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DRY MATTER PRODUCTION, YIELD COMPONENTS AND GRAIN YIELD OF THE MAIZE PLANT

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INTRODUCTION

Maize and rice rank second and third in importance among all crops for supplying foods to the people in the world. These two crops are especially important for people in developing countries. Improving the productivity of maize and rice is urgently needed to help solve world food problems.

To improve crop production, more emphasis has been given recently to physiology of dry matter production. Much information is being accumulated for several crops.

The authors have been studying the physiology of grain and dry matter production of rice and published critical discussions (TANAKA, NAVASERO, GARCIA, PARAO and RAMIREZ (1964), TANAKA, KAWANO and YAMAGUCHI (1966)). More recently, they have been working with maize and have published several reports in Japanese.

The object of this paper is to discuss critically the physiology of grain production of maize in relation to the dry matter production. For this we have used data presented in separate reports by the authors in Japanese and data available in the literature. References to the authors' experiences with rice are included. Detailed descriptions of experimental methods are omitted in this paper because they are available in previous reports.

I. GENERAL GROWTH PATTERN

Since increasing production of grain is the objective of improving maize cultivation, a general understanding of accumulation processes of dry matter and carbohydrates in each organ during growth is a prerequisite to discussing improvements of varieties and of cultural practices. For this reason, the following observations were made.

Growth Pattern and Dry Matter Accumulation

Ko No. 504, a standard dent corn variety in Hokkaido, was planted in a field of Hokkaido University with a standard cultivation method which includes sowing by mid-May at a spacing of 50 cm × 50 cm, one plant per hill, and applying 150 kg/ha each of N, P_2O_5 and K_2O (TANAKA and ISHIZUKA (1969)). Unless stated otherwise, this cultivation method was used in all following experiments.

Seedlings emerged about two weeks after sowing. Leaves developed in succession with a leafing interval of about 4.5 days. Elongation of internodes began 40 days after sowing, became vigorous 20 days later and stopped 10 days after silking. Tasseling occurred 70 days after sowing and silking started two weeks later. No tiller developed (Fig. 1).

An increase of the weight of the leaves, the culm, and the cob-and-husks occurred in this sequence. The weight of these organs decreased slightly during grain-filling. The weight of the grains increased slowly for about two weeks after silking and then increased rapidly until growth ceased.

It took about one month for the ear-primordium to complete its elongation after initiation. The weight of the husks increased first, then the cob. Increase of the weight of these organs continued for about two weeks after silking. The weight of the grains started to increase before the weight of the husks and the cob reached their maximum and continued to increase until harvest. The weight of the husks and the cob decreased when the increase of the grain weight became active. The decrease started in the husks first and then in the cob.

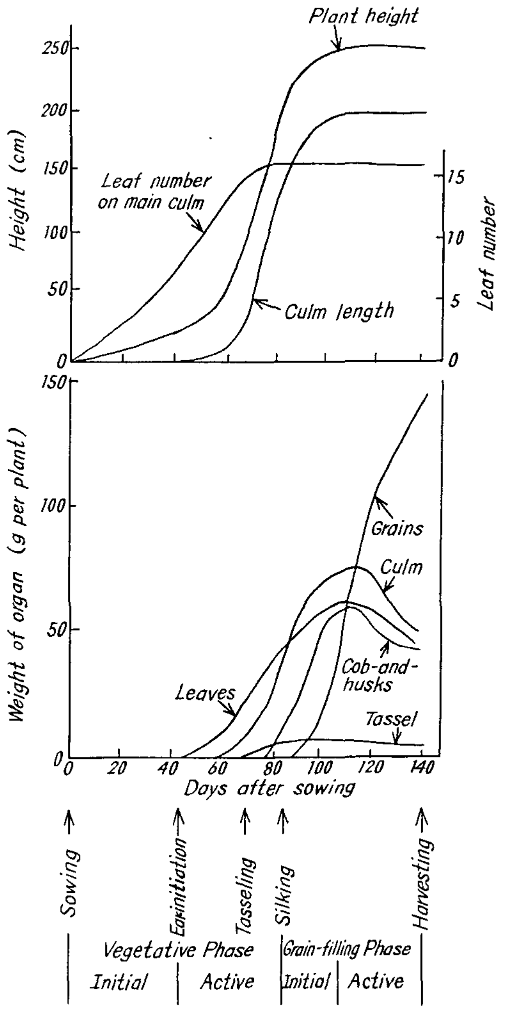


Fig. 1. Outline of growth process (Ko No. 504, 1967)

Based on these observations, the growth process of the maize plant can be divided into the following four phases.

Initial vegetative phase: The leaves are initiated and then develop in succession from the lower to the upper. The dry matter production is slow. This phase is terminated by the initiation of reproductive organs or by the beginning of internode elongation, or both.

Active vegetative phase: The leaves, the culm and the primordia of reproductive organs develop. An active increase of the weight of the leaves occurs first and then that of the culm. This phase is terminated by silking.

Initial grain-filling phase: The weight of the leaves and the culm continues to increase at a slower rate. The husks and the cob continue to gain weight. The weight of the grains increases slowly. This can be considered a transitory phase from the vegetative phase to the grain-filling.

Active grain-filling phase: A rapid increase in the weight of the grains occurs. This increase is accompanied by a slight decrease of the weight of the leaves, the culm, the husks and the cob.

Carbohydrate Accumulation

"Carbohydrates" is used to mean the total amount of sugars and starch. In the vegetative organs, there was almost no starch.

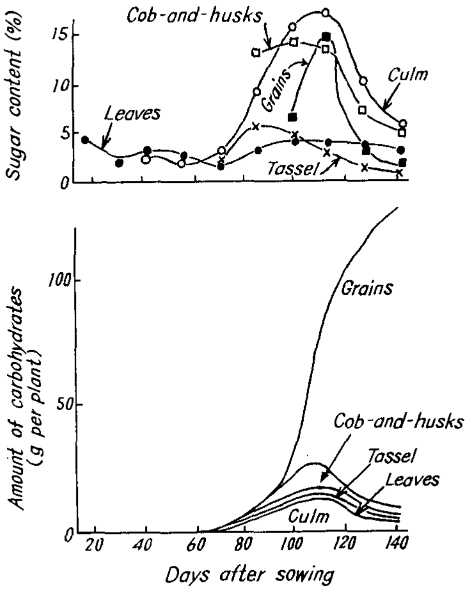


Fig. 2. Fluctuation of sugar content (top) and amount of total carbohydrates in the plant (battom) during growth (Ko No. 504, 1967)

The sugar content of the leaves was low throughout growth (Fig. 2, top). For the culm, it was low at early growth stages, started to increase before silking, increased considerably after silking, reached a maximum at the end of the initial grain-filling phase and then decreased. The sugar content of the cob-and-husks and the grains was relatively high during the initial grain-filling phase, and then decreased during the active grain-filling phase.

Only a small amount of carbohydrates accumulated in the vegetative organs (Fig. 2, bottom). However, the accumulation in the culm and in the cob-and-husks during the initial grain-filling phase was significant. During the active grain-filling phase, the amount of carbohydrates in these organs decreased and the amount in the grains increased rapidly. With a conventional substruction method described elsewhere (Ishizuka and Tanaka (1953)), about 90 percent of the carbohydrates in the grains at harvest were the photosynthetic products during grain-filling.

Although data are not presented, the translocation of nitrogen compounds from leaves and culm to grains during grain-filling was considerable.

Characteristics of Each Leaf

Fukko No. 8, a standard dent corn variety in Hokkaido, was grown with the standard cultivation method. There were 16 leaves on the culm and no tiller developed. Twelve leaves were alive and four leaves at the bottom were dead at silking. A fully developed ear formed at the node of the tenth leaf. Sometimes a second ear formed at the node of the ninth leaf, but only limited kernels developed on it.

The length and the width of the leaves, consequently the leaf area, increased from the lower to the upper leaves, reached a maximum at the tenth or the eleventh leaf and then gradually decreased (Table 1). The thickness of the leaves increased from the bottom to the top. The tenth to twelfth leaves were heaviest. The five leaves including the one below

TABLE 1. Morphological characteristics* and nutrient content at silking of each leaf on the main culm (Fukko No. 8, 1969)

Leaf position**	Length (cm)	Width (cm)	Area (cm^2)	Thickness (mg·dm^{-2})	Weight (g)	Nutrient content (%)		
						N	P	K
16	48	7.8	271	458	1.24	3.27	0.45	2.40
15	61	9.5	462	429	1.98	3.51	0.40	2.63
14	70	10.8	580	432	2.51	3.37	0.43	2.76
13	76	11.8	743	423	3.14	3.61	0.39	2.89
12	81	11.8	811	410	3.33	3.59	0.38	2.89
11	83	11.9	860	382	3.29	3.43	0.35	3.00
10	86	11.7	863	387	3.34	3.08	0.30	3.43
9	83	11.2	795	365	2.90	2.81	0.28	3.36
8	71	9.8	576	355	2.04	2.77	0.22	3.50
7	59	7.6	390	324	1.26	2.67	0.21	3.12
6	49	6.4	285	319	0.91	2.46	0.23	3.07
5	38	4.6	147	310	0.46	—	—	—
4	28	3.1	69	308	0.21	—	—	—
3	20	2.0	31	286	0.09	—	—	—
2	12	1.5	15.3	275	0.04	—	—	—
1	5.0	1.7	6.6	276	0.02	—	—	—

* Obseavations were made at growth stages when each leaf completed expansion. .
** Counted from the bottom.

and the three above the first ear were largest. They accounted for more than 60 percent of the total leaf area. At silking the nitrogen content was higher in the thirteenth leaf than in leaves above or below. The phosphorus content was highest in the top leaf and decreased towards the bottom leaf. Conversely, the potassium content was lowest in the top leaf and increased in successively lower leaves, except for a few leaves at the bottom.

Discussions

The growth process of the maize plant described here is almost identical with that reported by HANWAY (1963). It can be divided into four phases: initial vegetative phase, active vegetative phase, initial grain-filling phase, and active grain-filling phase.

During the initial grain-filling phase some sugars accumulate in the culm and the cob-and-husks. The largest accumulation in the culm is in the internode from which the ear exerts (VAN REEN and SINGLETON (1952), ASANUMA, NAKA and TAMAKI (1967)). The sugar content of the grains increases during the initial grain-filling phase and then decreases during the active grain-filling phase (EARLEY (1952)). These are indications of an imbalance between rate of photosynthesis of the leaves and rate of starch formation in the developing kernels during the initial grain-filling phase. In this sense, the sugars in the culm or in the cob-and-husks are transitory.

During the active grain-filling phase, the weight of the grains increases rapidly and the weight of the vegetative organs decreases slightly. This suggests that there is probably some retranslocation of substances from the vegetative organs to the grains during this phase. However, this decrease of the weight of the vegetative organs was not observed by HANWAY (1963). From the evidence available, it seems that this type of retranslocation does not make a very important contribution to grain weight. This decrease is quite large in the rice plant, at least under some circumstances (MURAYAMA, et al. (1955)).

The sugars accumulated in the culm or in the cob-and-husks decreased during the active grain-filling phase. The amount stored in the vegetative organs and then translocated to the grains accounts for less than 10 percent of the total carbohydrate accumulated in the grains at harvest. Although the amount of sugars stored in the culm is not large, this transitory sugar is important to maintain a constant kernel growth rate irrespective of daily fluctuations in the rate of photosynthesis (DUNCAN, HATFIELD and RAGLAND (1965)). In the rice plant, the growth rate of grains is higher in the day time than at night (MATSUSHIMA, OKADA and WADA (1957)).

More than 90 percent of the weight of the grains is derived from the product of photosynthesis during grain-filling and is translocated to the grains directly. Therefore, dry matter production after silking is important for grain production. The five leaves at or just above the ear are probably most important during grain-filling.

In several ways the growth of the maize plant described here is similar to the growth of the rice plant (ISHIZUKA and TANAKA (1953), ARASHI (1954), TOGARI, et al. (1954), TANAKA et al. (1964), ISHIZUKA (1965), MURAYAMA (1955, 1965)). Major differences between rice and maize are : (1) maize does not tiller as actively as rice and (2) in rice some starch or sugars are accumulated in the vegetative organs during the vegetative growth and are subsequently translocated rapidly into the grains after flowering. In maize, carbohydrate accumulation is less and vegetative growth continues after silking to some extent. In both crops, however, most starch accumulating in the grains is the product of photosynthesis during grain-filling.

II. CONTRIBUTION OF LEAVES AT VARIOUS POSITIONS TO GRAIN YIELD AND DRY MATTER PRODUCTION

In the previous chapter it was demonstrated that the photosynthetic products of the leaves during grain-filling are the major components of the grains. As there are many leaves at various positions on a culm, differential contribution among leaves for grain-filling can be expected. Experiments to demonstrate such a division of function among leaves were conducted by removing leaves or feeding $^{14}CO_2$ from leaves at various positions.

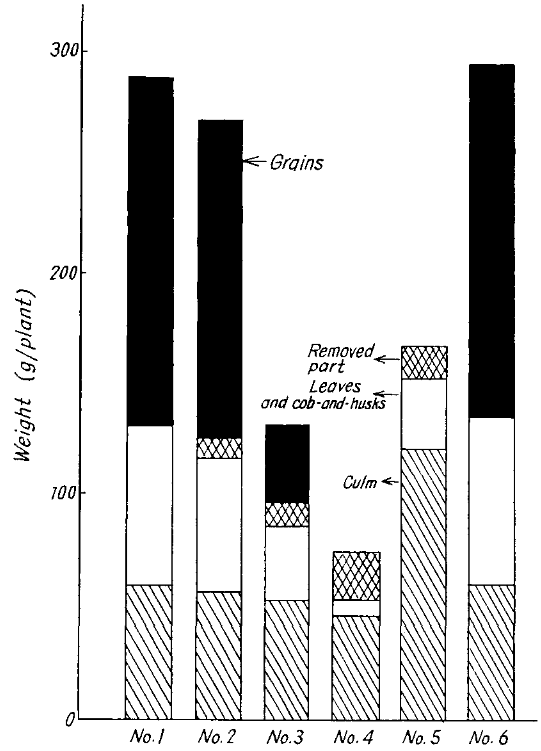
The source-sink theory is a handy tool when discussing dry matter production. In the maize plant during grain-filling the leaves and the ears can be considered as the source and the sink, respectively. Thus, various treatments of removing leaves or ears were tested to determine the relation between source and sink.

Effect of Removing Leaves or Ears

Using a Fukko No. 8 population, six treatments (Fig. 3) were differentiated by removing the leaf-blade or the ear at silking (TANAKA and FUJITA (1971)).

Removing all leaves (No. 4) resulted in no grain production and a decrease of the culm weight. Removing leaves above the ear (No. 3) caused a drastic decrease of grain weight. However, removing leaves below the ear (No. 2) caused almost no decrease of grain weight. Removing ears (No. 5) caused a significant increase of culm weight and a decrease of total plant weight. Removing neighboring plants (No. 6) did not result in a remarkable change of weight of any organs.

Removing all leaves (No. 4) decreased nitrogen content and increased



No. 1	*Control.*
No. 2	*The leaves at or above the 1st ear were kept intact and the leaf-blades of the lower leaves were removed.*
No. 3	*The leaves below the 1st ear were kept intact and the leaf-blades of the upper leaves were removed.*
No. 4	*All leaf-blades were removed.*
No. 5	*The ears were removed.*
No. 6	*The plants in the rows at the both sides of the test row were removed.*

Fig. 3. Effect of removing leaves or ears on weight of various organs at harvest (Fukko No. 8, 1968)

culm sugar content (Table 2). Removing ears (No. 5) caused a remarkable incease of sugar content of the leaf-blades and the culm. Also, it resulted in earlier senescence of the leaves.

TABLE 2. Effect of removing leaves or ears on sugar and nitrogen content of the leaf-blades and the culm* (Fukko No. 8, 1968)

Treatment**	Sugar (%)		Nitrogen (%)	
	Leaf-blades	Culm	Leaf-blades	Culm
No. 1	1.2	5.6	4.18	1.83
No. 2	2.4	7.8	2.24	1.48
No. 3	1.6	4.4	2.09	1.39
No. 4	—	11.8	—	1.08
No. 5	5.0	16.4	2.32	1.49
No. 6	1.6	4.9	4.00	1.43

* Including the leaf-sheath.

