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STUDIES ON THE NUTRIO-PHYSIOLOGY OF LEAVES OF RICE PLANT

By

Akira TANAKA

Faculty of Agriculture
Hokkaido University, Sapporo, Japan

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INTRODUCTION

At an early stage of agricultural science, generally, yields of crops were discussed in connected with the treatments which were given to the crops at sowing or planting. This was due to the fact that agricultural practices in early years, various treatments, such as plowing, adjustment of soil pH, application of composts, manures or fertilizers and spacing etc., were given at sowing or planting, however, almost no attention was paid during the growth and the crops were simply harvested when mature. So, it was quite reasonable to consider yields of crops as functions of the treatments which were given before or at the time of sowing or planting.

On the basis of this idea, effect of fertilizers was generally expressed by using the formula: $Y=F(x)$, where Y is yield of a crop and x is amount of fertilizer which was given to the crop. The studies which were carried out by MITSCHERLICH[1] and WILLCOX[2] are typical works along with this line. These works have supplied a great amount of valuable information and have contributed remarkably to agricultural practices.

However, in recent years, farmers have become more careful with their crops. They are anxious to get greater yields from their limited holdings on which their management is bound to be operated. The demands are very serious in countries where agricultural lands are limited, like Japan. Farmers in these countries have become more mindful of growth process of their crops. Agricultural operations during the growth process of crops, such as weeding, harrowing, top-dressing of fertilizers, application of pesticides or insecticides etc., have become more and more popular in recent years. Such agricultural conditions reflected upon agricultural science. Consequently, agricultural scientists have become more interested in growth processes of crops.

On the other hand, by the year 1920, techniques of water culture had been completed and it was ready to be utilized in the field of studies on nutrio-physiology of crops. Under such conditions, GERICKE carried out water culture experiments to estimate the effect of various nutrients at successive stages of growth of wheat plants[3] as well as of rice plants.[4] After his works were reported, Japanese scientists, such as ISHIZUKA,[5] KASUGAI[6] and OSUGI,[7] carried out many experiments of this type by using rice plants. In 1947, ISHIZUKA[8] again reported the studies on the nutrient absorption and utilization by wheat plants at different stages of growth. It was concluded in his report that nitrogen, phosphorus and sulphur are efficiently utilized at early stages of growth. If these elements are given to the crop at early stages of growth in sufficient amount, there is no need to supply these elements at later stages of growth. On the other hand, the crop requires potassium and calcium throughout its life cycle. Magnesium is effectively utilized during the growth period between the ear-initiation stage and the flowering stage. On the basis of these discussions, ISHIZUKA stated that to get successful yields of rice plants, nitrogen must be supplied for nine weeks from the beginning of growth, phosphorus must be given for seven weeks and potassium must be supplied throughout the growth process.

KIMURA et al.[9] carried out a series of experiments and they worked out the partial productivity for nitrogen at different stages of growth by using data obtained from their experiments. According to their results, if nitrogen is given at a high level, the partial productivity of nitrogen is high at early stages of growth and it decreases with the growth, but if the nitrogen level is low, there are two stages when the partial productivity is high. The first peak comes at early stage of growth and the second peak comes between the ear-initiation stage and the heading stage.

In this way, the requirements of crops for nutrients at successive stages of growth have been clarified. Methods of top-dressing with fertilizers have been improved on the basis of these studies.

Beside these water culture experiments, growth processes of crops which are grown under field conditions have been also studied. In early years, generally, growth was expressed by the growth curve which was proposed by ROBERTSON. For example, the growth process of rice plants was expressed by NOGUCHI[10] by the equation: $\mathrm{Log}\, y/45.00 - y = 0.20208\ (t - 8.0650)$, in which, y is the weight of the rice plants per hill at the growth stage t, and t is the time after transplanting expressed by weeks. This type of equation has only approximate meaning. In this curve, the growth process is considered to be a simple quantitative change. However, growth involves not only quantitative

increase, but also qualitative development.

GARNER and ALLARD[11] proposed the theory of photoperiodism, in which, it was pointed out that there is a phase, during growth process, when the plant demands a definite day-length. Vernalization was also found by LYSENKO,[12] who pointed out existance of the thermal sensitive phase during growth process. By these works, the theory of phasal development was established. Now, there is no doubt that ontogeny of anual plants invloves not only quantitatitve growth, but also phasal development. The studies on growth process of crops must be carried out on this basis.

The growth process of rice plants is not only a process of dry weight increase, but also a process which involves several phases.

Generally speaking, at an early phase of growth, tillering is vigorous. This suggests that in this phase, formation of new organs is active. After ear-inititation, enlargement of ear-primordium and elongation of stem are the main feature of growth. This suggests that in this phase, the enlargement of organs which are formed during previous phases is remarkable. After flowering, increase of ear weight and decrease of straw weight are remarkable, suggesting that in this phase, reconstruction of the rice body is the most important feature of growth. Accordingly, the ontogeny of rice plants seems to be divided into three phases by the stages of ear-initiation and flowering. The first phase is from the beginning of growth to the ear-initiation stage; the second phase is from the ear-initiation stage to the flowering stage; and the third phase is from the flowering stage to the maturity. These phases are the vegetative phase, the reproductive phase and the ripening phase, respectively.

ISHIZUKA and the author[13] carried out a series of studies in which it was aimed to characterize the physiological conditions of these three phases from the stand point of biochemistry. By classifying organic constituents of the plant body into three groups, i. e. protein, carbohydrates and cell-wall substances, accumulation process of these compounds during growth process of rice plants was traced and the following conclusions were obtained; in the first phase of growth, accumulation of protein is active, in the second phase accumutation of cellulose and lignin which are components of cell-wall takes place, predominantly and in the third phase, accumulation of carbohydrates in the ear is active. FUJIWARA et al.[14] carried out studies on growth process of rice plants. They stated that early stages of growth are the "protein phase", because accumulation of protein is very rapid and the later stages are the "carbon phase", because accumulation of non-nitrogenous compounds such as cellulose, lignin or starch is active. Their results are in agreement with our conclusions. Studies by TAKAHASHI and MURAYAMA[15] also supported our conclusions. ISHIZUKA and

the author[16] extended their studies to the fluctuation of some enzymatic activities during growth process to characterize the physiological condition of each phase of growth. By these studies, it was concluded that at the first phase of growth, the chlorophyll content is high, and catalase, amylase and invertase are active. These suggest that in this phase, photosynthesis is active and assimilation products are actively translocated into growing points and are consumed there. At the second phase, the content of chlorophyll is high and the catalase is active as at the first phase, while the activity of amylase and invertase are lower. Photosynthesis is kept active from the first phase on, but its products are accumulated where the photosynthesis is going on. At the third phase, both the content of chlorophyll and the activity of catalase decrease, while the activity of amylase and invertase increase. During this phase, products of photosynthesis in the leaf move actively into the ear to form rice grain. The fluctuation of photosynthetic activity during the growth process was studied by DASTUR[17] and also by several Japanese workers.[18][19] The conclusions of these studies are that there are two stages of growth when photosynthesis is very active. The first peak comes at the early stage of growth and the second peak comes just before flowering. YAMADA et al.[20] reported that under high light intensity, there are two peaks of photosynthetic activity during growth. The author's biochemical studies[21] were in agreement with these reports.

