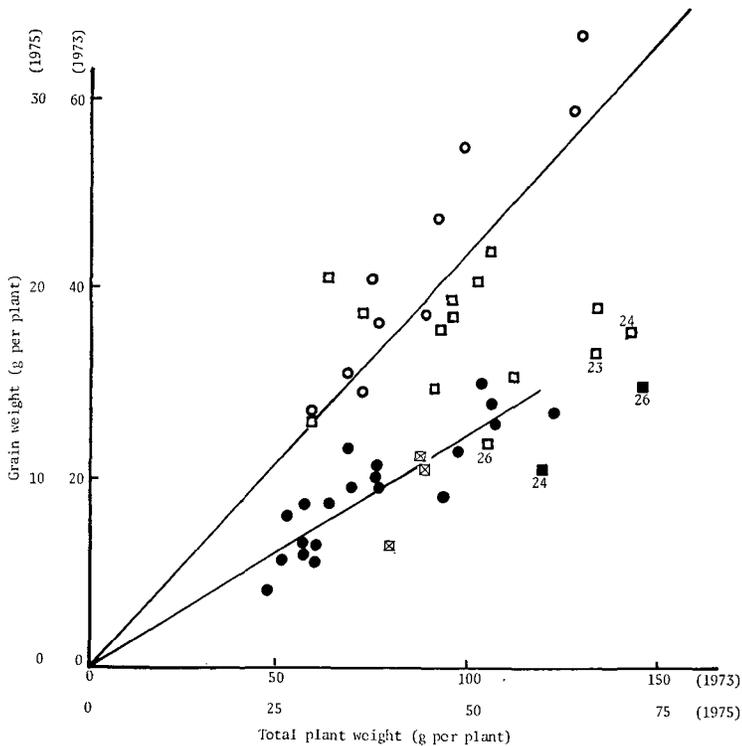


Fig. 40. Relation between total plant weight and grain weight.

The larger the total plant weight at harvest, the larger the grain yield, although the harvest index was larger in 1975 than 1973 (Fig. 40). Smaller harvest indexes were more frequent among the tropical varieties, especially the tropical determinates, than among the Hokkaido varieties.

Only with the Hokkaido varieties did the total plant weight tend to increase with an increase of the node number on the main stem, especially

in 1975 (Fig. 41, top). However, there was no such trend if tropical determinates were included, because these varieties were large in the total plant weight due to their many branches, although the node number on the main stem was small.

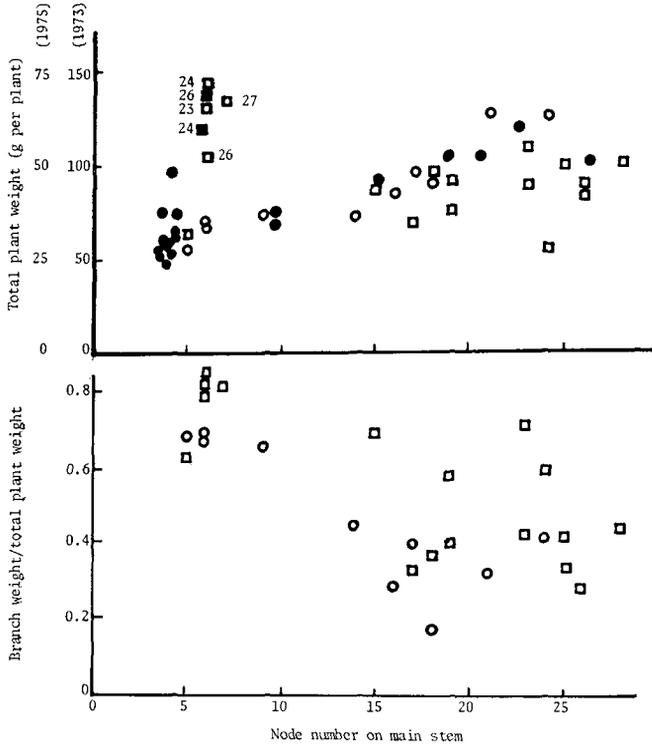


Fig. 41. Relations between node number on the main stem and the total plant weight (top), and branch weight/total plant weight ratio (bottom).

In 1975 the ratio of the branch weight to the total plant weight decreased with an increase in the node number on the main stem, and was larger in the tropical varieties than the Hokkaido varieties at a given node number (Fig. 41, bottom).