** See Fig. 3.

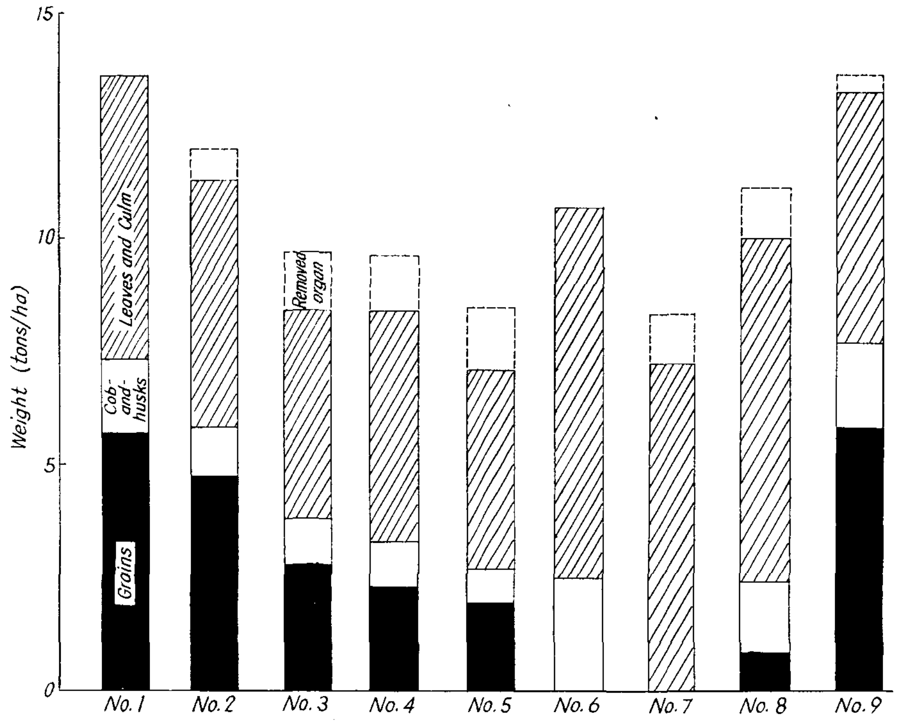
Another experiment using a Fukko No. 8 population included nine treatments (Fig. 4) differentiated at silking.

With a decrease of leaf area (No.2 – No.5), grain weight and total plant weight decreased. Removing lower leaves (No. 2) caused only a small decrease of grain weight. Interception of pollination (No. 6) resulted in no grain production, a decrease of total plant weight and an increase of the weight of vegetative organs. Removing the first ear (No. 7 and No. 8) caused a decrease of total plant weight, an increase of the weight of the leaf-and-culm and a slight increase of the weight of the second ear when it was kept intact. Removing the second ear (No. 9) caused almost no change.

Decreasing leaf area by removing the leaves (No.2 – No.5) caused an increase of the rate of dry matter production per unit leaf area during grain-filling (Table 3). Removing the first ear (No. 7 and No. 8) or the interception of pollination (No. 6) caused a decrease of the rate of dry matter production per unit leaf area and also caused an increase of sugar content of vegetative organs, especially in the sheath-and-culm.

Translocation of Photosynthetic Products

D403 × D405 was water cultured with a standard culture soltution.



No. 1	Control.
No. 2	The lower leaves* were removed.
No. 3	The lower and the middle leaves* were removed.
No. 4	The lower leaves and ½ area at the tip of the middle and the upper leaves were removed.
No. 5	The lower leaves and ⅔ area at the tip of the middle and the upper leaves were removed.
No. 6	Pollination intercepted by buging the ears.
No. 7	The ears were removed.
No. 8	The 1st ear was removed.
No. 9	The 2nd ear was removed.

* Two leaves at and just above the 1st ear were designated the middle leaves. The lower and the upper leaves designate the leaves at lower or upper positions of the middle leaves, respectively.

Fig. 4. Effect of removing leaves or ears on weight of various organs at harvest (Fukko No. 8, 1969)

At the beginning of silking, $^{14}CO_2$ was fed to the leaves at three different positions: two positions above the first ear (the twelfth leaf), the position of the first ear (the tenth leaf), and two positions below the first ear (the eighth leaf). Distribution of ^{14}C among the organs 24 hours after the ^{14}C feeding was traced (TANAKA and FUJITA (1971)). At this stage the upper leaves and the cob-and-husks, especially those of the second ear, were still growing vigorously.

TABLE 3. Effect of removing leaves or ears on rate of dry matter production per unit leaf area (DMP Rate) and sugar content of the leaf-blades and the culm* (Fukko No. 8, 1969)

Treatment**	DMP Rate*** ($g \cdot m^{-2} \cdot day^{-1}$)	Sugar (%)	
		Leaf-blades	Culm
No. 1	4.77	3.96	2.7
No. 2	5.11	—	—
No. 3	5.52	—	—
No. 4	5.34	—	—
No. 5	5.51	—	—
No. 6	2.95	1.70	17.6
No. 7	1.54	6.25	9.8
No. 8	3.28	1.98	6.3
No. 9	4.67	—	2.7

* Including the leaf-sheath.

** See Fig. 4.

*** DMP Rate = Dry matter production during grain-filling/leaf area at silking/days from silking to harvest.

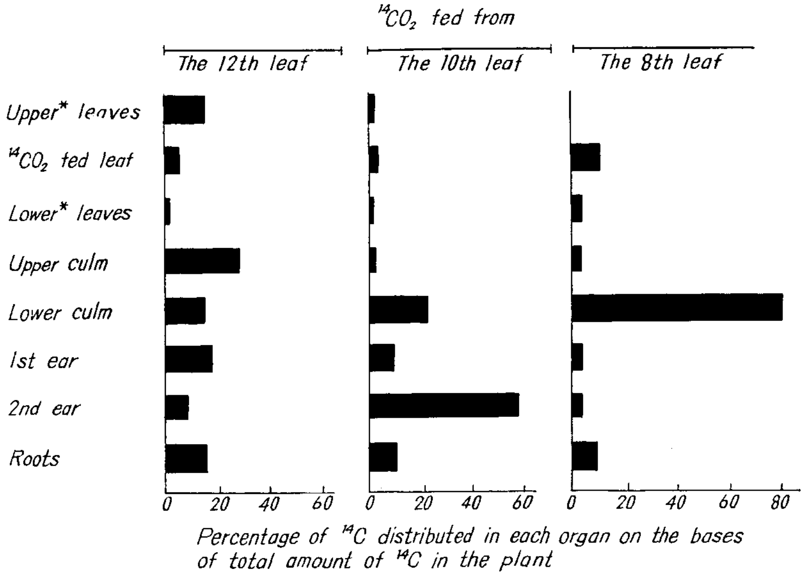


Fig. 5. Distribution of ^{14}C assimilated from the leaves at various positions (D403×D405, water cultured)

* "Upper" or "lower" indicate relative to the ^{14}C fed leaf.

The amount of ^{14}C remaining in the ^{14}C fed leaf was small in all cases (Fig. 5). The ^{14}C fed to the twelfth leaf was distributed uniformly in the plant, except in the lower leaves. More ^{14}C was detected in the first ear than the second ear and in the leaves and the culm above the fed leaf than below it. Most of the ^{14}C introduced from the tenth leaf was detected in the second ear and in the culm below the fed leaf. The ^{14}C fed to the eighth leaf was recovered mostly in the culm below the fed leaf.

Another $^{14}CO_2$ feeding experiment was conducted by using plants in selected plots of the experiment described in Fig. 4. $^{14}CO_2$ was fed to the leaf immediately above the first ear of the plants in treatments No. 1, No. 2, No. 6, No. 7 and No. 8. In No. 3, the lowermost remaining leaf was chosen to feed $^{14}CO_2$. Distribution of ^{14}C was determined 20 days after the ^{14}C feeding.

In the control (No. 1), most ^{14}C was found in the first ear and only two percent remained in the ^{14}C fed leaf (Table 4). With the removal of the leaves (No. 2 and No. 3), a distribution pattern similar to the control was

TABLE 4. Effect of removing leaves or ears on ^{14}C* distribution among organs (percentage of total amount of ^{14}C remaining in the plant) (Fukko No. 8, 1969)

Treatment**		No. 1	No. 2	No. 3	No. 6	No. 7	No. 8
^{14}C fed leaf		2.3	2.3	4.6	12.4	20.9	31.1
Leaves	Upper***	2.8	0.7	0.2	0.3	2.0	0.6
	Lower***	0.4	0.6	0.3	0.5	0.9	2.1
Culm	Upper	2.5	3.5	1.0	6.0	11.2	6.0
	Middle	1.2	2.4	0.7	6.4	7.9	4.0
	Lower	2.0	10.0	1.5	49.7	57.0	47.9
Ear	1st	88.7	79.6	91.6	1.9	—	—
	2nd	0.1	0.9	0.1	22.8	—	8.3
Percentage of ^{14}C released from plant****		38	33	38	45	52	53

* $^{14}CO_2$ was fed to the leaf one position above the 1st ear.

** See Fig. 4.

*** "Upper" or "lower" indicate the position relative to the $^{14}CO_2$ fed leaf.

**** In all treatments the amount assimilated was almost the same, about 13×10^7 cpm (a). From the data of cpm/mg and weight of each organ the total amount of ^{14}C remaining in the plant (b) was worked out : Percentage released $=(a-b)/a \times 100$.

observed. With removal of the lower leaves (No. 2), however, ^{14}C was distributed more in the lower culm. With removal of the ears (No. 7 and No. 8) or the interception of pollination (No. 6), more ^{14}C remained in the ^{14}C fed leaf, most of the ^{14}C translocated from the fed leaf was detected in the lower culm. Some was also found in the second ear when it was kept intact.

The percentage of ^{14}C released as CO_2 by respiration from the plant during the 20-day period after $^{14}CO_2$ feeding on the basis of the amount of ^{14}C assimilated at the time of feeding was less than 40 percent with the control or with the removal of the leaves. The percentage was, however, higher when the development of the kernels was interrupted.

Discussions

Many reports indicate that the more leaves removed and the earlier, the less the grain yield from the maize plant (CORNELIUS, RUSSELL and WOOLEY (1961), MACK (1965)). Similar results were obtained in the experiments described above. This provides further evidence of the importance of photosynthesis after silking for grain production.

However, removing leaves removes not only their contribution to photosynthesis, but also the nutrients they contain. For this reason, shortage of some nutrients, especially of nitrogen, might become one of the limiting factors to kernel development.

Removing all leaves at the beginning of silking resulted in no grain yield. In this case, increased sugar content in the culm was observed. This may indicate that with such treatments, failure of fertilization at the time of flowering rather than shortage of carbohydrates during grain-filling is the cause of no grain production.

Removing leaves above the ear causes a remarkable decrease of grain production. Removing leaves below the ear causes only a slight decrease of the grain yield. Similar results have been reported by several workers (HOYT and BRADFIELD (1962)). This indicates that the upper leaves play the most important role in grain-filling and that the contribution to the grain from the lower leaves is limited.

The results of the experiment with $^{14}CO_2$ fed to the leaves at different positions on the culm demonstrate that the upper leaves contribute more to the grains than the lower leaves. The results indicate a preferential translocation of photosynthetic products from the upper leaves to the grains and from the lower leaves to the lower culm. This was demonstrated by PALMER (1969). According to him, the photosynthetic products of the leaves above the ear translocate to the grains efficiently and translocation of photosynthetic products from the leaves below the ear to the grains decreases progressively towards the base of the plant. A similar division of function among leaves has also been observed in the rice plant (TANAKA (1961)). In rice, the upper three leaves on a culm send their photosynthetic products to the grains of the panicle on the culm and the lower leaves send theirs to the culm or the roots. One important difference is that the major flow of photosynthetic products to the grains is downward in the maize plant and upward in the rice plant.

Another possible explanation for the small contribution from the lower leaves to the grains is that under field conditions the lower leaves are shaded (HOYT and BRADFIELD (1962)).

For these reasons the dry weight increase of the grains in a crop of maize depends mostly on the photosynthesis of the leaves above the ear. Only a limited contribution comes from the lower leaves.

Under favorable conditions, translocation of photosynthetic products from the leaves is rapid and efficient in the maize plant. Only a small fraction of the photosynthetic products of a leaf remains in the leaf for more than 24 hours. The efficient translocation is a characteristic of the maize plant (EASTIN (1970)). The efficiency is lower in the rice plant (TANAKA (1961)).

A partial removal of the upper leaves increases the rate of dry matter production per unit leaf area of the remaining leaves. Such an increased photosynthetic activity by partial defoliation was reported by KIESSELBACH (1948). Since the developing kernels are demanding photosynthetic products from the leaves, a partial removal of leaves increases the demand on the remaining leaves and the photosynthetic efficiency of these leaves increases.

Similarly, it has been shown that in the maize plant the availability of storage sites affects production and movement of carbohydrates (MOSS (1962)). Thus, removing the ear or pollination interception causes a decrease of the rate of dry matter production per unit leaf area. It appears that if the demand of the developing kernels is interrupted, photosynthesis by the leaves is adversely affected.

It has also been demonstrated that the growth rate of the kernels is positively correlated with temperature during grain-filling (RAGLAND, HATFIELD and BENOIT (1965)). Consequently, an increase of temperature accelerates demand of the developing kernels and this affects the rate of photosynthesis by the leaves.

These phenomena can be explained in terms of sources and sinks for the products of photosynthesis where the leaves are the source and the kernels are the sink.

Removing the kernels decreases sink size and increases sugar accumulation in the vegetative organs. This type of accumulation of sugars in the culm, especially that of sucrose, has been reported by several workers (VERDUIN and LOOMIS (1944), VAN REEN and SINGLETON (1952)). The culm and the cob act as an additional sink to some extent by accumulating sucrose when the major sink, the kernels, is missing.

Accumulation of sugars in these organs increases respiration. In normal plants, about 40 percent of the photosynthetic products are consumed by respiration. With plants in which sugars have accumulated because development of the kernels has been prevented, more than 50 percent is consumed. Accumulation of sugars in the leaf-blades results in a decrease in the photosynthetic rate. Also, it accelerates the senescence of leaves (ALLISON and WEINMANN (1970)).

A decrease in the rate of photosynthesis, an increase in the rate of respiration and earlier senescence of the leaves result in reduced total dry matter production.

In the rice plant, removing the ears causes an accumulation of starch in the culm and in the leaf-sheath and eventually, development of new tillers. This was not observed in maize plants.

Removing adjacent plants at silking from a maize population spaced 50 cm × 50 cm which had a leaf area index (LAI) of about four did not cause a significant increase of the dry matter production of the remaining plants. This indicates that the solar energy available to individual plant was not the limiting factor for the dry matter production after silking, at least under the given environmental condition.

The evidence from these experiments and from others to which reference has been made, supports the view that the grains are formed from the products of photosynthesis in the leaves above the ear during grain-filling. Photosynthetic activity of these upper leaves is, however, controlled by the activity of the kernels as the sink.

III. DRY MATTER PRODUCTION, PHOTOSYNTHESIS AND RESPIRATION

Dry matter production is the balance between photosynthesis and respiration. The rates of these physiological processes differ among organs, ages, cultural conditions, etc. Discussions in the previous chapter revealed that the situation of the relation between source and sink interacts with the rates of photosynthesis and respiration.

Various data on photosynthesis and respiration were collected for a better understanding of dry matter production.

Photosynthetic Rate

Apparent rate of photosynthesis of each organ of a Fukko No. 8 population was determined during grain-filling (TANAKA, YAMAGUCHI and IMAI (1971)). In full sunlight the apparent rate of photosynthesis was large in the leaf-blade, small in the sheath-and-culm and negative in the ear (5.08, 0.16 and -0.55 g $CO_2 \cdot m^{-2}$field$\cdot hr^{-1}$, respectively). The rate of photosynthesis of the ear at the milky stage was about half its respiratory rate.

This indicates that maize photosynthesis depends mostly on the leaf-blade and only slightly on the sheath-and-culm.

By using the plants in the same population, the rate of photosynthesis per unit leaf area (po) of leaves at various positions on the culm was measured at successive growth stages.