Using rice plants grown under normal field conditions, the absorption process of the macro-elements and the translocation of these elements between the straw and ear during growth were studied by ISHIZUKA and the author.[22] On the basis of this study, the macro-elements were classified into three groups:

The first group: Nitrogen, phosphorus and sulphur:—Rice plants vigorously absorb these elements from the beginning of growth and continuing upto the flowering stage, but after this stage, no remarkable uptake takes place. These elements are stored in the straw until the flowering stage and are then translocated into ear.

The second group: Potassium and calcium:—Rice plants absorb these elements continuously from the beginning of growth to maturity.

The third group: Magnesium:—This element is absorbed most vigorously during the period of ear development.

The elements classified as the first group are called the "energy stores"[23] and are the elements which constitute protein. These elements have special importance during the first phase, because during this phase, cell division is active, and accordingly the increase of protein is active. Magnesium, which is classified as the third group seems to have special importance to the second phase of growth. This fact suggests that this element has some special meaning on the

formation of cellulose and lignin. The elements classified as the second group are called the "translocation regulators"[23] and absorption of these elements is necessary at all phases of growth so far as expansion of plant body takes place.

According to the results obtained by ISHIZUKA[8] using wheat plants under water culture conditions, the requirement of the plants for nitrogen, phosphorus and sulphur is great during the growth phase from germination to the flowering stage. The requirement for potassium and calcium is great throughout the growth, and that for magnesium is great during the period between ear-initiation and flowering.

From these findings, it can be stated that the period when active uptake of an element takes place is the period when the requirment for the element is great; in other words, plants which are grown under favorable conditions absorb mineral constituents vigorously when the requiremeut of the plants for these elements is great. So, the application of mineral elements at the time when the requirement for these elements is great, seems to be favorable for increasing the yield.

The above mentioned studies were carried out to meet the demands of practical agriculture, and based on the results of these studies, methods of top-dressing rice plants with fertilizers have been greatly improved.

However, demands of farmers for agricultural science, especially requests by rice growing farmers in Japan, are increasing. Farmers are more and more eagar to get greater yields from their limited fields. They want to know what to do for their rice plants every day by daily diagnoses. Unfortunately the studies which have been carried out are insufficient to meet these farmers' demands.

So far, agricultural scientists and nutrio-physiologists treat the plant as a whole, but the plant is constructed from many tillers. These tillers consist of many leaves, stem and ear and even the leaf is constructed from the leaf-blade and leaf-sheath. At a given stage of growth, many organs which construct a whole plant are at different stages of growth. Some organs are just completing differentiation, some are growing vigorously, some are functioning very actively, some are old and the others are dead. Data of the chemical analyses on a whole plant have very little meaning in expressing the physiological condition of the plant, because the sample is a mixture of organs which are completely different in nature or are at different stages of growth. If it is intended to clarify the physiological condition of a plant, more attention must be paid in each organ. The studies in which plants are treated as a whole have only qualitative meaning. If it is desired to know the physiological condition of the rice plant at any stage of growth qualitatively, analytical studies

on the many organs that make up the whole plant under study must be conducted. By these studies, morphological constructions can be connected with physiological functions from the view point of nutrio-physiology. If the physiological characters and functions of each leaf could be clarified by these studies, the diagnoses of rice plants at any given stage of growth could be done by the leaves which are growing or functioning at that stage of growth. The results of these studies are very useful to meet the above mentioned farmers' demands.

A rice plant grown under normal field conditions possesses 50 to 60 leaves. The number of leaves is so great that, it is too difficult to carry out studies on each leaf, so no nutrio-physiological study on individual leaves has been conducted so far.

KATAYAMA[24] carried out very intensive observations on the leafing processes of rice plants. He established a rule of leafing and proposed the theory of synchronous leaves. According to the theory, the leaf on a tiller has its corresponding synchronous leaf on the main stem which differentiates and elongates simultaneously. For example, the synchronous leaf of the first leaf on the first tiller is the fourth leaf on the main stem. The fifth leaf on the main stem, the second leaf on the first tiller and the first leaf on the second tiller are synchronous each other.

On the main stem of rice plants, there are 11–16 leaves according to the duration of growth. The later the duration, the greater the leaf number.[25][26] If there are 12 leaves on the main stem, the leaves of the rice plant can be classified into 12 groups by the theory of synchronous leaves. The 12 leaves on the main stem represent the 12 groups.

Since the study of leaves is simplified by the KATAYAMA's work, the author started a series of studies in which it was intended to know the characteristics of physiological conditions and functions of leaves on the main stem to meet the above mentioned farmers' demands. This report dealts with this series of studies.

After the author had started these studies, ARASHI[27][28] studied the *Akiochi* from the assumption that environmental conditions reflected on the length of leaf-blade which was formed under the conditions. TOGARI et al[29] studied the fluctuation of starch in each leaf on the main stem during growth of rice plants and MURAYAMA[30] carried out the same type of studies on nitrogen. These studies were very suggestive and also encouraging for the author's work.

The use of radio-active isotopes has become very popular in studies on nutrio-physiology in recent years. Especially studies on translocation of elements within the plant body have advanced remarkably.[31][32]

In this series of studies, radio-active isotopes, such as P^{32} and Ca^{45} were used to trace translocation of these elements among leaves. C^{14} was also used to compare photosynthetic activities of leaves and also to trace the translocation of assimilation products among leaves and other organs.

These tracers helped these studies by the extent that without them the results could not have been obtained.

By Yoshiaki ISHIZUKA and the author, a series of studies on the nutrio-physiology of rice plant is being conducted since 1948. The present report is a part of the series of studies.

The author is indebted to Dr. Y. ISHIZUKA, Professor of Soil Science and Plant Nutrition, Hokkaido University, for his valuable directions and cordial encouragements.

He wishes to thank Dr. T. TAGAWA, Professor of Plant Physiology, Hokkaido University, for his suggestions and encouragements and Dr. M. DRAKE, Research Professor of Chemistry, University of Massachusetts and Chief of ICA Party University of Massachusetts to Hokkaido University, for his kind help in preparing this report.

MATERIALS AND ANALYTICAL METHODS

Rice variety, *Chuseieiko*, medium duration variety in Hokkaido, was employed throughout these studies.