The grain weight correlated positively with the dry matter production after full blooming if a few varieties were excluded (Fig. 42, top). In many varieties, 70% of the dry matter produced after full blooming became the constituents of grains. This partition percentage of the field bean is smaller than in rice or maize where it is almost 100%. In the tropical determinates,

i. e. ICA Guali, ICA DUVA, Argentina 2, and PI 172.017, the partition percentage was lower than 70%: These varieties were active in branching; and the partition percentage was low because of the growth of branches after full blooming.

The relation between the LAI at full blooming and the dry matter production after this stage demonstrates that when the LAI was above 6,

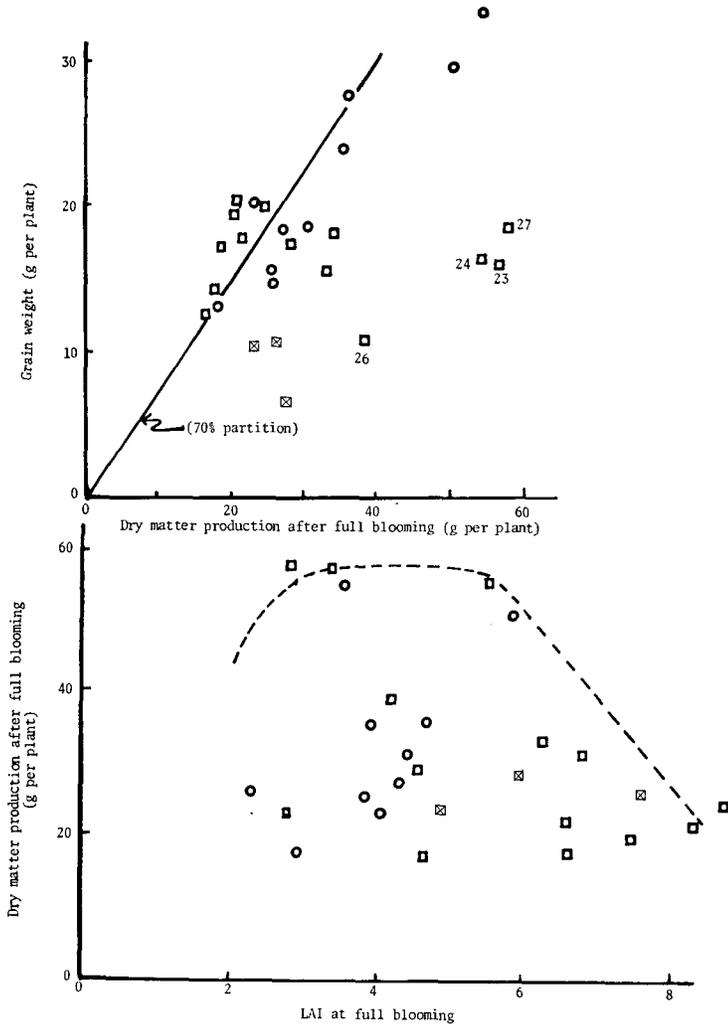


Fig. 42. Relations between dry matter production after full blooming and grain weight (top) and between the LAI at full blooming and dry matter production after blooming (bottom).

the dry matter production was bound to be small (Fig. 42, bottom). This low efficiency of leaves at a large LAI may be due to the mutual shading among overcrowded leaves. Within the range of LAI from 2.5 to 6 there was no relation between LAI and dry matter production. Thus, it can be considered that dry matter production after full blooming is not governed by the source capacity but by the sink capacity.

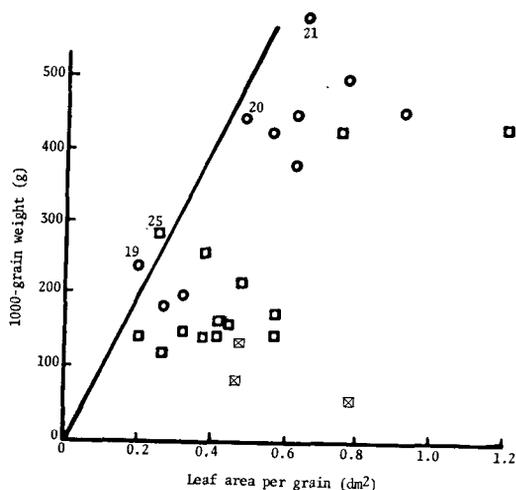


Fig. 43. Relation between leaf area per grain and 1000-grain weight.