The po of a lower leaf (the sixth leaf) was about 60 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$ at full expansion and decreased with age (Fig. 6). The po of a middle leaf

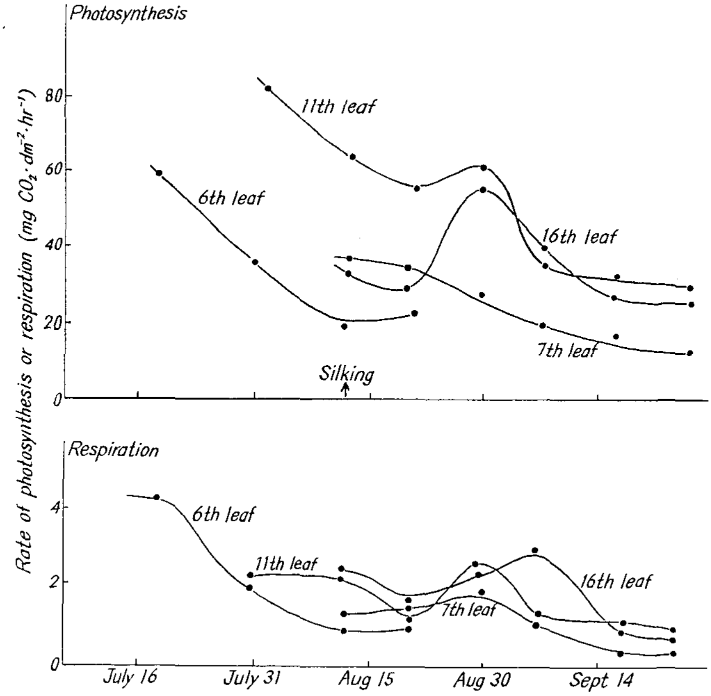


Fig. 6. Fluctuation of rates of photosynthesis and respiration of the leaves at various positions during growth (Fukko No. 8, 1969)

(the eleventh leaf) was as high as 80 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$ at full expansion, decreased slowly with age, increased again during the initial grain-filling phase, reached a maximum at the beginning of the active grain-filling phase and then decreased again. The po of the top leaf (the sixteenth leaf) was rather low when it completed expansion, started to increase from about 10 days after silking, reached a maximum of about 60 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$ at the beginning of the active grain-filling phase and then decreased.

At a given growth stage, the po was higher in the leaves which had just completed their expansion than in younger or older leaves (Table 5). Leaves with a high po contained less sugar than those with a low po.

These data show that the po of a leaf is low when it is expanding, reaches a maximum when it has completed expansion and then decreases with age. Translocation of photosynthetic products is more active from leaves which have just completed expansion and the active photosynthesis of these leaves appears to be associated with an active translocation. The rate of translocation decreases, sugar content increases and the po decreases with age. The low content of nitrogen and phosphorus of old leaves (Table 1) may also be

TABLE 5. Photosynthetic rate (po)* and sugar content of leaves at various positions on the culm at silking (Fukko No. 8, 1969)

Leaf position**	po (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	Sugar (%)
16	36	2.09
15	44	1.96
14	43	2.07
13	72	1.10
12	69	1.24
11	64	1.72
10	59	1.81
9	45	2.01
8	44	2.74
7	37	2.71
6	20	5.30

* Measured at 80 klux.

** Counted from the bottom.

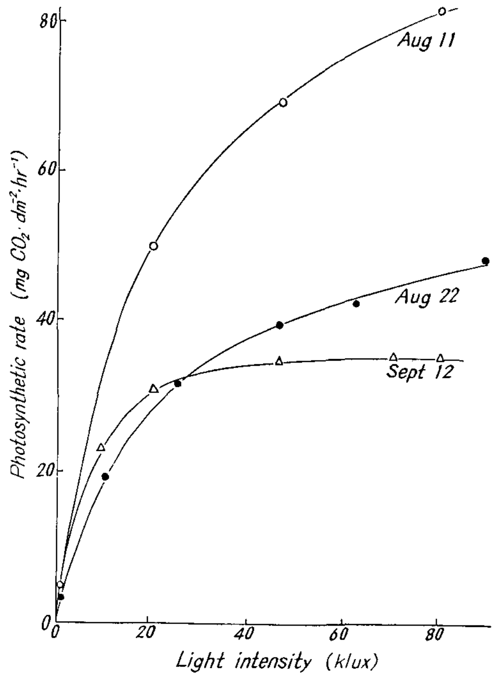
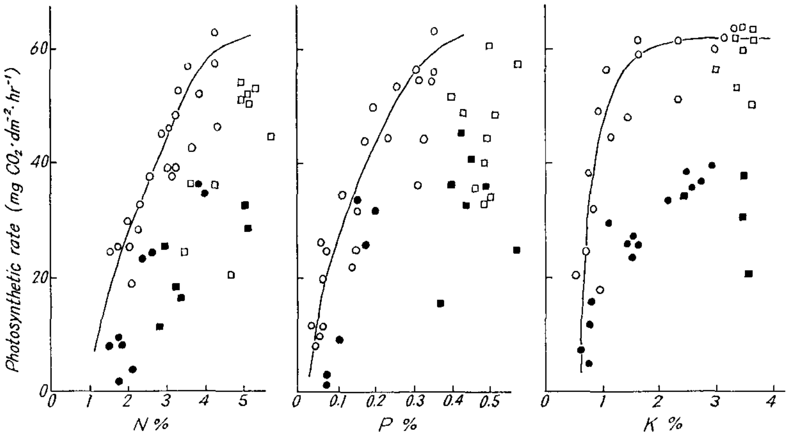


Fig. 7. Photoresponse curves of photosynthetic rate of the 11th leaf at various growth stages (Fukko No. 8, 1969)

related to the low po values of these leaves.

Leaves which have recently expanded had a high rate of photosynthesis and responded to high light intensity. For example, the po of the eleventh leaf did not show photosaturation up to 80 klux. However, the po and the response of the po to light intensity decreased with age (Fig. 7).

The po is also affected by the nutritional status of leaves. D403 x D405 was grown in water culture with graded levels of nitrogen, phosphorus and potassium in the culture solution. The po of the leaves and the content of these three elements in the leaves at different positions were measured at successive stages of growth (Tanaka and Hara (1970, 1971a)).



○ *Element deficient or normal leaves.*
□ *Leaves from plants grown with culture solutions at higher concentrations than 150 ppm N, 50 ppm P or 150 ppm K.*
(Open and solid symbols represent young and old leaves, respectively).

Fig. 8. Relation between nutrient content and photosynthetic rate (D403×D405, water cultured)

There was an association between po and nutrient content (Fig. 8). In newly expanded leaves, the greater the content of N, P or K, the larger was the po. However, the increase in po ceased when the content of N, P and K reached 4 percent, 0.4 percent and 1.5 percent, respectively. The po of old leaves or of leaves from plants grown with excess nitrogen or phosphorus was lower than the expected value from their nutrient content.

Response of the po to light intensity is also affected by the nutrient status of leaves. Leaves deficient in nutrients have a low po and also a low photosaturation point (Fig. 9).

The first ear of a Fukko No. 8 plant was removed at silking. The po of the leaf immediately above the ear of a control plant and the po of

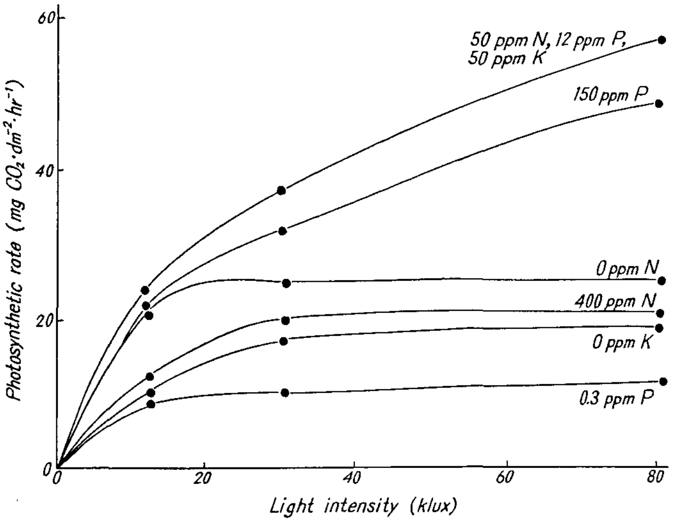


Fig. 9. Photoresponse curves of photosynthetic rate of the 15th leaf affected by nitrogen, phosphorus and potassium status (D403×D405, water cultured) (Letters in the figure indicate the concentration of elements in culture solution)

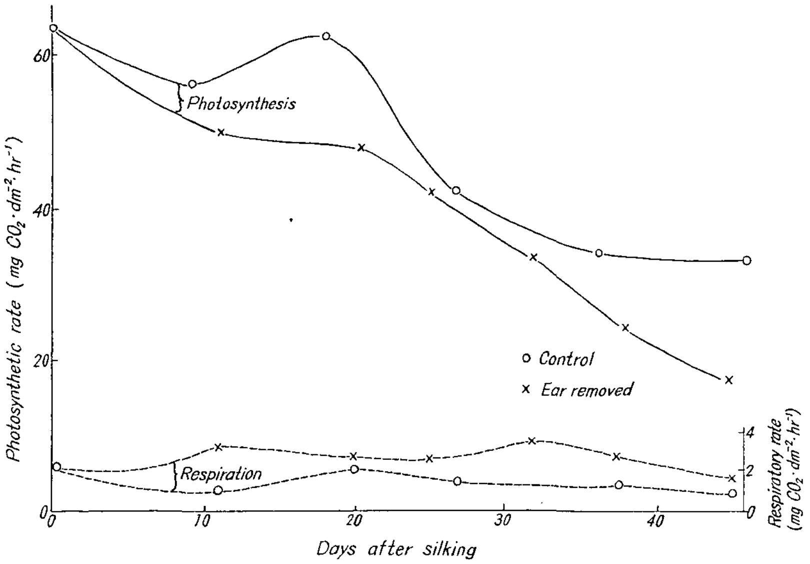


Fig. 10. Effect of removing ear on rates of photosynthesis and respiration of the leaf at one position above the ear (Fukko No. 8)

the corresponding leaf of a plant from which the ear had been removed were measured for 50 days from the removal of the ear (TANAKA and FUJITA (1971)). The po of the plant without an ear was apparently lower than that of the control plant (Fig. 10). This indicates the importance of sink for maintenance of a high po.

The diurnal fluctuation in the rate of photosynthesis of the Fukko No. 8 population which was used to collect the data in Fig. 7 was traced at three growth stages by the methods described elsewhere (TANAKA, KAWANO and YAMAGUCHI (1966)) and the data are plotted against the corresponding light intensities for each measurement (Fig. 11) (TANAKA, YAMAGUCHI and IMAI (1971)).

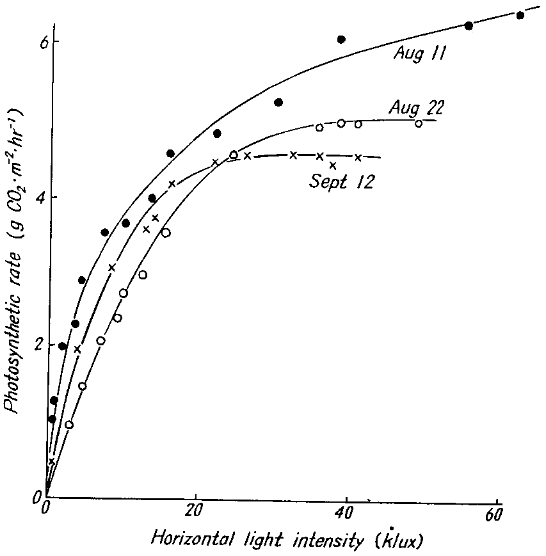


Fig. 11. Photoresponse curves of photosynthetic rate of a population at various growth stages (Fukko No. 8, 1969)

On August 11, the rate of photosynthesis was high and its response to light intensity was high, also. The LAI on August 11 and on August 22 was about 4. However, the rate of photosynthesis and the response of this rate to change in light intensity decreased from August 11 to August 22. There was a further decrease in the response to light intensity from August 22 to September 12, although the rate at lower light intensities was somewhat higher on September 12 than on August 22. These changes can be well interpreted on the basis of changes of the po of each leaf which were illustrated in Fig. 7.

Respiratory Rate

The respiratory rate per unit leaf area decreased with age (Fig. 6) (TANAKA, YAMAGUCHI and HARA (1971a)). However, there was an increase during the active grain-filling phase in the middle and the upper leaves. At a given growth stage, the respiratory rate was high in very young leaves and low in old leaves which were dying. With these exceptions, differences in the rates of respiration of the leaves were small.

Data from the water-culture experiment with graded levels of nutrients indicate a positive correlation between the respiratory rate and the po (Fig. 12). The correlation is not lineal. At low po, the respiration-photosynthesis ratio was higher than at high po.

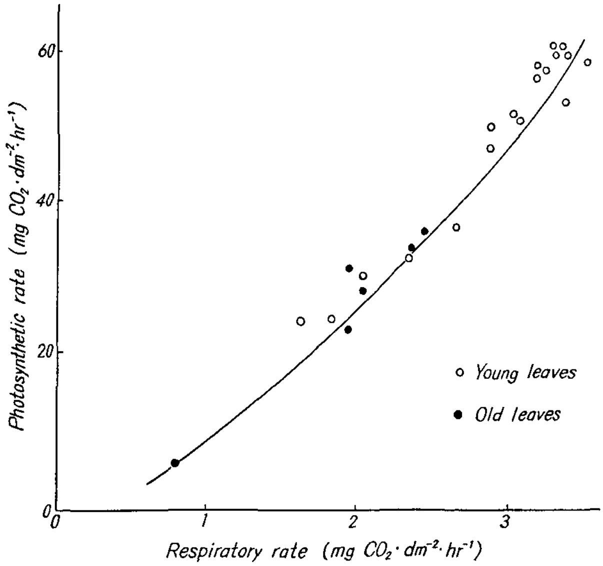


Fig. 12. Relation between respiratory rate and photosynthetic rate

This relationship between po and respiratory rate does not always hold true. For example, the ear removing experiment cited in Fig. 10 demonstrated that removing the ear increased the respiratory rate and decreased po.

The respiratory rate per unit weight of the leaf-blades, the sheath-and-culm and the ear was measured at successive stages of growth. It was higher in the leaf-blades than in the sheath-and-culm (Table 6). At silking, the respiratory rate of the tassel and the ear was higher than that of the leaf-blades. The rate of each organ decreased with age.

During the early part of the vegetative phase, the respiration of the leaf-blades was greater than that of the sheath-and-culm. However, at

TABLE 6. Respiratory rate of various organs at various stages of growth (Fukko No. 8, 1969)

Growth stage		Organ	Dry weight ($g \cdot m^{-2}$field)	Respiratory rate (mg $CO_2 \cdot g^{-1} \cdot hr^{-1}$)
Ear-initiation		Leaf-blades	65	4.25
		Sheath-and-culm	50	3.99
Tasseling		Leaf-blades	150	1.96
		Sheath-and-culm	250	1.40
Days after silking	3	Tassel	31	2.30
	15		25	2.03
	25		20	1.00
	37		20	0.84
Days after silking	3	Ear	52	2.38
	15		200	2.03
	25		390	1.55
	37		655	0.90
	47		835	0.46

tasseling the dry weight of the sheath-and-culm was greater than that of the leaf-blades and its respiration also was greater. The tassel respiration was about 5 percent of the respiration of the whole plant at silking and decreased rapidly. The proportion of the respiration of the whole plant that was accounted for by the ears increased after silking, reached 60 percent by the end of the initial grain-filling phase, was maintained at this level for more than 20 days and then decreased to about 40 percent at maturity.

Dry Matter Production Related to Photosynthesis and Respiration

Growth efficiency (GE) was defined here as the ratio of the amount of dry matter produced to the amount of materials used for the production (TANAKA and YAMAGUCHI (1968)).

Seeds of Wisconsin Hyb. Corn No. 95 were germinated in the dark at different temperatures (TANAKA and YAMAGUCHI (1969)). The higher the temperature, the higher was the growth rate of seedlings (Fig. 13). The GE of seedlings, calculated as the ratio of the seedling weight increase to the seed weight decrease, was maintained at about 70 percent regardless of temperature between 15°C and 35°C until the materials in the seeds were exhausted.