It was grown in the fields at the Hokkaido Agricultural Experiment Station or under water-culture conditions in the glass-house at Hokkaido University during the years between 1952 and 1957. Conditions of cultivation were as follows: In the cases of field cultures, in the middle of May, seeds were sown on upland protected nursary beds which had received sufficient nutrient supply. Transplanting was made about 30 days after sowing, when the forth leaf started to emerge, on well paddled flooded main fields which had received fertilizers at the rate of 2 kan/tan (ca. 75 kg/hect.) of N, P_2O_5 and K_2O as ammonium sulphate, superphosphate and potassium sulphate. The spacing was 7.5×7.5 sun (ca. 23×23 cm), with one plant per hill. After transplanting, irrigation, weeding, application of insecticides and pesticides were given by methods common to this locality. Under such management, rice plants were ready to harvest by the end of September. In the case of water-cultures, seedlings were raised on sand in the glass-house, regularly irrigated with tap water, transplanted to water-culture at the stage of the third leaf. Six seedlings were planted in a pot which contains 4 liters of culture solution. After one week, seedlings were thinned so that a pot had two uniform seedlings. A culture solution was composed of

NH_4NO_3, NaH_2PO_4, KCI, $CaCl_2$, $MgCl_2$ and Na_2SO_4. Supplying concentrations of N, P_2O_5, K_2O, CaO, MgO and SO_3 at 40, 30, 40, 30, 30, 30, ppm, respectively.[33] Distilled water obtained by metal apparatus using steam from boiler was used. The pH of the culture solution was adjusted at 4.6 initially, with no other adjustment until the renewal of the culture solution. Culture solutions were renewed once every five to seven days. Small amount of Fe and Mn were given. Treatments were duplicated.

Samples were taken periodically. In the cases of field culture, 10–30 plants showing almost the same tillering system were collected for each sample. In the cases of water-culture, 2 plants from one pot were uprooted for each sample. These plants were washed thoroughly and were separated into individual organs immediately, and were dried in an oven at 70–80°C. Dried samples were ground into powder with a grinding mill and were stored for analysis.

Nitrogen was determined by the micro-Kjeldahl method. Phosphorus was determined colorimetrically by the method of FISKE-SABBAROW.[34] Potassium was determined by precipitating potassium as cobalti-nitrite, then the cobalt was estimated colorimetrically by NH_4CNS in acetone.[35] Calcium was determined volumetrically by titrating with potassium permanganate after precipitating calcium as the oxalate. Magnesium was determined by precipitating magnesium with phosphorus under alkaline condition after removing calcium as oxalate and the phosphorus was determined colorimetrically.

Determination of sugars, starch and hemicellulose were carried out by the methods described by MURAYAMA et al.[16] Sugars were extracted by 80% alcohol and the extracted non-reducing sugars were hydrolysed by 2% H_2SO_4. Starch was extracted by 4.6 N $HClO_4$ and hydrolysed by the acid. Hemicellulose was hydrolysed by 0.7 N HCl. Impurities were removed by $Ba(OH)_2$ and $ZnSO_4$. Reducing power of sugars was estimated by the SOMOGYI method.[37]

The method of application and determination of radio-isotopes are described on each occasion.

LEAFING PROCESS AND LONGEVITY OF LEAVES

The rice variety, *Chuseieiko*, was grown in the fields at the Hokkaido Agricultural Experiment Station, under the conditions mentioned above. Transplanting was made on June 9, 1952. Samples were obtained once every two weeks from transplanting to harvest.

On these samples, observations on leafing of the main stem as well as that of the tillers were carried out. The results are given in figure 1.

In this figure, the nomenclature of leaves by KATAYAMA[24] was employed. By this method, for example, the third leaf on the main stem is symbolized by

3/0, where the denominator is the name of stem and the numerator is the position of the leaf on the stem. The main stem is symbolized by 0 and tillers of first order are symbolized by the number of node on the main stem from which the tiller emerges. P shows the profile. The tiller of the second order, which comes out from the first order tiller, is symbolized as follows. For example, the tiller at the second node on the 3-tiller is symbolized by 32, where the first figure suggests the name of tiller and the second figure suggests the name of node.

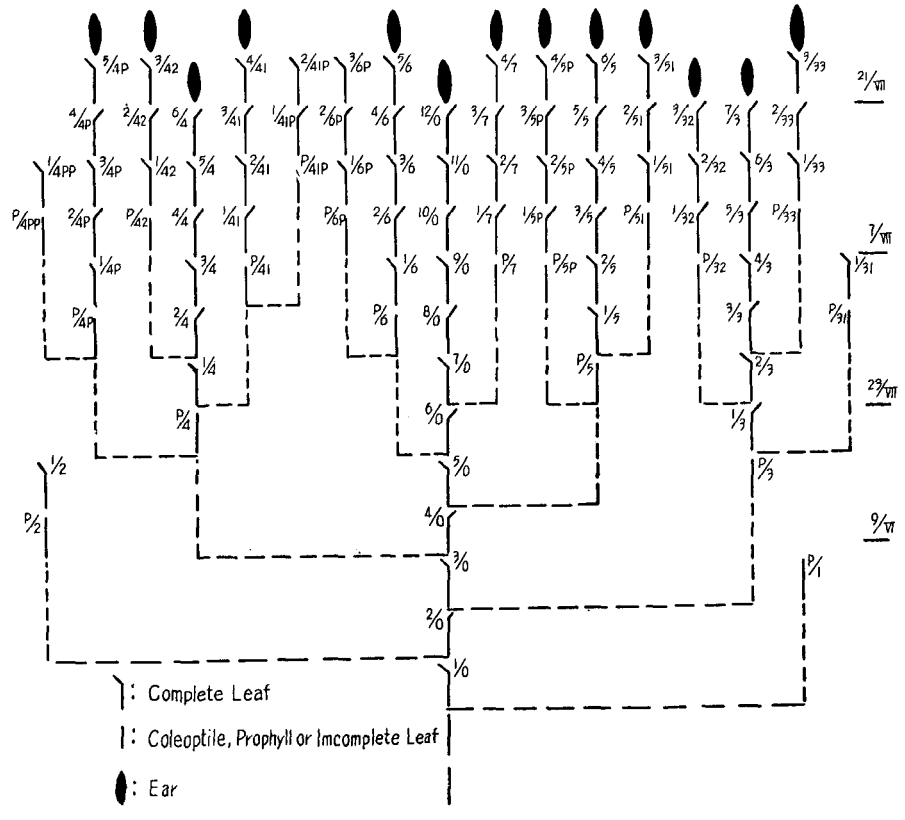


Fig. 1. Process of leafing.

At the time of transplanting, seedlings had four leaves and no tiller.