The relation between the leaf area at full blooming per mature grain and the 1000-grain weight demonstrates that 1 dm² leaf produced about 1 g of grains in high yielding varieties (Fig. 43). If the period of active grain growth is assumed to be 30 days, the rate of grain production per unit leaf area is about 33 mg·dm⁻²·day⁻¹. This value is lower than that of maize which is above 60 mg·dm⁻²·day⁻¹ ³⁷⁾. In low yielding varieties this rate was much lower: In the determinates with large grains the efficiency of leaves to produce the grains was low because of the limitation in the sink (the grain number). In these varieties it appears that by having a limited number of grains in relation to the leaf area, the source capacity exceeds the sink capacity under normal conditions as demonstrated by the accumulation of carbohydrates in the vegetative organs at later growth stages, and the characteristics of large grains can be expressed even if the environmental condition is not entirely favorable. On the other hand, in the tropical tall with small grains the efficiency of leaves to produce the grains is low because

of the mutual shading among leaves due to an excessive leaf area and also, probably, because of limitations in the sink size (the grain size).

3. Discussion

Plant height and node number on the main stem are characteristics under strong genetic control. The number of branches, on the other hand, is more responsive to different growing conditions, although there are varietal differences in branching ability.

Among the yield components, the grain number per pod and the 1000-grain weight are under strong genetic control, while the pod number varies markedly with growing conditions.

The grain yield is the product of the grain number per plant and the 1000-grain weight. There is a negative correlation between the grain number per plant and the 1000-grain weight among varieties. The grain yield, however, tends to increase with an increase of the grain number per plant, because the decrease of 1000-grain weight associated with an increase of the grain number is generally not so large as to nullify the increase in grain number. Thus, high yielding varieties are more frequently found among varieties that produce many small grains than those which produce a limited number of large grains^{2,8}. Some high yielding varieties with large grains and some low yielding varieties with many grains, however, were found so that exceptions to these general trends are recognized.

The grain number per plant increases with an increase in the pod number per plant. At close spacings varieties with more than 20 nodes on the main stem and of tall stature have more chances to produce many pods and a high grain yield than those with fewer nodes. The more the node number on the main stem, the longer the growth duration. Thus, a higher yielding variety is generally one with a long growth duration.

Determinates which have a limited number of nodes on the main stem have possibilities to produce many pods per plant when they have pronounced branching ability. The branching ability is, however, often obscured when such plants are grown at close spacings to obtain a very high grain yield.

Based on the data collected in this series of varietal comparison, varieties of the field bean can be classified into the following four groups by the source-sink relationship during the grain growth phase:

(a) The dry matter production is high because the grains are active as the sink and grain yield is high (Gin-tebō, Ō-tebō, Ōfuku, Toramame, etc.: Semi-indeterminates and indeterminates).

(b) The dry matter production is high because the branches, which develop during later growth stages, are active as the sink, and the grain

yield is not high (ICA DUVA, ICA Guali, Argentina 2, PI 172.017: Tropical determinates).

(c) The dry matter production is low because neither the grains nor the branches are active as the sink, the grain yield is relatively low while the 1000-grain weight is large (Hokkaido determinates).

(d) The dry matter production is low because of excessive leaf area (tropical indeterminates).

This classification is based on the growth behavior in Hokkaido. The climatic conditions in Hokkaido may not be optimal for the tropical varieties, and the growth behavior of these varieties in the tropics may be different from that observed in Hokkaido. Thus, a classification based on behavior in the tropics might be different.

By examining the characteristics of available commercial varieties which are popular among farmers, it can be speculated that :

(a) Hokkaido indeterminates have been developed to give a high grain yield with high quality (large grains). Since the quality of grains commands a high price, farmers can afford to use bamboo support.

(b) Hokkaido determinates have been developed to obtain large grains without support at the expense of the grain yield.

(c) Hokkaido semi-indeterminates have been developed to obtain a high grain yield without support at the expense of the grain size.