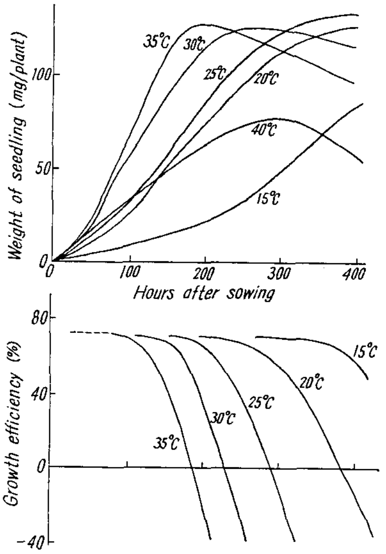


Fig. 13. Effect of temperature on weight of seedlings and growth efficiency at successive stages of germination

The GE decreased abruptly when the reserved materials for germination in the seeds were exhausted. After this growth stage, the weight of old leaves and roots starts to decrease. The GE should then be expressed as the ratio of the increased weight of new organs to the deceased weight of old organs. The GE calculated on this basis was about 50 percent for a longer period.

This demonstrates that the GE is low when reutilization of materials in old organs is occurring.

Using a Fukko No. 8 population, the plant weight and the rate of dark respiration were measured regularly during growth (YAMAGUCHI, HARA, and TANAKA (1970)). The relative growth rate ($RGR = \Delta W/(W \cdot \Delta t)$, where W is the plant weight and ΔW is the dry matter production during a period of Δt), and the rate of respiration per unit plant weight (R) were computed from the data obtained. The GE was calculated by the formula, $GE = RGR/(RGR + R)$. The rate of respiration is assumed to be the same in the light and in the dark.

The RGR and the R increased for 40 days after sowing and then decreased gradually until maturity (Fig. 14). Low values at early growth stages were probably due to low spring temperatures. The GE was kept between 60 percent and 65 percent until silking, decreased gradually for some time and then decreased more rapidly to about 40 percent at maturity.

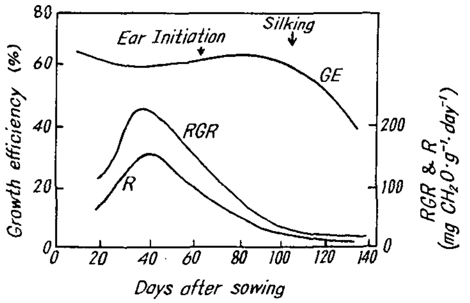


Fig. 14. Fluctuation of respiratory rate (R), relative growth rate (RGR) and growth efficiency (GE) of a population during growth (Fukko No. 8, 1968)

The rate of respiration and the dry weight of the ears were measured at successive stages of grain-filling. Then the GE of the ear at successive stages of growth was computed (TANAKA, YAMAGUCHI, and HARA (1971)). The GE of the ear was maintained between 70 percent and 75 percent throughout the grain-filling phase.

Photosynthesis and Respiration at Stratified Strata of Population

The dry weight, the rate of photosynthesis at a full sunlight and the rate of respiration in the dark of 40 cm strata within the canopy of a population of a Fukko No. 8 were measured at the milky stage (TANAKA, YAMAGUCHI and HARA (1971a)).

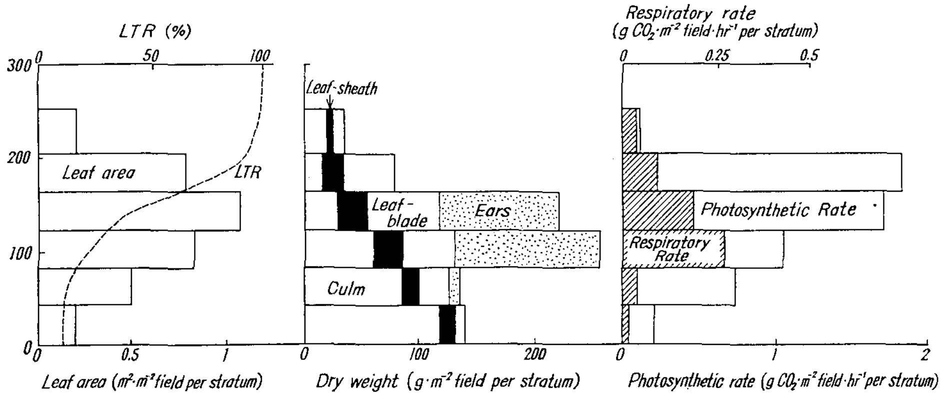


Fig. 15. Leaf area, light transmission ratio (LTR), dry weight, photosynthetic rate and respiratory rate at various strata of a population during grain-filling (Fukko No. 8, 1969)

The light transmission ratio decreased from the top to the bottom of the canopy (Fig. 15). The decrerse was significant at the upper and the middle strata. A large proportion of the leaf area was situated in the middle strata where the ears were formed. There was very little leaf area in the lower strata but a large fraction of the culm weight is at this level.

With the exception of the top stratum where the tassels were located, the rate of photosynthesis was high in the upper strata of the canopy. The rate of respiration in the 120–80 cm stratum was the highest because of the active respiration of the ears.

From these data, the balance between photosynthesis and respiration during a one day cycle were estimated for each stratum. For estimating the amount of photosynthesis, the rate of photosynthesis of each stratum at full sunlight, the light transmission ratio at various height, the light response curves of the photosynthetic rate of the population presented in Fig. 11 and a typical fluctuation curve of solar radiation during a day in this season were used. The rate of respiration was assumed to be kept constant at the rate in the dark.

TABLE 7. Estimated amount of photosynthesis and respiration at each stratum of a crop canopy during grain-filling (g $CH_2O \cdot m^{-2} \cdot day^{-1}$) (Fukko No. 8, 1969)

Stratum* (cm)	Photosynthesis (a)	Respiration (b)	(a−b)	$\frac{(a-b)}{(a)}$ (%)
246–200	1.21	0.59	0.62	51
200–160	13.51	1.48	12.03	89
160–120	10.64	3.17	7.47	70
120– 80	4.81	4.69	0.12	2.5
80– 40	1.73	0.63	1.10	64
40– 0	0.36	0.18	0.18	50
Total	32.26	10.74	21.52	67

* Height from the ground.

The estimates presented in Table 7 indicate that photosynthesis was largest in the 200–160 cm stratum and respiration was largest in the 120–80 cm stratum. The balance between photosynthesis and respiration was largest in the 200–160 cm stratum. The balance was about 90 percent of the total photosynthesis in the 200–160 cm stratum, about 3 percent in the 120–80 cm stratum and 50–60 percent in the 80–0 cm stratum.

The method of estimation used here is based on various assamptions and subjects to criticisms. However, it indicates fairly clearly that the 200–160 cm stratum is the site of production and the 120–80 cm stratum where the ears are located is the site of consumption and storage.

Discussions

It was reported that there is no photosaturation point in the photosynthesis of maize populations (BAKER and MUSGRAVE (1964)). In rice populations there is a photosaturation point when LAI is small, but it does not exist when the LAI is large (TAKEDA (1961), MURATA (1961)). However, there is a photosaturation point, even in maize populations with a reasonably large LAI, at later stages of grain-filling when all the leaves are old. The changes in the rate of photosynthesis of a population can be explained by the variation in the po.

It has been pointed out that the po is apparently higher in the maize plant than in other crops (HESKETH (1963), WAGGONER, MOSS and HESKETH

(1963)), including rice (MURATA (1961), TANAKA, KAWANO and YAMAGUCHI (1966)). The po of maize increases with an increase of light intensity and does not show photosaturation even at full sunlight, whereas rice is light saturated at about 40 klux. High po is an extremely important characteristic of maize for it is the basis of high yielding ability.

The po increases with an increase of nutrient content in the leaf up to a certain value. The critical percentages in the leaves of maize appear to be approximately the same as those of rice (TANAKA (1961)). Old leaves, however, generally show a lower po, even though they have an adequate nutrient content. It has been noted that the photosynthesis of a leaf declines with age due to translocation of nutrients from the leaf, especially potassium (MOSS and PEASLEE (1965)). In the observations reported in this paper, the po decreased without any significant decrease of potassium content. The decrease of po with age can not always be considered a simple nutritional deficiency.

The translocation of photosynthetic products from a leaf is active when it has just completed its expansion. With age, the translocation becomes slower because younger leaves become the major source to the growing point. Under such conditions, sugars accumulate in the old leaves and the po of these leaves decreases.

Although the po of a healthy, newly expanded leaf is higher and responds better to high light intensity in the maize plant than in the rice plant, the po is strongly influenced by age and by nutritional status. It can be low even in maize under some circumstances.

The po of several leaves at or above the ear, the major source for the developing kernels, increases when grain-filling is active. This type of increase has been reported in the flag leaf of the rice plant under certain conditions (MURATA (1961)). By removing the ear, the po of these leaves decreases. This indicates that these leaves are performing an important role in grain-filling and the rate of dry matter accumulation in the kernels influences the po of these leaves.

The GE of germinating maize seedlings is about 70 percent between 15°C and 35°C. This value is slightly higher than that of rice (TANAKA and YAMAGUCHI (1969)).

During the vegetative growth phase, the GE of maize populations is kept almost constant between 60 percent and 65 percent. During grain-filling, however, it decreases. A lower GE value during this phase is due to the respiration of organs other than the ears. Reutilization of substances, especially nitrogen compounds in the leaves and in the culm for grain-filling may be another low GE value factor. The GE of rice is almost the same as maize during early stages of growth, but is lower during grain-filling (TANAKA and YAMAGUCHI (1968)).

In maize high night temperatures promote respiration and result in accelerated photosynthesis in the day time. So, activated respiration caused by a high temperature can not be considered a negative factor for grain yield (MOSS, MUSGRAVE and LEMON (1961)). On the other hand, in rice many reports indicate that higher temperatures than a certain limit may accelerate respiratory loss and result in a decreased grain yield (MURATA (1964)). The difference may be that in rice a higher proportion of respiration is not directly linked with grain-filling.

Most of the photosynthesis in maize is at the top of canopy (WRIGHT and LEMON (1966), UCHIJIMA, UDAGAWA, HORIE and KOBAYASHI (1967)). During grain-filling, the upper strata of the crop where the active leaves are located are the main producers. Photosynthetic products from the upper strata are translocated to the middle strata where the ears are located. Part of the translocated material is respired and the remaining part is converted to starch in the kernels. In the lower strata, photosynthesis and respiration are reasonably well balanced.

In rice, respiration and photosynthesis is high in the upper strata where the panicles and the leaves are located. It is in this layer that most of the production, consumption and storage occurs. In the lower strata, where leaves are shaded and the sheath-and-culm are located, there is more respiration than photosynthesis. There appears to be more respiration in the lower strata in rice than in maize (TANAKA and YAMAGUCHI (1968)). However, it should be mentioned that the data for rice was obtained using varieties with a poor plant type. For improved varieties with good plant type, the lower stratum does not consume a large amount of the photosynthetic products of the upper stratum (YOSHIDA, COCK and PARAO (1971)).

To summarize, the po of young leaves of maize is larger than that of rice. However, as a leaf ages the demand on it for photosynthetic products decreases and this results in a low po even if the leaf maintains a high potential productivity. The efficiency of respiration in dry matter production during grain-filling is higher in maize than in rice, Also, the demands of the lower layers of the crop canopy for respiratory substrates from the upper layers is smaller in maize than in rice. For these reasons, it seems that the rate of photosynthesis of the crop during grain-filling is more intimately controlled by the demand of the developing kernels for photosynthetic products in maize than in rice.

IV. VARIETAL TRAITS ASSOCIATED WITH YIELDING ABILITY

Hybrids generally give higher grain yield than their parental inbreds. Varietal difference in yielding ability is also obvious. It is needless to mention that many plant traits are associated with the yielding ability.

With these backgrounds varietal comparisons of various traits were

TABLE 8. Grain yield, total plant weight and photosynthetic rate (po) of hybrids and their parents (1968)

Line	Grain yield (g/plant)	Total plant weight (g/plant)	Grain : total weight ratio	po* (mg CO_2· dm^{-2}·hr^{-1})
WF9	17	173	0.10	24.7
$OH51^A$	70	163	0.43	28.0
OH43	44	113	0.39	17.0
OH45	59	150	0.39	28.4
WF9×$OH51^A$	217	452	0.48	25.9
OH43×OH45	124	264	0.47	31.3
Ko No. 504**	185	336	0.55	28.1

* Measured on the leaf just above the ear during grain-filling at 55 klux.

** Ko No. 504=[(WF9×$OH51^A$)×(OH43×OH45)].

TABLE 9. Hybrids and their parents tested (1969)

Combination No.	Parental inbred				Hybrid	
		Mark		Mark		Mark
1	$W153^R$	A	W25	B	$W153^R$×W25	AB
2	OH43	C	OH45	D	OH43×OH45	CD
3	W9	E	$WM13^R$	F	W9×$WM13^R$	EF
4	W23	G	W28	H	W23×W28	GH
5	C13	I	C30	J	C13×C30	IJ
6	P39	K	$P51^B$	L	Golden Cross Bantam	KL
7	D403	M	D405	N	D403×D405	MN
8	T102	O	T107	P	T102×T107	OP
9	$OH51^A$	Q	WF9	R	$OH51^A$×WF9	QR
10	Ma21547	S	C13	I	Golden Beauty	SI
11	W49	U	WH	V	W49×WH	UV
12	A357	W	$OH40^B$	X	A357×$OH40^B$	WX
13	N21	Y	N19	Z	N21×N19	YZ

made in this chapter to pinpoint the key factor of varietal difference in yielding ability.

Heterosis and Yielding Ability

Seven lines (or varieties) related to each other as indicated in Table 8 were planted at 60 cm × 60 cm. Heterosis in the grain yield was positive in the single crosses but was not observed in the double cross. The same

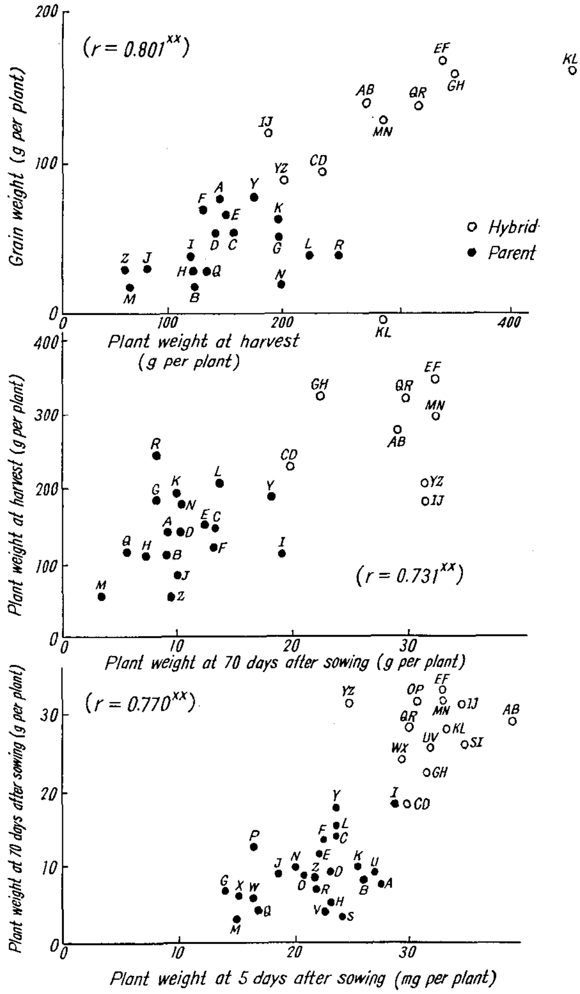


Fig. 16. Relation among grain weight, plant weight at harvest, at 70 days and at 5 days after sowing in thirteen hybrids and their parents (1969) (Letters in figure indicate lines listed in Table 9)

trend was observed in total plant weigtht and in the ratio of grain : total plant weight. Varietal differences in the po were statistically significant. A positive heterosis in the po was observed in OH43 x OH45 but not in the other combinations. There was no association between grain yield and po.

In another experiment, 13 F_1 hybrids and their parents listed in Table 9 were sown at a wide spacing (TANAKA and HAYAKAWA (1971)). There was positive heterosis in grain yield and in total plant weight at harvest (Fig. 16, top). A statistically significant positive correlation between grain yield and total plant weight at harvest was observed. The ratio of grain : total plant weight tended to be smaller in the parents.