On June 23, when seedlings were established, the rice plants had six leaves on the main stem and two visible tillers. The 1-tiller had only the profile which had dried. The 2-tiller had the profile and the first leaf, however, these leaves were dead. These two are mortal tillers which could not continue to grow

due to shrinkage by transplanting. The 3-tiller had the profile and the first leaf. The 6/0 and 1/3 are synchronous leaves each other.

On July 7, the main stem had nine leaves and the 6-, 5-, 4-, 3-, 31 and 4p-tillers. Also the 9/0, 6/1, 5/2, 4/3, 3/4, 2/5, 1/6, 4/1p, 3/11, 2/12, 1/13, 3/2p, 2/21, 1/22, 2/3p, 1/31, 1/4p, 2/1pp, 1/1p1, 1/11p, and 1/2pp are synchronous leaves which are elongating at this growth stage. In fact, the 9/0, 4/3, 3/4, 2/5, 1/6, 1/31 and 1/4p were elongating. This suggests that the synchronous leaf theory is more or less applicable to this case.

On July 21, ear-primordia were observed on the main stem, and the 3-, 4- and 32-tillers. However, no ear-primordium was visible on other tillers. At this stage, there was some difference of growth among tillers.

On August 6, ear-primordia on all effective tillers had been formed and these were growing rapidly.

On August 20, all ears had imarged. There was difference of position among ears expressed by synchronous leaf system. The difference was one step as is shown in figure 1, with the result, there was about one week difference in heading date among tillers.

At the end of growth, the main stem had 12 leaves among which the 1/0 and 2/0 had mortal tillers, and the 3/0–7/0 had effective tillers. Internodes between the 9/0–10/0, 10/0–11/0, 11/0–12/0 and 12/0–ear elongated, namely the 10/0, 11/0, 12/0 and ear had elongated internode. Among these internodes, the lowest one was rather short. The 3-tiller had three secondary tillers, among which the 31-tiller was ineffective and the 32- and 33-tillers were effective. The 4-tiller was the most vigorous tiller, from which four tillers emerged among which the 4p, 41 and 42 were effective and the 41p was ineffective. The 5-tiller had two effective tillers, i.e., the 5p and 51. The 6-tiller had only one secondary tiller, the 6p, which was ineffective. The 7-tiller had no tiller. All effective tillers had at least three leaves which had elongated internode.

Generally, there were one or two leaves which had nither elongated internode nor tiller on a stem. The main stem and the 5-, 6- and 4p-tiller had two leaves of this type, the 3-, 4-, 7-, 41- and 5p-tillers had one, and the 32-, 33-, 42- and 51-tillers did not have any.

No mortal tiller had more than three leaves. The critical number of leaves on an effective tiller seems to be three, that is, tillers which could possess more than three healthy leaves are effective and tillers which failed to have three healthy leaves by some reason turn to be mortal.

These observations show that the theory of synchronous leaves can be well fitted in this case. Since synchronous leaves come out simultanenously, these leaves grow under approximately the same conditions and these leaves

seems to have almost the same physiological conditions and functions. By this reason, in this series of studies, discussions are limited only on the leaves on the main stem.

Table 1 shows length of leaf-blade and conditions of the leaves on the main stem at successive stages of growth.

TABLE 1. Length of leaf-blade on main stem (cm)

Name of leaf	Date of sampling							
	9/VI	23/VI	7/VII	21/VII	6/VIII	20/VIII	3/IX	17/IX
12/0				10 D	28 ○	29 ○	28 ○	29 ○
11/0				40 ○	41 ○	40 ○	41 ○	40 ◑
10/0				41 ○	42 ○	42 ○	41 ◑	42 ●
9/0			11 D	35 ○	35 ○	34 ◑	35 ●	34 ●
8/0			30 ○	30 ○	31 ○	30 ●	30 ●	31 ●
7/0			23 ○	22 ○	23 ○	22 ●	22 ●	23 ●
6/0		5.0 D	17 ○	17 ○	16 ○	17 ●	18 ●	17 ●
5/0		12.4 ○	13 ○	13 ○	13 ●	12 ●	13 ●	12 ●
4/0	2.9 D	10.5 ○	10 ○	10 ●	10 ●			
3/0	8.2 ○	9.0 ○	9 ◑	9 ●				
2/0	5.2 ○	5.8 ◑	5.8 ●	6 ●				
1/0	1.9 ○	1.9 ●						

○ : Complete leaf. D : Elongating leaf. ◑ : Half dead leaf. ● : Dead leaf.

Figure 2 was prepared to show leafing intervals of successive leaves on the main stem. In this figure, date of observation is taken in the lateral axis and the number of leaves on the main stem in the vertical axis. The plotted figure is almost a strait line. The leafing intervals are almost constant from the 3/0 to 12/0. The intervals between the emergence of one leaf and the next leaf are about 5–6 days, regardless to position of leaves. KATAYAMA[24] pointed out that leafing interval is almost constant until a certain stage of growth and then it becomes longer. He called this stage the "transitional period of leafing interval". However, in the data described here, there was no such transitional period, though the observations carried out here are not in such detail. On this subject, the author made detailed studies and it was concluded

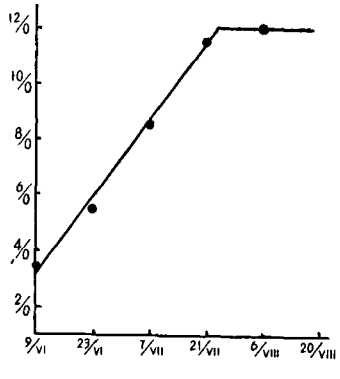


Fig. 2. Leafing process of leaves on main stem.

that if environmental conditions are kept constant throughout growth, the intervals are kept constant.[25]

Longevity of leaves at various positions on the main stem can be estimated by table 1.

On June 10, the 3/0 was elongating and on July 7, the leaf had started to dry, so the longevity of 3/0 is approximately 30 days. On June 23, the 4/0 had finished its elongation and on July 21, the leaf was dead, so the longevity of 5/0 is about 40 days. It seems the longevity of 6/0 is nearly 45 days. The longevity of 7/0–10/0 is approximately same to that of 6/0. The 11/0 is kept active more than 50 days. The longevity of the flag leaf is longer than any other leaf.

Generally speaking, the longevity of leaves which are active during the tillering stages is shortest, that of leaves which are active during the elongation stages is longer and that of leaves which are active during the maturing stages is longest. This result is in agreement with the conclusions obtained by MORITA.[38]

GROWTH PROCESS OF LEAVES

Leaves on the main stem emerge from the lower one to the upper one successively with growth as described above. Since a rice plant is constructed from many leaves, the life history of the individual leaf should be clarified to understand the life history of a whole plant.

Physiologically speaking, the life history of a leaf is a process of increase and decrease of dry weight of the leaf or a process of accumulation and effluxion (outflow) of substances in or from the leaf.