(d) In the tropics bush types and climbers were established in connection with mono- and mixed-crop systems. As adverse environmental conditions are rather frequently encountered an active branching habit has been acquired to counteract against such conditions. Under favorable conditions, however, determinates produce excessive branches at later growth stages, and semi-indeterminates and indeterminates produce an excessive leaf area. All these varieties may produce rather low grain yields.

The merits and demerits of varieties with different traits depend closely upon the cultural conditions. Thus, it is difficult to depict a general picture of the ideo-type of the field bean^v.

In cases where farmers can afford to provide support, tall stature, many nodes on the main stem and rather weak branching activity are desirable traits.

A high yield per crop can be expected with varieties which have a long growth duration and many nodes on the main stem. However, a long duration variety can not be used when the growing season is limited due to climatic conditions or to the growing seasons of crops which are included in a cropping system, and providing support is impossible in most cases

because it is expensive and laborious.

Active branching is a desirable characteristic when spacing is sparse. However, this planting is impractical because the grain yield tends to be low under such a condition.

Under thick planting without support varieties with about 12 nodes on the main stem with moderate branching ability appear to be better. Among such varieties semi-indeterminates seems to be better favored than determinates. Of course, resistance to lodging is an indispensable characteristic under such a cultural condition.

VI. GENERAL DISCUSSION

In the field bean 3 t/ha is generally considered to be a good yield and 4.5 t/ha the maximum yield. In this series of experiments the maximum yield obtained from a sizable plot was 4.35 t/ha, although yields above 5 t/ha were recorded with indeterminates from a small plot. At CIAT yields of 5.65 t/ha in 96 days in a climbing variety and 3.8 t/ha in 75 days in a non-climbing variety were recorded under experimental conditions at a high planting density (with support for the climber)⁹.

In a farmers contest conducted since 1963 in the Tokachi district, which is the major bean producing area in Hokkaido, the maximum yield of the field bean (no indeterminate was included) so far obtained for 15 years was 4.45 t/ha, and the average of the top yields in each year was 3.44 t/ha. The maximum and the average yields of maize in the same contest were 8.14 t/ha and 6.34 t/ha, respectively. Thus, it can be said that the yield per crop is lower in the field bean than in the maize.

The growth duration of the field bean is generally shorter than for maize; approximately 100 days and 150 days for the field bean and maize in Hokkaido, respectively. Thus, it is necessary to compare the productivity of crops in terms of the weight of product per day of growth. Even with this expression the field bean is inferior to maize (see the following table).

		Yield per crop (t/ha)	Yield per growing day (kg/ha/day)
Maximum yield	Field bean (a)	4.45	44.5
	Maize (b)	8.14	54.3
	Ratio (a/b)	0.55	0.82
Average yield	Field bean (a')	3.44	34.4
	Maize (b')	6.25	41.7
	Ratio (a'/b')	0.55	0.82

The field bean is higher in protein than maize, and production of protein requires more energy than that of starch. By taking into account the difference in chemical composition of the grains it has been estimated that if the yield of field bean is expressed in weight as 90% of that of maize the productivity may be considered to be about equal²⁰. If this point is considered, the productivity is only slightly lower in the field bean than in maize. A similar statement can be made in a comparison between the field bean and rice. Thus, it can be said that the productivity of the field bean is slightly lower than or comparable to cereal crops.

In these studies the maximum value of the photosynthetic rate per unit leaf area of the field bean observed was about $40 \text{ mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{hr}^{-1}$; this value is comparable to that of rice, etc. (C-3 plants) although it is lower than that of maize, etc. (C-4 plants). The maximum leaf area index during growth was about 8; this value is comparable to other crops. The translocation percentage of photosynthates from the leaf was higher than 80% when a leaf was functioning efficiently; this value is also comparable to that of cereal crops although it is sometime above 90% in maize. All of these data indicate that the productivity of the field bean should be comparable to cereal crops at least as far as the potential capacity of photosynthesis is concerned.

The photosynthetic rate per unit leaf area and the translocation percentage of a leaf, however, decrease rapidly with the age of the leaf after reaching maximum values, especially during the grain growth phase, due to inability of the sink (the grain) to accept all the photosynthates produced by the source. The carbohydrates accumulate in the stem during the grain growth phase due to excessive photosynthesis. These phenomena suggest that the limiting factors of productivity of the field bean are generally related to the sink size during the grain growth phase.