There were statistically significant positive correlations between plant weight at harvest and at 70 days after sowing (Fig. 16, middle), and between plant weight at 70 days after sowing and weight of seedlings which were germinated in the dark for 5 days at 20°C (Fig. 16, bottom).

TABLE 10. Days from sowing to emergence and from sowing to silking of hybrids and their parents (1969)

Combination* No.	From sowing to emergence (days)			From sowing to silking (days)		
	Hybrid	MPV**	Difference	Hybrid	MPV**	Difference
1	18	25.5	7.5	81	93.5	12.5
2	22	24.5	2.5	92	99.5	7.5
3	18	22.0	2.0	81	87.5	6.5
4	20	23.0	3.0	85	102.0	17.0
5	21	21.5	0.5	81	80.5	−0.5
6	20	21.5	1.5	92	97.5	5.5
7	16	23.0	7.0	83	100.5	17.5
8***	20	24.5	4.5	—	—	—
9	20	26.5	6.5	89	100.5	11.5
10***	18	21.0	3.0	—	—	—
11***	20	25.5	5.5	—	—	—
12***	19	27.5	8.5	—	—	—
13	19	20.5	1.5	78	86.0	8.0
Average			4.9			9.5

* See Table 9.

** MPV : Mid Parents Value.

*** These combinations were discarded 70 days after sowing because of poor germination in parents.

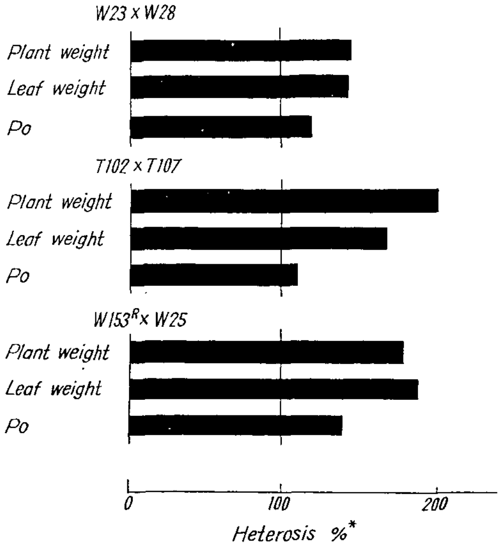


Fig. 17. Degree of heterosis in plant weight, leaf weight, and photosynthetic rate (po)** in three combinations at 50 days after sowing

* Taking the mid-parents value as 100.

** Average of several measurements on the most active leaves.

There was a close positive correlation between leaf area and plant weight during growth.

The time from sowing to emergence and from sowing to silking was shorter for hybrids than the mid-parent values by 5 days and 10 days, respectively (Table 10).

No significant heterosis was observed in the seed weight, the embryo weight or in the GE during germination.

Three sets of parents and their hybrids (No. 1, No. 4, and No. 8 in Table 9) were grown in standard culture solution. Fifty days after sowing, there was a significant positive heterosis in plant weight and leaf weight (Fig. 17). The po of hybrids was higher than that of the mid-parent value. However, the difference in the po was statistically significant only in W153^R × W25. In this set, the po of the hybrid exceeded the higher parent value. In other sets, however, the po of the hybrids was lower than that of their higher parents though the difference between the hybrid and its higher parent was not statistically significant.

Comparison among Varieties

Fifteen commercial varieties listed in Table 11 were planted at the spacing of 40 cm × 40 cm in 1968, a year of reasonably good weather.

The grain yield ranged from 4.78 to 10.6 tons/ha. Dates of silking ranged from July 22 to August 17. Ko No. 3 silked latest and its grain yield was lowest though its total plant weight at harvest was largest. This demonstrates that an extremely late silking results in a low grain yield.

The plant height ranged from 157 cm to 289 cm. There was no simple correlation between plant height and grain yield. There was a tendency for grain yield to increase with total dry matter production. The varietal difference in the ratio of grain : total plant weight was small, except for Ko No. 3 in which the ratio was small due to late silking. Golden Beauty

TABLE 11. Grain yield and various plant traits of fifteen varieties (1968)

No.	Varieties	Type*	Grain yield (tons/ha)	Date of silking	Plant height (cm)	LAI	Total weight at harvest (kg/m^2)	Grain : total weight ratio	Kernel number per m^2 field (10^3)	1000-kernel weight (g)
1	D403×D405	D	9.58	Aug. 2	233	3.14	1.56	0.54	2.95	325
2	Wis. Hyb. 95	D	8.41	Aug. 4	245	4.39	1.41	0.52	2.78	303
3	〃 100	D	6.39	Aug. 5	232	4.49	1.40	0.41	2.47	259
4	〃 105	D	8.07	Aug. 5	235	3.19	1.37	0.52	2.75	293
5	〃 110	D	10.64	Aug. 6	219	4.70	1.82	0.52	3.79	281
6	〃 115	D	9.29	Aug. 11	236	3.99	1.64	0.50	3.59	259
7	〃 120	D	8.93	Aug. 11	248	4.57	1.65	0.48	3.66	244
8	Giants	D	9.15	Aug. 12	289	5.62	1.89	0.43	3.44	266
9	Ko No. 3	DF	4.78	Aug. 17	269	5.34	2.08	0.20	2.26	212
10	Ko No. 4	F	7.52	Jul. 29	226	5.14	1.29	0.52	2.30	327
11	Ko No. 6	DF	9.89	Aug. 4	289	6.34	1.73	0.51	2.71	365
12	Sakashita	F	6.31	Jul. 31	235	3.72	1.08	0.53	1.76	359
13	Fukko No. 4	D	8.66	Jul. 29	235	3.62	1.34	0.57	2.62	330
14	Fukko No. 6	D	10.37	Aug. 4	229	4.36	1.63	0.56	3.40	305
15	Golden Beauty	S	6.43	Jul. 22	157	4.08	0.91	0.63	2.08	309

* D: Dent, F: Flint, S: Sweet, DF: Dent×Flint.

and Giants had a high and a low ratio of grain : total plant weight, respectively. These were the shortest and the tallest varieties.

There was a positive correlation between number of kernels per unit field area and grain yield, but no correlation between 1000-kernel weight and grain yield. However, the grain yield of Ko No. 3 was low because of a low 1000-kernel weight due to a short grain-filling period.

In 1969, 15 leading commercial varieties listed in Table 12 were compared (TANAKA and MORISADA (1971)). The weather was less favorable than normal. Two spacings, 60 cm × 60 cm and 30 cm × 30 cm, were used. In August, some plants in the 30 cm × 30 cm spacing lodged because of strong wind. All plants at this spacing were supported with strings.

The grain yield ranged from 2.61 to 4.69 tons/ha at 60 cm × 60 cm and from 2.52 to 7.55 tons/ha at 30 cm × 30 cm (Table 12). The grain yield at 30 cm × 30 cm was higher than at 60 cm × 60 cm. However, there was a varietal difference in response to spacing. In Fukko No. 8, D403 × D405 and Ko No. 8, the response to close spacing and the grain yield at 30 cm

TABLE 12. Grain yield, date of silking and photosynthetic rate (po) of fifteen commercial varieties (1969)

No.	Variety	Type*	Grain yield (tons/ha)		Date of silking	po** (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)	
			60 cm × 60 cm	30 cm × 30 cm		60 cm × 60 cm	30 cm × 30 cm
1	Ko No. 8	D	4.26	5.99	Aug. 19	41	33
2	Ko No. 504	D	3.01	5.34	Aug. 18	48	39
3	Long Fellow	F	2.90	3.69	Aug. 11	43	45
4	D403×D405	D	3.71	6.59	Aug. 13	57	32
5	Giants	D	2.89	3.43	Aug. 22	49	34
6	Ko No. 4	F	3.81	4.56	Aug. 6	38	30
7	Ko No. 6	DF	3.78	5.20	Aug. 16	44	37
8	Sakashita	F	2.61	2.89	Aug. 4	37	37
9	Fukko No. 4	D	4.69	5.25	Aug. 4	38	30
10	Fukko No. 8	D	4.53	7.55	Aug. 15	42	34
11	Golden Beauty	S	—***	—***	Jul. 29	47	41
12	Golden Cross Bantam	S	3.52	2.95	Aug. 15	41	29
13	Onowa	F	3.87	2.52	Aug. 13	52	27
14	Wis. Hyb. 100	D	3.86	5.42	Aug. 15	57	50
15	〃 110	D	4.06	5.11	Aug. 14	49	42

* D: Dent, F: Flint, S: Sweet, DF: Dent×Flint.

** Average of duplicate measurements on the leaf just above the 1st ear at silking at 60 klux.

*** Data are missing because of rats attack.

×30 cm were greater than for other varieties. Onowa and Golden Cross Bantam showed a negative response to a decrease of spacing and the grain yield at 30 cm×30 cm was low.

No correlation between grain yield and plant height was observed. There were, however, no extremely short or extremely tall varieties among high yielding varieties. At close spacings, the plants were more susceptible to lodging because the culms were taller and thinner. There was no correlation between grain yield and tiller number.

Grain yield was positively correlated with number of ears per unit field area at 30 cm×30 cm, but this tendency did not exist at 60 cm×60 cm (Fig. 18, top). At 30 cm×30 cm, the number of ears was less than the number of plants. This indicates that the number of ears at this spacing was determined by the barren plant percentage. A larger number of kernels per ear associated with a higher grain yield at 30 cm×30 cm, except in Giants which had an extremely low 1000-kernel weight due to late silking

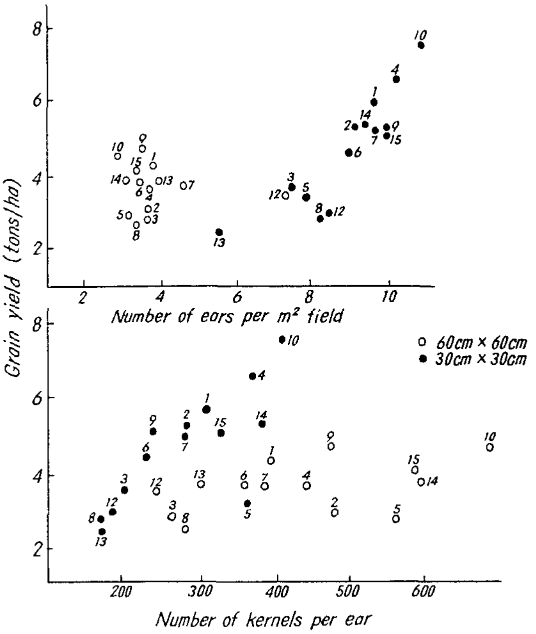


Fig. 18. Grain yield as related to number of ears per unit field area and with number of kernels per ear in fifteen varieties (1969) (Numbers in figure indicate varieties listed in Table 12)

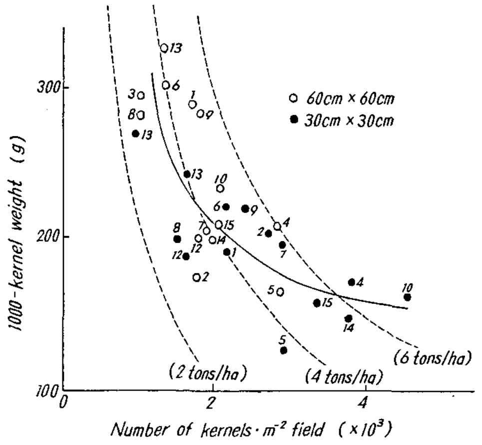


Fig. 19. Relation between number of kernels per unit field area and 1000-kernel weight in various varieties grown at two spacings (Numbers in figure indicate varieties listed in Table 12)

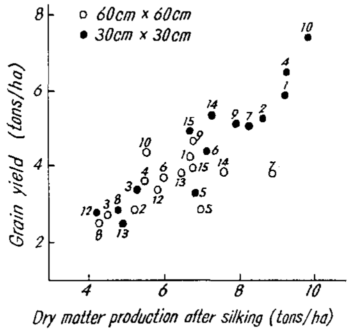


Fig. 20. Relation between dry matter production after silking and grain yield in fifteen varieties (1969)
(Numbers in figure indicate varieties listed in Table 12)

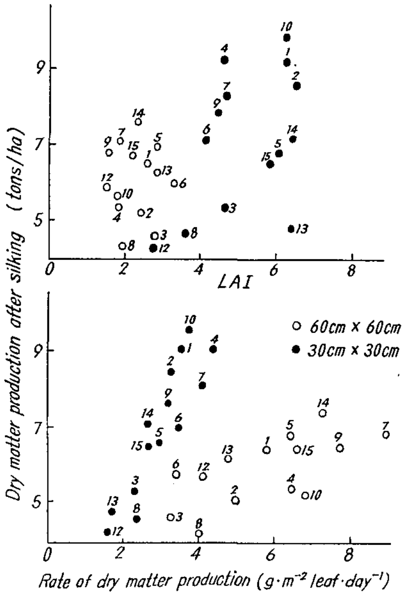


Fig. 21. Dry matter production after silking as related to LAI and rate of dry matter production per unit leaf area in fifteen varieties (1969)
(Numbers in figure indicate varieties listed in Table 12)

(Fig. 18, bottom). At 60 cm × 60 cm, however, there was no correlation between grain yield and number of kernels per ear.

The correlation between number of kernels per unit field area and grain yield was significant, including 30 cm × 30 cm and 60 cm × 60 cm. However, there was no clear relationship between grain yield and 1000-kernel weight.

There was a loose negative correlation between number of kernels per unit field area and 1000-kernel weight (Fig. 19). However, the equi-yield

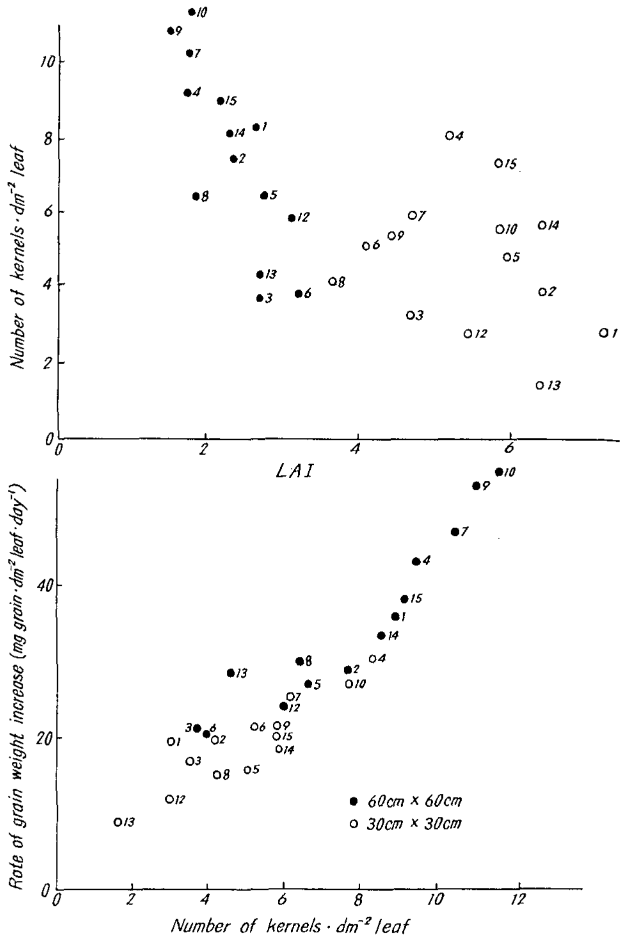


Fig. 22. Relations between LAI and number of kernels per unit leaf area (top) and between number of kernels per unit leaf area and rate of grain weight increase per unit leaf area (bottom)
(Numbers in figure indicate varieties listed in Table 12)

lines which are composed by assuming grain yield = number of kernels per unit field area × 1000-kernel weight, do not fit the observed data. The observed correlation indicates that the larger the number of kernels per unit field area, the higher was the grain yield.

The correlation between grain yield and dry matter production after silking was positive (Fig. 20). The dry matter production during grain-filling was more closely correlated with the rate of dry matter production per unit leaf area during this growth period than LAI, at least at a given spacing (Fig. 21).