By this reason, the determination of dry weight, content of elements and also content of carbohydrates of leaves on the main stem of rice plants grown under normal field conditions were carried out at successive stages of growth in the years 1952 and 1957. In these years, the rice plants under these studies, made normal growth due to favorable weather conditions.

Fluctuation of Dry Weight

Determination of the dry weight of leaves on the main stem at successive stages of growth were carried out in the years 1952 and 1957. In these two years, the data were more or less the same, so only the data[39] in 1952 are given in table 2 and figure 3.

The dry weight of a leaf increases at the early stage of growth of the leaf, reaches the maximum and then decreases. After some time, the decrease stops and then the weight of the leaf remains constant. The leaf dries, generally, when the decrease of weight of the leaf stops.

The maximum weight of 1/0 was reached at transplanting, on June 10. The flag leaf, 12/0, is at the maximum weight on August 20. The maximum weight of all leaves comes between June 10 and August 20 in sequence from the lower leaf to the upper leaf. This means that the lower leaves grow first and then the upper ones grow successively.

TABLE 2. Dry weight of leaves on main stem

(g per leaf)

Name of leaf	Date of sampling							
	10/VI	23/VI	7/VII	21/VII	6/VIII	20/VIII	3/IX	17/IX
Ear	—	—	—	—	0.27	0.64	1.75	2.25
12/0				0.036	0.35	0.38	0.29	0.27
11/0				0.21	0.51	0.56	0.42	0.35
10/0				0.23	0.47	0.47	0.34	0.31
9/0			0.012	0.25	0.32	0.28	0.20	0.21
8/0			0.096	0.17	0.21	0.18	0.18	0.18
7/0			0.082	0.14	0.14	0.12	0.12	0.12
6/0		0.012	0.063	0.087	0.068	0.073		
5/0		0.026	0.059	0.054	0.052	0.050		
4/0	0.008	0.026	0.033	0.030	0.032	0.030		
3/0	0.014	0.022	0.019	0.017	0.019			
2/0	0.006	0.012	0.009	0.010				
1/0	0.002	0.002						
Stem	0.001	0.003	0.017	0.081	0.462	1.30	1.19	1.10

From figure 3, it is very clear that, at some stage of growth of a rice plant, the weight of some leaves is increasing, while that of other leaves is decreasing. That is, the increase of total weight of a rice plant at a given moment means that the algebraic sum of increase and decrease of weights of individual leaves is positive and decrease of total weight means that the sum is negative. However, regardless of the increase or decrease of total weight, some leaves are gaining their weight and others are losing their weight.

Table 3 was prepared from table 2 and figure 3, in which the maximum dry weight of each leaf and the weight at the death of each leaf are given.

The higher the position (or insertion) of a leaf, the greater the maximum dry weight, except for the flag leaf. From this fact, it can be stated that 2/0 grows by the help of 1/0, so 2/0 is greater than 1/0 and 3/0 is greater than 2/0 by the same reason. By this way, the upper leaf is greater than the lower

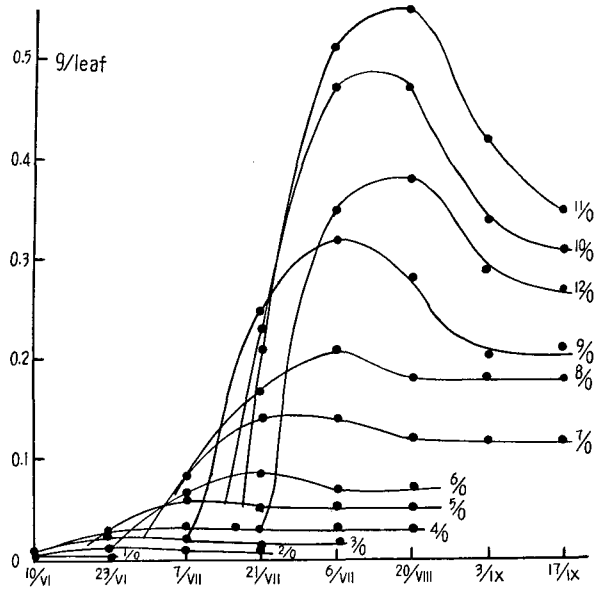


Fig. 3. Dry weight of leaves on main stem.

TABLE 3. Maximum weight and the translocation quotient

Name of leaves	Maximum weight (g)	Weight at death (g)	Translocation quotient
12/0	0.385	0.270	30
11/0	0.559	0.350	37
10/0	0.474	0.308	35
9/0	0.315	0.208	34
8/0	0.211	0.179	15
7/0	0.143	0.122	15
6/0	0.087	0.073	13
5/0	0.059	0.050	12
4/0	0.033	0.030	10
3/0	0.022	0.019	16
2/0	0.012	0.010	17
1/0	0.002	0.002	0

one. Growth of a rice plant can be considered to be a chain reaction. Growth of 1/0 is indispensable to the growth of 2/0 and 3/0 grows by the help of 2/0 and 1/0. Generally, $n/0$ is formed by the help of $n-1/0$, $n-2/0$ and $n-x/0$ and contribute to the growth of $n+1/0$, $n+2/0$ and $n+x/0$. In this way, the growth process of a whole rice plant has a character of auto-catalytic reaction.

The dry weight of a leaf decreases after reaching the maximum weight. This decrease is mainly due to translocation of materials from the leaf to the organs which grow later. It can be considered that the degree of translocation of materials from a leaf after having reached the maximum weight of the leaf suggests the grade of contribution of that leaf to the growth of a later stage by means of materials which were once stored in the leaf. The translocation quotient is calculated by the equation:

$$\text{Translocation quotient} = \frac{(\text{Maximum weight} - \text{Weight at death})}{\text{Maximum weight}} .$$

The translocation quotient of 1/0 is zero. The observations were started only at the time of transplanting, so it is quite possible that the decrease of dry weight of 1/0 had finished until the time of transplanting. This may be the reason why the quotient of 1/0 is zero. The quotient of 2/0 and 3/0 is 16 or 17. That of 4/0–6/0 is small. Between 4/0 and 11/0, the quotient becomes greater from the lower leaf to the upper leaf. The quotient of leaves between 9/0 and 11/0 is great and that of 12/0, the flag leaf, is also fairly great. These differences of the translocation quotients among leaves suggest that each leaf has its characteristics of the physiological conditions and functions corresponding to its position on stem.

The upper leaves have a greater capacity to store substances than the lower leaves.

Accumulation and effluxion of elements

Nitrogen: Determination of nitrogen content of each leaf on the main stem at successive stages of growth were carried out in the year 1952. The data are given in table 4.[40]

Figure 4 was prepared to show the fluctuation of nitrogen content of each leaf during growth.