The dry matter production during growth was generally below 10 t/ha, although the maximum value observed was about 14 t/ha. The harvest index ranged from 0.3-0.5, and was frequently below 0.4; this value is smaller than the value in cereal crops. The partition percentage of photosynthates between the grains and the vegetative organs during the grain growth phase was about 70% when the photosynthates were efficiently utilized by the grains; this value is lower than the equivalent value for cereal crops. The grain yield was highly correlated with the grain number: The more the grain number the higher was the grain yield. From these data it is apparent that the limitation of the sink (capacity of grains) to accept photosynthates during the grain growth phase is the major factor controlling the grain

yield as well as the total dry matter production.

The life cycle of the field bean can be divided into four phases: Vegetative growth, blooming, pod-wall growth and grain growth phases. However, as the vegetative growth phase continues on during the blooming and the pod-wall growth phases, there is overlapping of the growth phases and the overlapping is more acute and longer in indeterminates (including semi-indeterminates) than determinates, due to the continuous development of the leaves and flowers after the start of blooming.

During the blooming and the pod-wall growth phases the pod number is determined and the carbohydrate content of the stem is generally low. The grain number is positively correlated with the pod number, and the pod-setting percentage is generally low. This situation suggests that during these phases the sink capacity exceeds the source capacity because the flowers, the young pods and the vegetative organs compete with each other for photosynthates; under such circumstances many flowers and young pods abort; the sink capacity (the pod number) is adjusted to match with the source capacity; with this self-adjustment an excessive abortion generally takes place; and once the set-pod number is established, the source capacity is larger than the sink capacity during the grain growth phase. Thus, increasing the set-pod number by improving the competition for photosynthates between the reproductive and the vegetative organs during the blooming and the pod-wall growth phases is the key to increasing the grain yield.

The set-pod number can be increased by increasing the flower number, and/or the pod-setting percentage. However, it is very complicated to study these two factors separately because they interact with each other. Generally speaking, however, the flower number is more but the pod-setting percentage is less in indeterminates than in determinates because the node number on a stem is more, and the overlapping of the vegetative growth with the blooming and the pod-wall growth phases is more pronounced in indeterminates than determinates. Thus, it is not simple to decide that between determinates and indeterminates which has more chances to produce more pods.

The pod number per plant is the product of the node number and the pod number per node, and the node number is composed of the node number on the main stem and on the branches. Topping or branch-removing experiments revealed tendencies for a decrease of the node number on the main stem or the branches to result in an increase of the node number on the branches or the main stem, respectively, and a decrease of the node number on a stem results in an increase of the pod number per node of

the stem. These compensations pose difficulties in discussing the method to increase the pod number per plant or the pod number per unit field area by improving varieties and cultural practices.

A decrease in the plant spacing causes decreases of the branch number and the node number on the main stem, and the decrease is more prominent in the branch number than in the node number on the main stem. Such changes are more prominent in indeterminates than determinates. Thus, an increase in grain yield by a decrease in spacing is more prominent in determinates than in indeterminates. Generally speaking, at wide spacings the grain yield is higher in indeterminates than in determinates, and this difference becomes smaller with a decrease of spacing. As the grain yield is higher at closer than at wider spacings within the limit of practical farmers' practices, discussion to maximize the grain yield should be concentrated on the condition of dense planting where only a few branches are produced.

The field bean is grown under two distinctively different agronomic conditions; *i. e.* with and without support. By this difference in the growing condition the field bean is divided into bush beans and climbing beans, and the most desirable plant type for one condition naturally differs from one for the other.

For bush bean varieties at a close spacing, lodging resistance is one of the prerequisites; active branching is not necessarily an important characteristic because branching is limited anyway at close spacings although it is a desirable characteristic to counteract various adverse conditions; the optimum node number on the main stem appears to be about 12 (10 trifoliated leaves) because a smaller or a larger number than the optimum results in a smaller grain number due to limitations in the node number on the main stem or in the pod number per node, respectively; and the semi-indeterminate habit may be better than the determinate habit since the former has the potential to respond more favorably to adverse environmental conditions.

For climbing bean varieties at a close spacing, a node number on the main stem of more than 20 appears to be a desirable characteristic. In such varieties the upper portion of the main stem is typically composed of the source-sink units; the leaf of a unit takes care of the pods on the raceme within the unit, an increase of the number of nodes (the units) results in a proportional increase in grain yield, but an increase in node number accompanies an extension of the growth duration.