The po at silking ranged from 27 to 57 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$ (Table 12). Varietal difference was, however, statistically significant only at the 10 percent level. The difference of the po between two spacings was highly significant. No correlation was observed between the rate of dry matter production per unit leaf area during grain-filling and the po at silking.

The larger the LAI, the smaller the number of kernels per unit leaf area though there were several exceptions at 30 cm × 30 cm (Fig. 22, top). There was a positive correlation between number of kernels per unit leaf area and rate of grain weight increase per unit leaf area (Fig. 22, bottom).

Discussions

There are varietal differences in yielding ability. Positive heterosis in the grain yield is apparent. New varieties in Hokkaido are hybrids with a high positive response to dense planting and with high yielding ability.

The seeds or the embryo of a hybrid are not necessarily larger than its parental inbreds. A heterosis in the po has been reported (HEICHEL and MUSGRAVE (1969)). Some combinations reported in this paper showed a heterosis in the po. In other combinations, however, the heterosis was not statistically significant. Among commercial varieties in Hokkaido, varietal differences in the po were statistically significant only at the 10 percent level. On the other hand, the growth rate of hybrids was higher from germination. The higher growth rate results in a higher rate of leaf expansion. Because of a larger leaf area, the rate of photosynthesis per plant is higher, and consequently, plant weight is larger in hybrids. Moreover, the time from sowing to silking is shorter, and the grain-filling period is longer in hybrids. For these reasons, hybrids give a higher grain yield than their parental inbreds.

These differences indicate the importance of vegetative vigor. Hybrids are capable of producing a high grain yield even with mediocre cultural practices of their vegetative vigor. A careful examination is needed to determine whether vegetative vigor is an indispensable trait for high yielding varieties, even with good management.

In rice there is heterosis in vegetative vigor (JENNINGS (1967)). However, it is not necessarily associated with high grain yields under intensive cultural conditions (JENNINGS and JESUS (1968), KAWANO and TANAKA (1969)).

By comparing commercial varieties in Hokkaido, it becomes apparent that grain yield is positively correlated with dry matter production during grain-filling. Dry matter production during this growth phase is more closely correlated with rate of dry matter production per unit leaf area than LAI at least for a specific planting density. There is no simple correlation between rate of dry matter production per unit leaf area during grain-filling and po at silking. Grain yield is more closely correlated with kernel number per unit field area than with 1000-kernel weight. On unit leaf area basis rate of grain weight increase is positively correlated with number of kernels.

These results suggest that the potential photosynthesis of the leaves is not the limiting factor, but the number of kernels, the sink, is the factor intimately controlling rate of grain-filling and grain yield.

In rice, there is ample evidence of a positive relation between spikelet number per unit field area and grain yield. However, this correlation is more evident at low yield levels. At high yield levels, the percentage of sterility is an important factor in controlling grain yield. In this instance, it is the source rather than the sink that is the yield limiting factor.

The concept of the plant type has been well established in rice on the basis of physiology related to the dry matter production (HAYASHI and ITO (1961), TSUNODA (1965), TANAKA, KAWANO and YAMAGUCHI (1966)).

There are several reports on maize indicating the importance of plant type. The importance of erect leaves was demonstrated by PENDLETON, SMITH, WINTER and JOHNSTON (1968). The association between leaf display and dry matter production had been studied on the basis of light interception by the leaves and response of po to light intensity (LOOMIS, WILLIAMS, DUNCAN, DOVRAT and NUNEZ (1968)). On the basis of these studies, simulation analyses are being developed (DUNCAN, LOOMIS, WILLIAMS and HANAU (1967)).

Removing tassels increases grain yield, especially at close spacings. This is explained by the tassels shading the leaves (DUNCAN, WILLIAMS and LOOMIS (1967), HUNTER, DAYNARD, HUME, TANNER, CURTIS and KANNENBERG (1969)). However, competition for photosynthetic products (CHINWUBA, GROGAN and ZUBER (1961)) or for nitrogen (SANFORD, GROGAN, JORDAN and SARVELLA (1965)) between the developing ears and the tassels or the pollen is also considered to be one of the causes of a positive effect of detasseling or male sterility on the grain yield.

Although these reports indicate the importance of plant type in maize, the experiments reported in this paper did not support the view that leaf display is important in relation to the grain yield in maize.

V. CULTURAL FACTORS AFFECTING GRAIN YIELD

In the previous chapter it was demonstrated that the number of kernels per unit field area, the sink, is the key factor controlling varietal difference in yielding ability. In addition to this varietal difference, grain yield and various traits of a variety are influenced by cultural conditions.

The objective of this chapter is to find out the key traits which control the fluctuation of grain yield of a variety caused by cultural conditions such as climatic condition, fertilizer level and spacing. Interactions between varietal characteristics and cultural conditions were also discussed.

Date of Planting

Fukko No. 8 was sown on four dates at two-week intervals (on May 1, 15, 29, and June 12 in 1970) (TANAKA and HARA (1971b)). These sowing dates were designated treatments No. I, No, II, No. III, and No. IV,

TABLE 13. Effect of planting date on various plant traits (Fukko No. 8, 1970)

Treatment No.	I	II	III	IV
Date of sowing	May 1	May 25	May 29	June 12
Days				
From To				
Sowing-Emergence	20	17	15	12
Emergence-Silking	71	69	61	58
Silking-Harvest	67	58	54	46
Plant height* (cm)	239	244	241	203
LAI*	4.39	4.57	4.46	3.61
Grain yield (tons/ha)	9.21	9.04	7.97	4.96
Grain : total weight ratio	0.58	0.53	0.46	0.35
Kernel number per m^2 field ($\times 10^3$)	3.36	3.15	3.02	3.02
1000-kernel weight (g)	274	284	264	164

* Maximum value during growth.

respectively. All plots were harvested on October 6 because of a heavy frost.

The later the sowing, the fewer the days from sowing to emergence and from emergence to silking (Table 13). This was an effect of differences in temperature at sowing. Though the interval from sowing to silking was shorter in later sowings, the date of silking was earlier and the interval from silking to harvest was longer in the earlier sowings than in later ones.

The rate of dry matter production for two months following sowing was higher in later sowings, but then the rate was almost the same in all sowings (Fig. 23, top). The total plant weight at harvest was greatest for treatment No. III and smallest for No. IV.

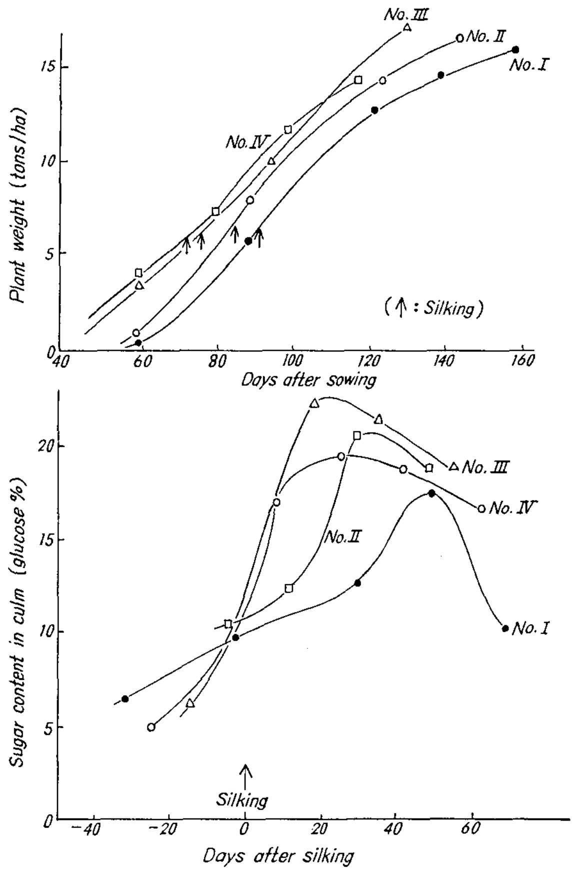


Fig. 23. Changes of plant weight and sugar content in the culm during growth as influenced by date of sowing (Fukko No. 8, 1970)

There was a more rapid increrse in sugar content of the culm after silking for treatment No. III than for No. I. This indicates a better balance between photosynthesis of the leaves and starch formation in the kernels for treatment No. I than for No. III.

The plant height and the LAI were largest for No. II and decreased with delay in sowing (Table 13). The grain yield and the ratio of grain : total plant weight were highest for treatment No. I and decreased with a delay of sowing, especially from treatment No. III to No. IV. The number of kernels per unit fleld area and the 1000-kernel weight decreased with a delay of sowing, especially from treatment No. III to No. IV.

Interactions among Spacing, Nitrogen Level and Variety

Two dent corn lines, OH43 × OH45 and D403 × D405, were tested. Combinations of three nitrogen levels (0, 100 and 300 kg N/ha) and three spacings (25 cm × 25 cm, 50 cm × 50 cm and 75 cm × 75 cm) gave nine

TABLE 14. Effect of spacing and nitrogen level on grain yield, amount of nitrogen absorbed and some plant traits in two lines (1967)

Spacing (cm) / N level (kg/ha)		Line					
		OH43×OH45			D403×D405		
		25×25	50×50	75×75	25×25	50×50	75×75
Grain yield (tons/ha)	0	3.01	3.79	2.34	5.18	5.12	3.42
	100	6.13	5.13	2.92	8.03	6.80	3.74
	300	7.14	5.63	2.55	10.65	7.30	4.44
Nitrogen absorbed (kg N/ha)	0	66	70	77	74	65	70
	100	125	145	115	124	171	94
	300	155	111	114	163	185	139
Plant height (cm)	0	151	176	166	191	227	216
	100	190	187	170	243	253	236
	300	209	189	170	265	251	239
Thickness of culm ($g \cdot m^{-1}$)	0	18	59	70	13	39	75
	100	23	67	84	21	59	78
	300	29	63	80	24	54	81
LAI	0	3.37	1.65	0.82	3.59	1.52	1.00
	100	4.88	2.05	0.92	5.34	1.99	0.88
	300	5.77	1.48	0.89	6.25	2.09	0.95

treatments (TANAKA, YAMAGUCHI and FUJITA (1969)).

Silking was earlier in D403×D405 than in OH43×OH45 and was earlier at wide spacings than at close spacings.

The grain yield of D403×D405 was higher than that of OH43×OH45 (Table 14). The higher the nitrogen level or the closer the spacing, the higher was the grain yield in both varieties.

Nitrogen increased the plant height, especially at close spacings. At close spacings with no nitrogen the plants were short because of a nitrogen deficiency. Culm thickness, expressed as the weight per unit culm length, increased markedly with an increase in spacing and increased much less with the addition of nitrogen. The LAI was larger at close spacings and it increased with an increase of nitrogen application at close spacings.

With no nitrogen application, about 70 kg N/ha was absorbed regardless of lines or spacings. This indicates the amount of nitrogen that was available from the soil. At close spacings with no nitrogen, plants suffered

TABLE 15. Effect of spacing and nitrogen level on yield components in two lines (1967)

Spacing (cm) / N (kg/ha)			Line					
			OH43×OH45			D403×D405		
			25×25	50×50	75×75	25×25	50×50	75×75
Percentage of plants having	1st ear	0	75	100	100	100	100	100
		100	94	100	100	100	100	100
		300	100	100	100	100	100	100
	2nd ear	0	0	0	18	0	0	58
		100	0	0	19	0	0	38
		300	0	0	16	0	0	71
Row number per cob		0	13.7	15.0	15.3	13.6	14.5	14.6
		100	14.3	15.3	15.1	13.8	15.3	14.6
		300	14.8	14.7	14.3	15.0	14.7	14.8
Kernel number per m² field (×10³)		0	2.32	1.84	1.04	2.89	1.89	1.16
		100	4.22	2.40	1.29	4.13	2.46	1.30
		300	4.07	2.75	1.18	4.72	2.72	1.56
1000-kernel weight (g)		0	136	216	238	188	285	309
		100	153	225	238	205	290	303
		300	184	215	228	238	282	299

seriously from nitrogen deficiency. The higher the nitrogen level, the larger the amount of nitrogen absorbed by the plants.

There were no barren plants except in the plot of OH43 × OH45 at 25 cm × 25 cm with no nitrogen application (Table 15). Second ears formed at 75 cm × 75 cm, but they did not produce many kernels. The number of rows per cob is almost constant except for a slightly lower value with no nitrogen application at 25 cm × 25 cm. The number of kernels per row was larger at wide spacings or at high nitrogen levels. The number of kernels per unit field area increased with a decrease of spacing and with an increase of nitrogen application. The 1000-kernel weight increased with an increase of spacing and with an increase of nitrogen application, especially at 25 cm × 25 cm. Grain yield was positively correlated with dry matter production after silking (Fig. 24).

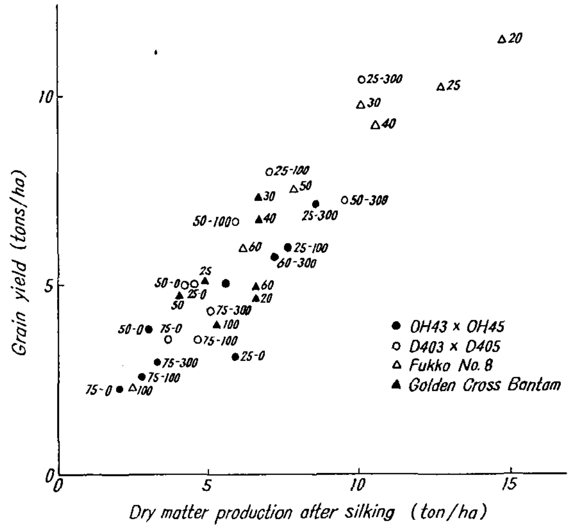


Fig. 24. Relation between dry matter production after silking and grain yield (Numbers in figure are: For example, 20–200 means 20 cm × 20 cm with 200 kg N/ha, and 20 means 20 cm × 20 cm)

In a separate experiment, two varieties, Fukko No. 8 and Golden Cross Bantam, were tested at nine spacings from 10 cm × 10 cm to 100 cm × 100 cm (TANAKA, YAMAGUCHI and YAMAGAMI (1970)).

The plants at 10 cm × 10 cm and 15 cm × 15 cm lodged seriously before tasseling and were discarded. Since plants in plots with closer spacings than 30 cm × 30 cm tended to lodge at about silking, they were supported artificially.

TABLE 16. Effect of spacing on grain yield (GY), total plant weight (TPW) and yield components in Fukko No. 8 and Golden Cross Bantam (1968)

Variety	Fukko No. 8							Golden Cross Bantam						
Spacing (cm)	20×20	25×25	30×30	40×40	50×50	60×60	100×100	20×20	25×25	30×30	40×40	50×50	60×60	100×100
GY (tons/ha)	11.66	10.36	9.82	9.28	7.55	6.00	2.29	4.84	5.09	7.36	6.71	4.64	4.85	3.99
TPW (tons/ha)	25.3	21.0	18.4	16.2	12.8	10.2	4.1	13.3	13.2	14.4	12.9	11.8	11.0	7.9
GY/TPW	0.40	0.43	0.47	0.50	0.52	0.52	0.49	0.31	0.34	0.45	0.46	0.35	0.39	0.45
1000-kernel weight (g)	195	213	226	243	278	298	299	178	195	213	226	234	231	230
Kernel number per m^2 ($\times 10^3$)	6.00	4.86	4.34	3.82	2.71	2.01	0.77	2.72	2.61	3.45	2.97	1.98	2.10	1.74
Ear number per m^2	20.3	13.4	11.0	6.3	4.0	3.0	1.2	17.5	12.1	12.2	8.1	7.3	6.4	3.2
Kernel number per ear	296	361	394	605	671	670	621	156	216	283	356	273	330	337
Barren plant percentage	19	14	1	0	0	0	0	30	24	0	0	0	0	0
Tiller number per m^2*	25	16	11.1	6.3	4.0	2.8	1.0	25	16	11.1	12.0	11.7	10.8	5.3
Tiller number per plant*	1	1	1	1	1	1	1	1	1	1	1.9	2.9	3.9	5.3

* Including the main culm.

Silking was August 7 and 15 for Fukko No. 8 and Golden Cross Bantam, respectively. The closer the spacing, the later was the silking. The difference in the silking date between 100 cm × 100 cm and 20 cm × 20 cm was 8 days in Fukko No. 8 and 4 days in Golden Cross Bantam. Harvest was October 5–8, about 150 days after sowing.