The nitrogen content of 1/0 and 2/0 drops very quickly after transplanting. These leaves die in a short time. The nitrogen content of 1/0 and 2/0 at their death are 0.73 and 0.90%, respectively. The nitrogen content of 3/0–5/0 decreases quickly with the elongation of these leaves. After this rapid decrease, the rate to decrease diminishes. The higher the position of leaf, the higher the nitrogen content at which the rapid decrease of nitrogen content stops.

TABLE 4. Nitrogen content of each leaf on main stem
(N% on dry matter basis)

Name of leaf	Date of sampling							
	10/VI	23/VI	7/VII	21/VII	6/VIII	20/VIII	3/IX	17/IX
12/0				5.03	1.65	1.64	1.33	0.58
11/0				3.60	1.67	1.51	1.16	0.58
10/0				3.12	1.64	1.48	1.07	0.58
9/0			5.58	2.80	1.64	1.23	0.80	
8/0			4.21	2.79	1.58	0.92	0.75	
7/0			3.59	2.62	1.05	0.80		
6/0		5.63	3.10	2.37	0.95			
5/0		3.60	2.88	1.80	1.28			
4/0	5.52	2.79	2.13	1.59				
3/0	3.85	2.48	1.97	1.57				
2/0	3.28	1.50	0.90					
1/0	2.20	0.73						

These leaves die with a rather high nitrogen content (1.28–1.59%). This means that the cause of death of these leaves is not protein decomposition. In the cases of 6/0–9/0, the nitrogen content drops very quickly during the stage of elongation of these leaves, then the drop slows down for some time. However, the drop becomes rapid again after July 20. The nitrogen content of these leaves at death is 0.75–0.95% which is not so high as in the cases of 3/0–5/0. The content of 10/0–12/0 drops very quickly in company with their growth, but when the elongation finishes, the content is maintained at an almost constant level for a fairly long time and it starts to drop again after flowering. The nitrogen content of these leaves at their death is very low (about 0.6%). This suggest that the protein in these leaves is decomposed remarkably and translocates from them to ear. The death of these leaves may be due in part to the decomposition of protein.

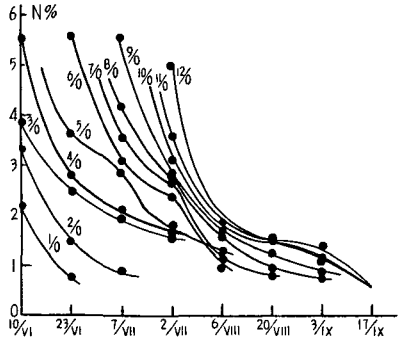


Fig. 4. Nitrogen content of each leaf on main stem at successive stages of growth.

Figure 5 shows the nitrogen content of leaves at the various positions on the main stem.

During the growth periods, between June 10, transplanting, and July 21, ear-initiation, the upper leaves are higher in nitrogen content than the lower leaves. At these stages of growth, tillering is going on and primordia of new leaves are being formed. The nitrogen content of new leaves is higher than that of the older leaves. This means that nitrogen in the older leaves translocates to new leaves. Nitrogen which comes from the older leaves and also which is absorbed by roots at these stages of growth goes into the growing points instead of into the lower leaves. At the growing point, new leaves are initiated and these leaves elongate by using the incoming nitrogen. This means that initiation and expansion of new organs cause accumulation of nitrogen. After the ear-initiation stage, the difference of nitrogen content among leaves becomes smaller. On August 6, there is not much difference of nitrogen content among leaves. Even at this growth stage, death of the leaves goes on from lower leaves, upward. After the flowering stage, the nitrogen content of the lower leaves starts to decrease quickly, so, in this phase of growth, again the upper leaves are higher in nitrogen content than the lower leaves.

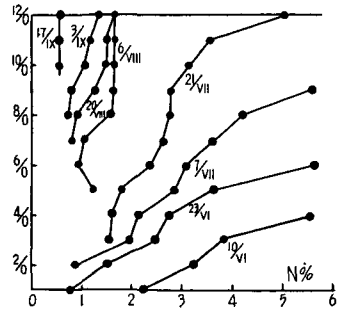


Fig. 5. Nitrogen content of leaves at various positions on main stem.

TABLE 5. Amount of nitrogen in each leaf on main stem

(N mg per leaf)

Name of leaf	Date of sampling							
	10/VI	23/VI	7/VII	21/VII	6/VIII	20/VIII	3/IX	17/IX
12/0				1.8	5.8	6.2	3.9	1.6
11/0				7.6	8.5	8.5	4.9	2.0
10/0				7.2	7.7	7.0	3.6	1.8
9/0			0.7	7.0	5.2	3.4	1.6	
8/0			4.0	4.7	3.3	1.7	1.4	
7/0			2.9	3.4	1.5	1.0		
6/0		0.68	2.0	2.1	0.65			
5/0		0.94	1.7	0.97	0.66			
4/0	0.44	0.73	0.70	0.48				
3/0	0.54	0.55	0.37	0.27				
2/0	0.20	0.18	0.08					
1/0	0.08	0.02						

The amount of nitrogen in each leaf at successive stages of growth was calculated by multiplying the dry weight of a leaf by its nitrogen content. The results are given in table 5. In figure 6, the amount of nitrogen is plotted against the date of determination.

The amount of nitrogen in each leaf increases in relation to the growth, and after reaching the maximum value, it decreases. This result is in agreement with many reports.[41)42)] Accumulation and effluxion of nitrogen in or from a leaf are related to the activity of the leaf. If a leaf is active, nitrogen accumulates in the leaf and if it is not active, nitrogen efflux from the leaf.

The time when the maximum nitrogen accumulation is attained, comes in sequence from lower leaf to upper leaf in the same manner as the dry weight.

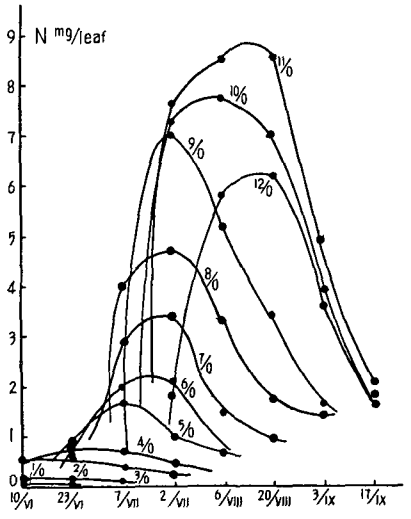


Fig. 6. Amount of nitrogen in each leaf at successive stages of growth.