The yielding ability among varieties should be compared on the basis of the yield per day of growth because the more the node number on the main stem, the higher the grain yield and also the longer the growth duration.

A long duration indeterminate may produce a high grain yield, but may not be high in the yield per day of growth.

There is a loose negative association between the grain number and the 1000-grain weight with present commercial varieties. However, there is no genetic basis for this association, and recombinations are possible. Thus, effort should be made to increase the 1000-grain weight in the breeding of all growth habit varieties. In this effort it should be borne in mind that the fluctuation of 1000-grain weight caused by the growing condition is larger when the 1000-grain weight is larger.

So far as the data obtained in these experiments reported here are concerned, the nitrogen fixing capacity of the field bean is low. Of course, it is necessary to look into the situation more close by using wider ranges of field bean varieties and rhizobium strains. But in obtaining a very high yield for the field bean, an application of considerable amounts of nitrogen seems to be indispensable.

VII. SUMMARY

For increasing grain yield of the field bean (*Phaseolus vulgaris*) through breeding and improvement of cultural practices it is necessary to identify the yield limiting factors under presently available good cultural conditions and also to find out plant traits which are associated with the potential productivity of varieties by analyzing the source-sink relationship.

For this purpose (a) growth pattern, photosynthetic rate of leaves, and translocation of photosynthates among various organs were compared between a determinate and a semi-indeterminate (Taishō-kintoki and Gin-tebō, respectively, standard Hokkaido commercial varieties), (b) the source-sink relationship was analyzed through manipulation of relative strength of the source and the sink by removing leaves, branches or pods, (c) responses of various plant traits to nitrogen, plant spacing and support were studied by using a few standard Hokkaido commercial varieties, and (d) relationships between the grain yield, total dry matter production, yield components and other plant traits were studied by using 22 Hokkaido varieties and 17 tropical varieties. The following are the results obtained:

1. The grain yield of presently available varieties of field bean is generally lower than for cereal crops due to shorter growth durations. The productivity per day of growth of the field bean is slightly lower than or almost comparable to that of cereal crops. However, as far as potential capacity of photosynthesis is concerned, the productivity of the field bean should be comparable to cereal crops. Thus, the limiting factor of grain

yield appears to be the sink size.

2. The life cycle of the field bean can be divided into four phases: Vegetative growth, blooming, pod-wall growth and grain growth phases. The vegetative phase overlaps with the blooming and the pod-wall growth phases.

3. During the blooming and pod-wall growth phases, when the pod-setting percentage is determined depending upon the availability of carbohydrates to the developing pods, the sink capacity generally exceeds the source capacity due to the overlapping of growth phases, and also to active consumption of photosynthates for nitrogen fixation by root-nodules. Thus, the set-pod number is controlled by the source capacity during the blooming and the pod-wall growth phases. The source capacity is frequently larger than the sink size during the grain growth phase. Thus, the limiting factor of yield is generally the set-pod number.

4. Indeterminates or semi-indeterminates produce more flowers by having more nodes on each stem, but are lower in setting percentage than determinates due to more active and longer overlapping between the vegetative growth phase and the blooming and pod-wall growth phases. Thus, the question of which type is better, is complicated. But, determinates are often lower yielders than other types.

5. The grain yield is higher at closer than at wider spacings. At close spacings only a small number of branches are produced. Thus, an active branching habit is not necessarily an important characteristic although it is desirable to counteract various adverse growing conditions.

6. In bush beans which are grown without support, varieties with about 12 nodes on the main stem with moderate branching ability are desirable, and the semi-indeterminate habit seems to be better than the determinate habit because the former responds more favorably to adverse environmental conditions. Whereas, in climbing beans which are grown with support, a node number of more than 20 on the main stem is a desirable characteristic.

7. Although there is a loose negative association between the grain number per plant and the 1000-grain weight among presently available varieties, recombinations of these two traits are possible. Efforts should be made to increase the 1000-grain weight in the breeding of all growth habit varieties.

8. Application of a considerable amount of nitrogen is indispensable to obtain a very high yield, because the nitrogen fixing capacity of this crop is not very high, although it is higher in indeterminates than determinates.

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