The grain yield at 100 cm × 100 cm was higher for Golden Cross Bantam than for Fukko No. 8 (Table 16). However, at closer spacings, Fukko No. 8 yielded more than Golden Cross Bantam and the difference became larger as plant population increased. The grain yield of Fukko No. 8 continued to increase with a decrease of spacing to 20 cm × 20 cm. In contrast, the yield of Golden Cross Bantam reached a maximum at 30 cm × 30 cm and then decreased with a further decrease of spacing.

The number of ears per unit field area increased with a decrease of spacing. At wide spacings it was larger for Golden Cross Bantam than for Fukko No. 8 because Golden Cross Bantam formed tillers. The difference became smaller with a decrease of spacing and at close spacings the difference was reversed because there was a higher percentage of barren plant in Golden Gross Bantam. Even at wide spacings, there was rarely more than one well developed ear on a culm in either variety.

The number of kernels per ear remained almost constant between 100 cm × 100 cm and 50 cm × 50 cm. The number was larger for Fukko No. 8 than for Golden Cross Bantam. It decreased with a decrease of spacing below 50 cm × 50 cm for Fukko No. 8. For Golden Cross Bantam, however, it was lower at 50 cm × 50 cm than at 40 cm × 40 cm and below 40 cm × 40 cm it decreased with a decrease of spacing. The lower value at 50 cm × 50 cm was due to many small ears on tillers.

The number of kernels per unit field area increased with a decreased spacing for Fukko No. 8. For Golden Cross Bantam, it increased with a decrease of spacing, reached a maximum at 30 cm × 30 cm and then decreased with a further decrease of spacing. The 1000-kernel weight was greater for Fukko No. 8 than for Golden Cross Bantam and it decreased with a decrease of spacing in both varieties.

For Fukko No. 8, the closer the spacing, the greater the total dry matter production, the greater the grain yield and the smaller the ratio of grain : total plant weight. For Golden Cross Bantam, a decrease of spacing did not always result in an increase of the total plant weight. The ratio of grain : total plant weight of this variety was smaller than that of Fukko No. 8.

The LAI was larger at closer spacings (Fig. 25). At 10 cm × 10 cm at

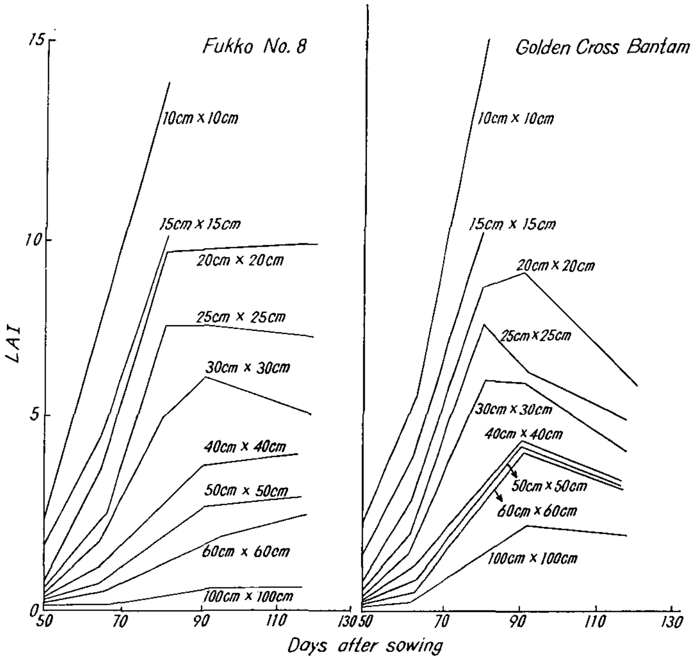


Fig. 25 Changes of LAI with growth at various spacings in two varieties (1968)

80 days after sowing when lodging became serious, the LAI reached 15 in both varieties. At wider spacings, Golden Cross Bantam had a larger LAI than Fukko No. 8 due to tillering ability. The LAI increased with growth and reached a maximum at about silking. The leaves of Fukko No. 8 remained green longer after silking than those of Golden Cross Bantam. Death of the lower leaves was more rapid at close spacings.

There was a positive correlation between grain yield and dry matter produlction after silking in both varieties (Fig. 24). The crop growth rate (CGR) increased with an increase of LAI and there was no optimum LAI in either variety until silking (Fig. 26). After silking CGR of Fukko No. 8 continued to increase as plant population and LAI increased, but in Golden Cross Bantam there was an optimum LAI at about 4 to 5. This indicates that the efficiency of leaves in dry matter production was almost the same for both varieties during early growth stages, but after silking a varietal difference was apparent. The efficiency remained high in Fukko No. 8, but it decreased in Golden Cross Bantam, especially at closer spacings.

The percentage nitrogen content of the shoot was lower, but the amount of nitrogen absorbed by the plants was greater at close spacings than at wider spacings (Table 17). These results show that at close spacings less nitrogen is available per plant than at wider spacings.

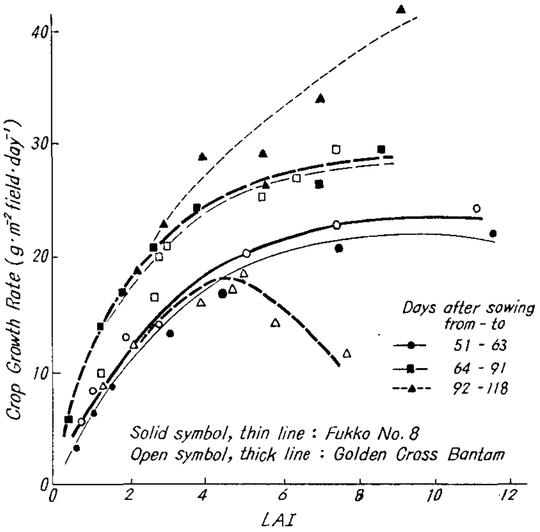


Fig. 26. Relation between LAI and crop growth rate at successive stages of growth (Fukko No. 8 and Golden Cross Bantam, 1968)

TABLE 17. Nitrogen content of shoot and amount of nitrogen absorbed by the plants as affected by spacing in Fukko No. 8 (F 8) and Golden Cross Bantam (GCB) (1968)

Growth stage	80 days after sowing				Silking			
Spacing	N (%)		N absorbed (kg/ha)		N (%)		N absorbed (kg/ha)	
(cm)	F 8	GCB	F 8	GCB	F 8	GCB	F 8	GCB
10×10	2.54	3.99	92	118	—	—	—	—
15×15	3.02	3.93	73	87	—	—	—	—
20×20	3.54	4.01	73	74	1.95	2.64	182	257
25×25	3.82	3.77	52	48	2.03	2.57	176	215
30×30	3.62	4.15	35	41	1.94	2.38	169	190
40×40	3.66	4.27	23	27	2.23	2.61	131	170
50×50	3.74	4.19	15	19	2.27	2.83	114	160
60×60	3.66	4.26	14	10	2.27	3.32	98	150
100×100	3.89	4.14	4	5	2.38	3.26	41	91

Interactions between Climatic and Cultural Conditions

A nitrogen level × phosphorus level × spacing experiment using Fukko No. 8 was conducted in a field of National Hokkaido Agricultural Experiment Station in 1968 and in 1969 (TANAKA, YAMAGUCHI and HARA

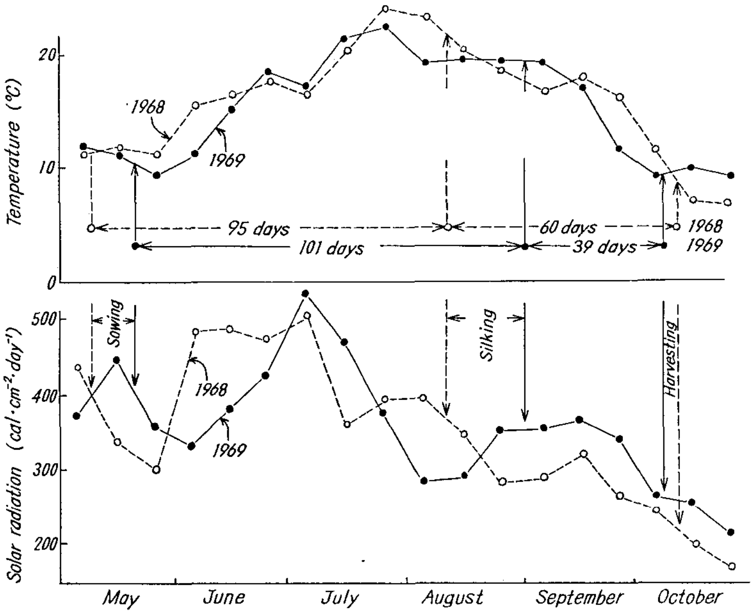


Fig. 27. Climatic conditions during growth and duration of each growth phase (Fukko No. 8, 1968 and 1969)

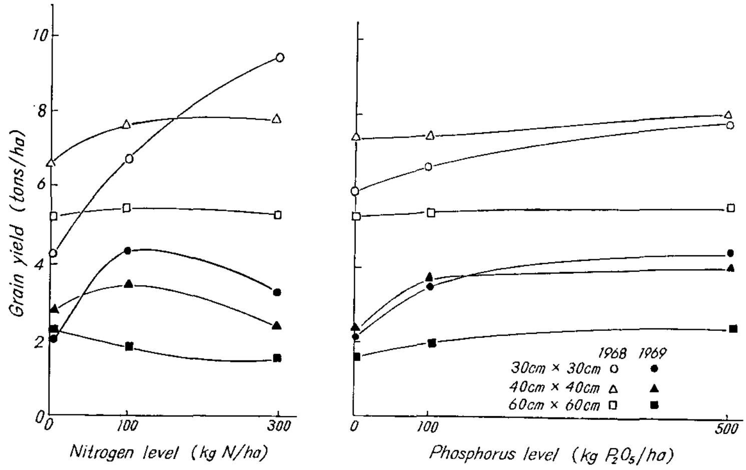


Fig. 28. Effect of nitrogen and phosphorus application on grain yield (Fukko No. 8, summarized figure)

(1971b)). The soil is volcanic ash origin and is low in phoshorus. Twenty-seven treatments were chosen. These were the factorial combinations of three nitrogen levels (0, 100 and 300 kg N/ha), three phosphorus levels (0, 100 and 500 kg P_2O_5/ha) and three spacings (30 cm × 30 cm, 40 cm × 40 cm and 60 cm × 60 cm). For convenience, the treatment of 30 cm × 30 cm with 100 kg N/ha and 500 kg P_2O_5/ha, for example, is designated as 30D·100N·500P. Sowing was made May 7–8, 1968, and May 19–20, 1969.

The 1968 weather was favorable and at 40D·100N·100P it took 95 days for the vegetative phase and 60 days for the grain-filling phase (Fig. 27). In 1969, sowing was 10 days later than in 1968 and growth was delayed because of low temperatures, especially in June. At 40D·100N·100P, it took 101 days for the vegetative phase and only 39 days for grain-filling.

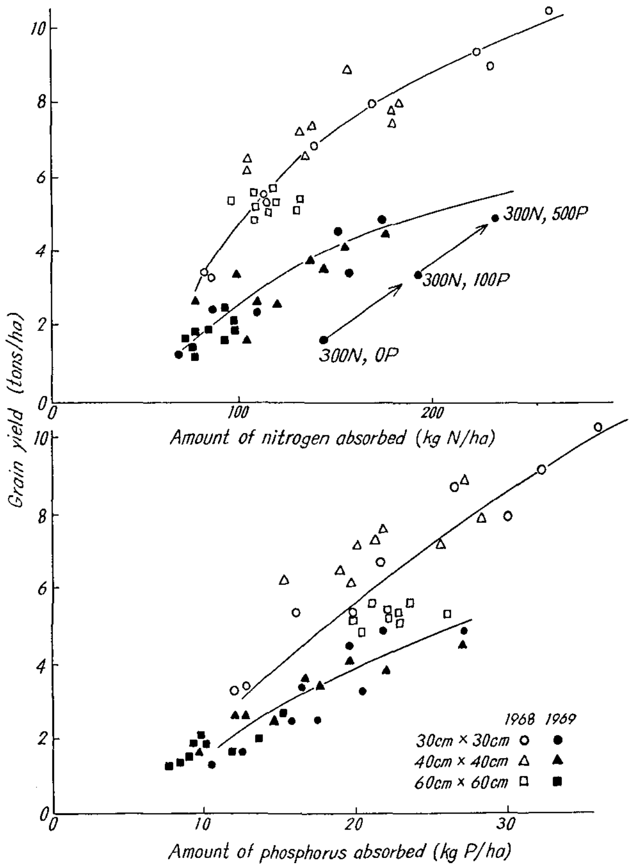


Fig. 29. Relation between amount of nitrogen or phosphorus absorbed by plants and grain yield (Fukko No. 8, 1968 and 1969)

In both years, silking tended to be later with dense planting, especially with no nitrogen application. Phosphorus application hastened silking in 1969.

In 1968, grain yield increased with a decrese of spacing at 300N (Fig. 28). However, at low nitrogen levels it was lower at 30D than at wider spacings. The effect of phosphorus application was small and was observed only at 30D. In 1969, grain yield was smaller, the effect of phosphorus was larger and the effect of nitrogen was smaller.

The amount of nitrogen and phosphorus absorbed by the phants is positively correlated with grain yield in a given year (Fig. 29). The efficiency of nitrogen or phosphorus absorbed by the plants in grain production is different between 1968 and 1969. With 30D·300N·0P in 1969, the

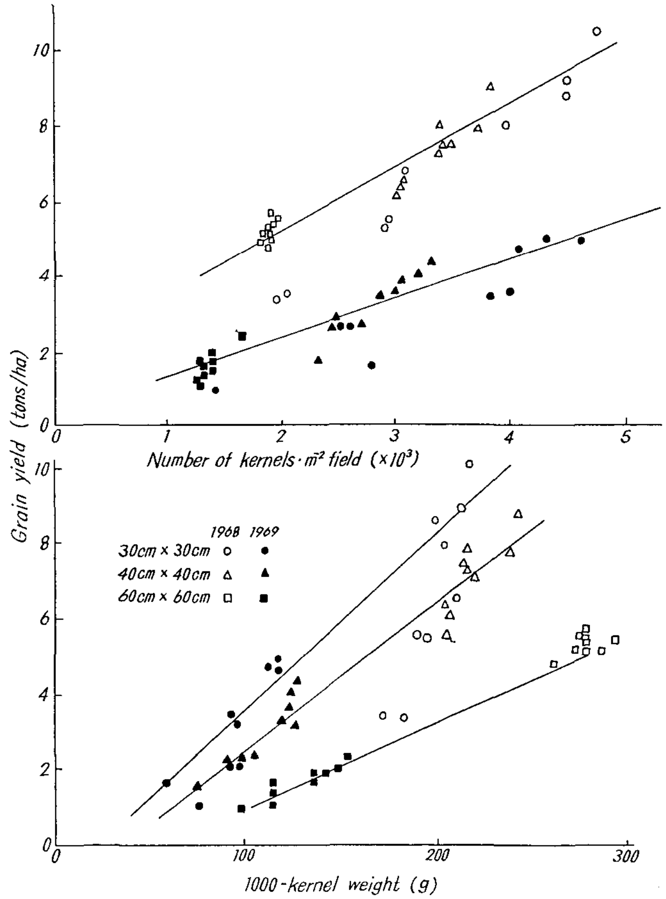


Fig. 30. Relation of grain yield to number of kernels per unit field area and to 1000-kernel weight (Fukko No. 8, 1968 and 1969)

efficiency of nitrogen was extremely low. However, it was improved by a phosphorus application as indicated by the arrow in the figure.

There was a close correlation between number of kernels per unit field area and grain yield in a given year, except for plots at closer spacings with low nitrogen application (Fig. 30, top). There was a remarkable difference in the 1000-kernel weight between these two years. The low 1000-kernel weight in 1969 was the cause of the low grain yield (Fig. 30, bottom).

With the data collected from the experiments described above in which Fukko No. 8 was grown under various cultural conditions, a loose negative correlation was demonstrated between number of kernels per unit field area and 1000-kernel weight for each experiment (Fig. 31). The equi-yield lines drawn in the figure indicate that the larger the number of kernels per field area the higher was the grain yield.