Phosphorus: Determinations of the phosphorus content of each leaf on the

TABLE 6. Phosphorus content of each leaf on main stem

(P_2O_5% on dry matter basis)

Name of leaf	Date of sampling							
	10/VI	23/VI	7/VII	21/VII	6/VIII	20/VIII	3/IX	17/IX
12/0				1.32	0.68	0.70	0.59	0.31
11/0				1.07	0.66	0.66	0.35	0.09
10/0				1.00	0.64	0.62	0.18	0.06
9/0			1.04	0.39	0.32	0.22	0.05	
8/0			0.55	0.25	0.29	0.12	0.05	
7/0			0.30	0.18	0.24	0.05		
6/0		0.94	0.17	0.15	0.20	0.04		
5/0		0.51	0.27	0.30	0.16			
4/0	1.10	0.32	0.25	0.19				
3/0	1.06	0.28	0.10	0.04				
2/0	1.21	0.24	0.02					
1/0	1.18	0.22						

main stem at successive stages of growth were carried out on the same samples used in determining nitrogen. The data[43] are given in table 6.

In figure 7, the phosphorus content of each leaf at successive stages of growth are taken against the date of sampling.

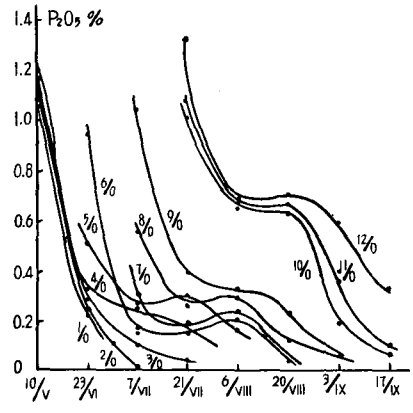


Fig. 7. Phosphorus content of each leaf on main stem at successive stages of growth.

The phosphorus content of 1/0 and 2/0 drops very quickly after transplanting similar to that of the nitrogen content. The phosphorus content of these leaves at death is 0.02% which is very low. Behavior of phosphorus in 3/0 is more or less the same as that in 2/0. The phosphorus content of 4/0 and 5/0 decreases quickly when these leaves elongate. After this rapid decrease, the phosphorus content remains almost constant at about 0.3–0.4% or rises slightly. After this stage, the content slowly drops again. The phosphorus content of 4/0 and 5/0 at the death of these leaves is 0.14–0.19% which is higher than that of other leaves. The behavior of phosphorus in 6/0–9/0 is more or less the same as that in 4/0 or 5/0. The content of these leaves reaches the maximum value on August 6, and then decreases. The phosphorus content of 10/0–12/0 drops very remarkably until August 6. After this stage, the content is maintained almost constant, between 0.6 and 0.8%, until the time of flowering. The constant level of these leaves is far higher than that of the lower leaves. After flowering, the phosphorus content of 10/0–12/0 starts to drop from lower leaf to upper leaf.

Figure 8 shows the relation between the position of leaves and the phosphorus content of these leaves at various stages of growth.

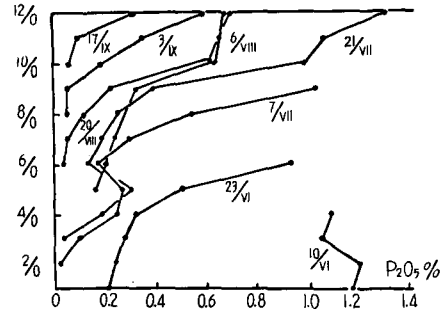


Fig. 8. Phosphorus content of leaves at various positions on main stem.

At the time of transplanting, there is not much difference in the phosphorus content among leaves. After seedlings are established, generally, the phosphorus content of the upper leaf is higher than that of the lower leaf. This condition is maintained until the end of growth.

However, differences of phosphorus content among leaves is large until the ear-initiation stage. During the growth phase between transplanting and ear-initiation, the nitrogen content of the upper leaves is also kept higher than that of the lower leaves. This suggests that the accumulation of phosphorus is governed by almost the same mechanism as that of nitrogen. After the ear-initiation stage, the difference of phosphorus content among leaves becomes smaller.

The amount of phosphorus in each leaf was worked out by the same method as in the case of nitrogen and the results are given in table 7.

Figure 9 shows the amount of phosphorus in each leaf at successive stages of growth.

The amount of phosphorus in each leaf increases with elongation of leaf, reaching the maximum amount and then decreases. The period when the maximum phosphorus amount is reached comes from the lower leaf to the upper leaf,

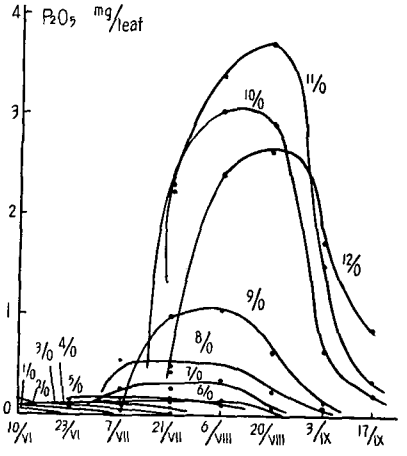


Fig. 9. Amount of phosphorus in each leaf at successive stages of growth.

TABLE 7. Amount of phosphorus in each leaf on main stem

(P_2O_5 mg per leaf)

Name of leaf	Date of sampling							
	10/VI	23/VI	7/VII	21/VII	6/VIII	20/VIII	3/IX	17/IX
12/0				0.48	2.38	2.66	1.71	0.84
11/0				2.25	3.37	3.70	1.47	0.32
10/0				2.30	3.01	2.90	0.61	0.19
9/0			0.01	0.98	1.02	0.62	0.10	
8/0			0.53	0.43	0.61	0.22	0.09	
7/0			0.25	0.25	0.34	0.06		
6/0		0.10	0.11	0.13	0.13	0.03		
5/0		0.13	0.16	0.16	0.08			
4/0	0.09	0.08	0.08	0.06				
3/0	0.15	0.06	0.02	0.01				
2/0	0.07	0.03	0.00					
1/0	0.03	0.00						

successively. This is just the same as in the case of the nitrogen amount. There are differences of fluctuation between the nitrogen and the phosphorus in the leaves which are on the positions lower than 9/0. In the case of these lower leaves, the maximum amount of phosphorus in each leaf remains constant for a long period. This may occur because during the growth stages of the lower leaves soluble phosphorus is not abundant in the soil and because the absorption of phosphorus is not active due to low temperature. Thus, phosphorus which is accumulated in a leaf stays in these leaves for a rather long time in order to maintain these leaves in active conditions. Phosphorus in these leaves flows out only after these leaves begin to dry. The process of accumulation and effluxion of phosphorus in 10/0–12/0 is similar to that of nitrogen in these leaves.

Potassium: Determinations of the potassium content of each leaf on the main stem at successive stages of growth were carried out on the same samples used for nitrogen determinations in the year 1952. The data[43] are given in table 8.