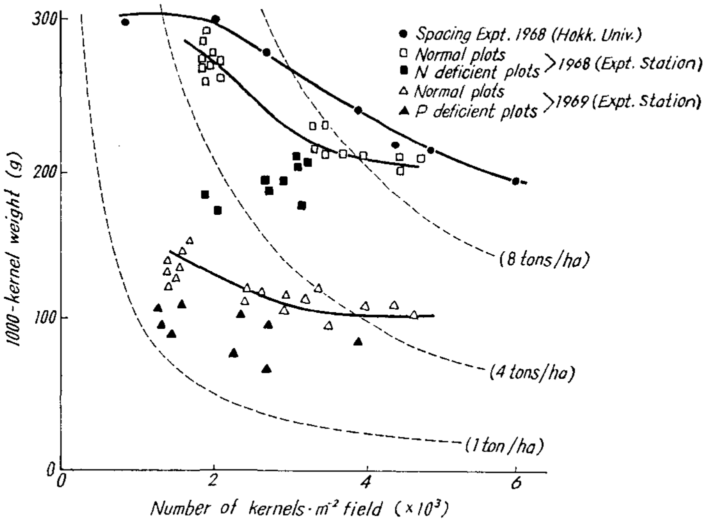


Fig. 31. Relation between number of kernels per unit field area and 1000-kernel weight in Fukko No. 8 under various cultural conditions

For the spacing experiment at Hokkaido University in 1968 an increase in plant population with adequate fertilizer resulted in an increase of grain yield. The increase was derived mainly from an increase of the number of kernels. In this case, the 1000-kernel weight decreased with a decrease of spacing, but this decrease did not compensate for the increase of kernel number. In the case of the experiment at National Hokkaido Agricultural

Experiment Station in 1968, a take-off from the above mentioned correlation, however, was observed when nitrogen was limiting. When nitrogen deficiency became serious at close spacings, the number of kernels as well as the 1000-kernel weight decreased and the grain yield decreased. When phosphorus level was low in this experiment in 1969 with adverse climatic conditions, the 1000-kernel weight was low due to a delay in silking.

An increase of LAI caused by an increase of planting density or of nitrogen application generally resulted in a decrease of number of kernels per unit leaf area (Fig. 32, top). However, at a given LAI the number

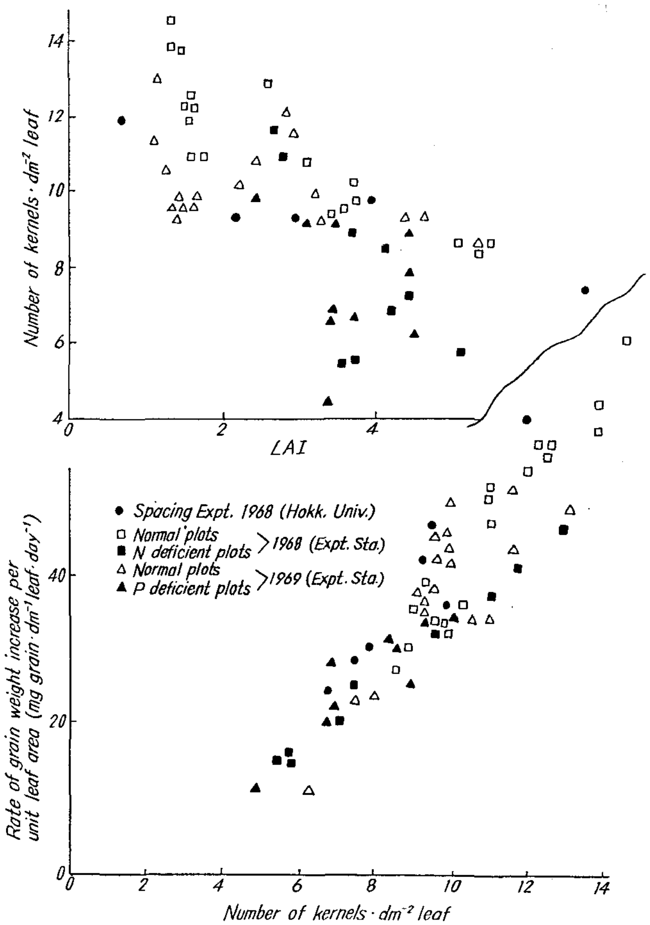


Fig. 32. Relations between LAI and number of kernels per unit leaf area (top) and between number of kernels per unit leaf area and rate of grain weight increase per unit leaf area (bottom)

was less when the plants were deficient in nitrogen. In addition to this tendency there was a trend that the larger the number of kernels per unit leaf area, the higher was the rate of grain weight increase per unit leaf area (Fig. 32, bottom).

Discussions

If the season is favorable, the duration of grain-filling is about 55 days though there are varietal differences ranging from 53 days to 61 days (HILLSON and PENNY (1965)). Extending grain-filling to 55 days increases 1000-kernel weight. Late sowing or low temperatures during the vegetative growth phase delay silking and result in a short grain-filling period. Dense planting, especially with a low nitrogen level, delays silking. Phosphorus application hastens silking, especially with low temperatures.

The LAI can reach 15 at very close spacings and with adequate fertilizer, but with such a large LAI, the plants lodge. Provided that there is no lodging, the CGR increases with an increase of LAI, at least during vegetative growth. Although the net assimilation rate (NAR) decreases with an increase of the LAI, there is no optimum LAI and above a certain LAI the CGR is kept constant. An asymptotic relation between the LAI and the CGR has been reported (WILLIAMS, LOOMIS, and LEPLY (1965b)). The major determinant of CGR is reported to be solar radiation intercepted by the population until tasseling (WILLIAMS, LOOMIS, DUNCAN, DOVRAT and NUNEZ (1968)). After silking, the situation becomes quite different. In high-yielding varieties like Fukko No. 8, there is no optimum LAI, even above a LAI of 8. For low-yielding varieties like Golden Cross Bantam, there is an optimum LAI between 4 and 5 above which the CGR decreases.

There is also a report indicating that rice varieties with low yielding ability have an optimum LAI of 6. However, for varieties with high yielding ability, there is no optimum LAI, but a ceiling LAI of about 6 (YOSHIDA (1969)).

At wide spacings, nitrogen application has only a limited effect on the LAI unless the nitrogen level in the soil is very low. This applies particularly to non-tillering varieties. Under these conditions, nitrogen application increases nitrogen content of the leaves which may result in an increased NAR (NUNEZ and KAMPRATH (1969)). Conversely, at close spacings, nitrogen frequently becomes the leaf expansion limiting factor. Then, nitrogen application increases the LAI as well as the nitrogen content of the leaves. The increase of nitirogen content, however, does not necessarily increase the NAR.

For a given grain-filling duration, grain yield is more closely correlated with the number of kernels per unit field area than with the 1000-kernel weight. This suggests that the CGR during grain-filling is closely controlled by the number of kernels.

The number of kernels per unit field area is the product of the number of ears per unit field area and the number of kernels per ear.

The number of kernels per unit field area tends to be smaller when the vegetative phase is less than 80 days.

The number of ears per unit field area increases with a decrease of spacings provided with adequate nitrogen. At close spacings, the percentage of barren plants increases. Nitrogen deficiency is one reason for this. Varieties which actively tiller produce more than one ear per plant at wide spacings. Limited information described above suggests that at close spacings active tillering varieties may have a higher barren plant percentage.

The number of kernels per ear is the product of the number of rows per ear and the number of kernels per row. For a given variety, the number of rows is constant under a wide range of cultural conditions and is under genetic control. The number of kernels per row decreases with a decrease of spacing and nitrogen level.

It has been reported that at close spacings where mutual shading is a problem, the activity of nitrate reductase tends to be low and the plants utilize nitrate in the soil poorly. For this reason, it has been argued that high nitrate reductase activity is a desirable varietal character (ZIESERL, RIVENBARK and HAGEMAN (1953)). Differences in the activity of this enzyme between parental inbreds and their hybrids have been discussed (SCHRADER, PETERSON, LENG and HAGEMAN (1966)). However, the results obtained from experiments reported here demonstrate that a low nitrogen percentage in the plants at close spacing is a result of the increased demand for the nitrogen available from the soil and not a decrease in the ability of the plants to absorb and utilize nitrogen. At close spacing, the plants usually absorbed more nitrogen per unit field area than at wide spacing.

Lodging limits the possibilities for combining close spacing with an adequate supply of nutrients. However, the maximum grain yield can be obtained under such combinations. The relation between lodging and potassium nutrition has been reported by LIEBHARDT and MURDOCK (1965). However, in the experiments reported here, the potassium content of the shoot remained high, even at close spacings. It is very necessary to find out how far the spacing can be decreased without lodging by using lodging resistant varieties and with reasonable cultural method.

VI. GENERAL DISCUSSIONS

The experiments described in this paper indicate that there are similarities between maize and rice. However, there are also several important differences which affect the measures needed to improve yield. These are:

1) Tillering is the characteristic which, more than any other, enables rice to respond to changes in cultural conditions. This facility is absent or weak in maize. Also, rice has smaller leaves but more of them than maize. These characteristics give rice wider adaptability than maize to changes in cultural conditions.

2) The maximum LAI reported under experimental condition is 20 for maize (WILLIAMS, LOOMIS and LEPLEY (1965a)) and 12 for rice. However, with a LAI of above 10, both crops generally lodge.

3) The rate of photosynthesis per unit area of newly developed healthy leaves is 60–80 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$ for maize and 30–40 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$ for rice. Also, translocation of photosynthetic products from the leaves is faster and more efficient in maize than in rice. Even so, good grain yields under experimental conditions in Hokkaido are 8 to 10 tons/ha of maize and 6 to 8 tons/ha of rice. Why then is the difference in the grain yield less than might be expected from so large difference in the photosynthetic rates?

4) The top three leaves on a culm in rice and the five leaves at or above the ear in maize are the most important for providing photosynthetic products to the developing grains. Translocation of photosynthetic products from these leaves to the kernels is upward in rice and downward in maize.

5) The vegetative growth of rice stops at flowering and active grain-filling starts after flowering. Some starch or sugars accumulate in the leaf-sheath or in the culm until flowering and they are then translocated to the grains after flowering. In maize, the vegetative growth overlaps the initial grain-filling phase for about two weeks after silking. There is no measurable starch accumulation in the vegetative organs and there is only a very limited accumulation of sugars in the culm.

6) The efficiency of respiration in dry matter production during grain-filling is higher in maize than in rice. In maize, the lower strata of the crop canopy do not consume a large amount of the photosynthetic products from the upper leaves by their respiration. In rice, the respiratory loss in the lower strata accounts for a relatively large proportion of the products of photosynthesis, at least under some conditions.

7) In rice, the plant type is important in efforts to improve yield.

However, in maize, observations on the leaf arrangement, the plant height, etc. did not give any evidence to demonstrate the relationship between yielding ability and plant type.

8) A reasonably good grain yield of 7 tons/ha can be obtained with the following combinations of yield components.

	Ear number per m^2 field	Grain number per ear	Grain number per m^2 field	1000-grain weight (g)
Rice	400	70	28000	25
Maize	4	700	2800	250

These figures illustrate big differences in the number of grains per unit field area and the 1000-grain weight for obtaining equal grain yields.

9) In both crops, the greater the production of dry matter after flowering, the higher the grain yield. The dry matter production during this growth phase can be considered in terms of the relation between source and sink. A breakthrough in the present yield level seems likely to come from an improvement of the source in rice and from an improvement of the sink in maize.

The relationships shown in these experiments described in this paper between grain yield and its separate components indicate that it is the number of kernels per unit field area, more than any other factor, that determines the grain yield of maize.

The number of kernels per unit field area, the sink size, is composed of (1) number of plants per unit field area, (2) number of ears per plant and (3) number of kernels per ear.

1) *Number of plants per unit field area* is under the control of cultivation method. It can be increased by increasing the planting density. The plant population required for high yield appears to be larger in rice than in maize.

2) *Number of ears per plant* is the product of number of culms per plant and average number of ears per culm. Rice produces more tillers and more ears, especially at wide spacings, than maize. In rice, the number of ears per plant is the product of number of culms per plant and percentage of ear bearing culms. Both components decrease with a decrease of spacing, but the number of ears per unit field area always increases with a decrease of spacing. In maize at wide spacings, varieties that tiller may produce several tillers bearing at least one ear and in some varieties there may be more than one ear on a culm. Consequently, the number of ears per plant is larger at wide spacings. However, this does not compensate for the decrease in plant population. Also, the ears on tillers are frequently

small and the second ear on a culm generally does not produce many kernels. Thus, at wide spacing, the grain yield is usually small, even with multi-ear varieties. The number of ears per unit field area can be increased most easily by increasing plant population. The percentage of barren plant then limits the number of ears per unit field area. The percentage of barren plants is higher when nitrogen is limiting and it is likely to be higher in active tillering varieties than varieties which produce few tillers.

3) *Number of grains per ear* in rice is the product of number of spikelets per ear and percentage of filled grains. With a decrease of spacing, both of these components decrease. With an increase of nitrogen level, number of spikelets increases and the percentage decreases. In maize the number of kernels per ear is the product of number of rows per ear and number of kernels per row. The number of rows is a genetic character which is not easily affected by cultural conditions. The number of kernels per row decreases with a decrease of spacing and nitrogen level. There are varietal differences in the number of kernels per row and also in the response of the number to cultural conditions.

The product of these three components, namely the number of grains per unit field area, generally increases with an increase of planting density in rice and maize provided all nutrients, especially nitrogen, are adequately supplied. Increasing the planting density and the level of nitrogen, the LAI increases and the number of grains per unit leaf area decreases. This decrease appears to be more significant in maize than in rice.

One more point to be mentioned is the potential size of grains. In rice, the husk, which limits grain size, is determined during spikelet development. It is not yet known whether the potential size of kernels of maize is determined before silking or later.

These discussions demonstrate the importance of discussing the dry matter production during grain-filling in relation to the number of kernels.

It follows that; (a) a high grain yield can be obtained if the dry matter production during grain-filling is large; (b) the dry matter production during this growth phase is the product of duration of grain-filling and crop growth rate; (c) if the duration is less than 55 days, there is a close correlation between the duration and the 1000-grain weight, hence the grain yield; and (d) the CGR increases with an increase of LAI provided the increase of LAI accompanies a reasonable increase of the number of kernels: However, (e) an increase of LAI generally causes a decrease of the number of kernels per unit leaf area and (f) this decrease of the sink size per unit leaf area results in a decrease of the rate of dry matter production per unit leaf area, namely the rate of grain weight increase per unit leaf area.

Thus, the key for a higher grain yield is maintaining a large number of kernels per unit leaf area combined with a large LAI. For this purpose maintaining a high percentage of ear bearing plants and a large number of kernels per ear at close spacings is critical.

CONCLUSION

From the foregoing discussions, the following conclusion can be drawn.

The potential rate of photosynthesis of the leaves is much higher for maize than for rice, but the difference in the grain yield is comparatively small. This is because the rate limiting factor of the dry matter production after flowering, which is closely correlated with the grain yield, is the "sink" in maize and is the "source" in rice at least at present yield levels. In maize, the limitation in the sink size interferes with the expression of potential photosynthetic capacity. In rice the solar radiation available to the plant and the respiratory loss from the lower strata of the crop canopy limit the expression of the sink size.

For this reason, the plant type which controls the efficiency of utilization of solar energy for dry matter production is important to improve rice grain yields, but not so important for maize. In maize, the sink size, the number of kernels per unit field area, is the key factor controlling grain yield.

Sufficient nitrogen with close plant spacing are the cultural conditions needed for a high grain yield. Under these conditions the leaf area index increases, but the number of kernels per unit leaf area decreases. This is the reason why the sink frequently limits the grain yield of maize.

Uniculm with one large ear having many rows of many kernels are desirable characteristics for high-yielding maize varieties. At close spacings, the percentage of barren plants and the number of kernels per row are the major factors limiting sink size. Physiology related to such factors should be studied more to improve cultural methods and varieties of maize.

A closer spacing than a critical one is not practical for farmers because under such conditions plants become susceptible to lodging. Breedging lodging resistant varieties is obviously important.

Varieties and cultural methods that provide 80 days for the vegetative growth and more than 55 days for ripening are prerequisites for high grain yields.

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