TABLE 8. Potassium content of each leaf on main stem

(K_2O% on dry matter basis)

Name of leaf	Date of sampling							
	10/VI	23/VI	7/VII	21/VII	6/VIII	20/VIII	3/IX	17/IX
12/0				6.02	1.90	1.90	1.91	2.05
11/0				3.52	1.96	2.05	2.38	2.45
10/0				2.90	1.90	1.90	2.23	2.20
9/0			4.97	2.31	1.45	1.63	1.91	
8/0			3.50	2.15	1.32	1.52	1.50	
7/0			2.82	1.32	1.20	1.42		
6/0		3.72	2.65	1.75	1.50	1.50		
5/0		3.15	2.15	1.60	1.50			
4/0	5.00	2.70	1.50	0.98				
3/0	4.47	1.24	1.01	0.90				
2/0	3.85	0.80	0.75					
1/0	2.73	0.42						

Figure 10 shows the flucation curves of potassium of each leaf.

The potassium content of 1/0 and 2/0 drops rapidly until the death of these leaves. This tendency is almost the same as in the cases of nitrogen and phosphorus. Because these leaves are withered after transplanting, the constituents of these leaves seems to go out almost completely. The 3/0 and

4/0 behave almost the same as 1/0 or 2/0, though the drop of potassium content is not so rapid. The fluctuation curves of the potassium content of the leaves on the positions higher than 5/0 are somewhat different from those of nitrogen or phosphorus content. The potassium content drops slowly with the growth of these leaves, and reaches the minimum value at the stage when the leaf stops its elongation. After this stage, the potassium content goes up very slowly. This rise is more remarkable in the cases of 10/0–12/0 than in the cases of the lower leaves. This rise in the potassium content takes place when the nitrogen and phosphorus content drops. This may occur because the translocation of potassium from these leaves is slower than that of nitrogen and phosphorus. Thus, the relative content of potassium rises with the translocation of nitrogen and phosphorus.

Figure 11 shows the relation between the position of leaves and the potassium content of these leaves at various stages of growth.

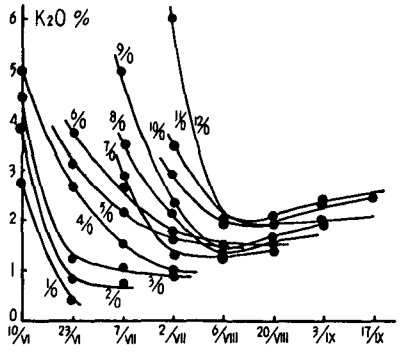


Fig. 10. Potassium content of each leaf at successive stages of growth.

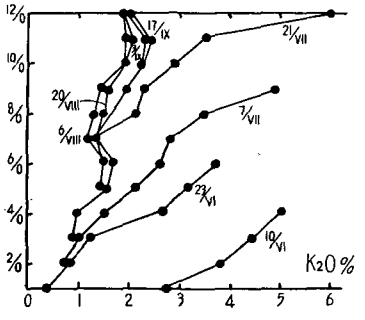


Fig. 11. Potassium content of leaves at various positions on main stem.

During the growth stages between the transplanting and the ear-initiation stage, the difference of potassium content among leaves diminishes. These tendency is almost the same as that for the nitrogen content.

The amount of potassium in each leaf at successive stages of growth was calculated and is given in table 9. Figure 12 shows the fluctuation curves of the amount of potassium in each leaf at successive stages of growth.

Potassium accumulates in a leaf in company with the growth of the leaf, reaches the maximum amount and then flows out from the leaf. The accumulation takes place in the lower leaf first and then in the upper leaf. This tendency is the same as the accumulation or effluxion of nitrogen and phosphorus.

TABLE 9. Amount of potassium in each leaf on main stem

(K_2O mg per leaf)

Name of leaf	Date of sampling							
	10/VI	23/VI	7/VII	21/VII	6/VIII	20/VIII	3/IX	17/IX
12/0				2.17	6.65	7.22	5.54	5.54
11/0				7.37	9.99	11.48	9.99	8.57
10/0				6.67	8.93	8.93	7.56	6.82
9/0			0.59	5.77	4.64	4.56	3.82	
8/0			3.37	3.65	2.77	2.74	2.70	
7/0			2.31	1.84	1.68	1.70		
6/0		0.45	1.67	1.52	1.02	1.09		
5/0		0.82	1.27	0.86	0.78			
4/0	0.40	0.70	0.50	0.29				
3/0	0.63	0.27	0.19	0.15				
2/0	0.23	0.07	0.07					
1/0	0.07	0.01						

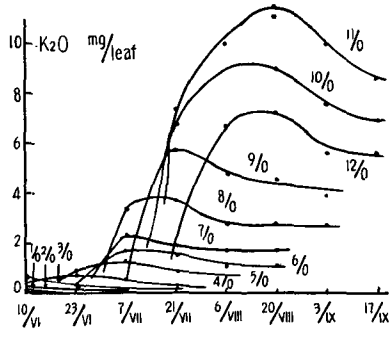


Fig. 12. Amount of potassium in each leaf at successive stages of growth.

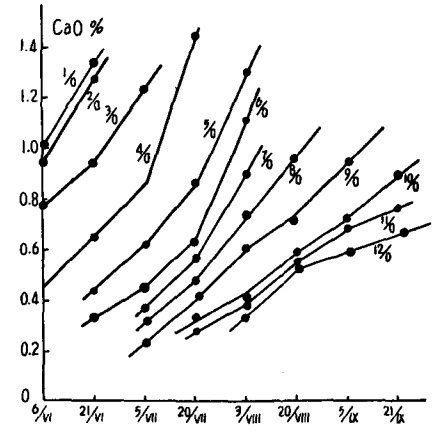


Fig. 13. Calcium content of each leaf at successive stages of growth.

Calcium: Determinations of the calcium content of leaves on the main stem at successive stages of growth were carried out in the year 1957. The results[44] are given in table 10. Figure 13 shows the fluctuation curves of the calcium content of each leaf during growth.

The fluctuation of the calcium content is greatly different from that of other elements which have been described above. The calcium content of a leaf

TABLE 10. Calcium content of each leaf on main stem

(CaO% on dry matter basis)

Name of leaf	Date of sampling							
	6/VI	21/VI	5/VII	21/VII	3/VIII	20/VIII	5/IX	21/IX
12/0					0.33	0.52	0.57	0.65
11/0				0.28	0.38	0.56	0.68	0.76
10/0				0.33	0.41	0.59	0.72	0.89
9/0			0.24	0.42	0.61	0.81	0.94	
8/0			0.32	0.48	0.74	0.95		
7/0			0.37	0.57	0.90			
6/0		0.33	0.45	0.63	1.11			
5/0		0.43	0.63	0.86	1.30			
4/0	0.45	0.65	0.87	1.45				
3/0	0.78	0.94	1.24					
2/0	0.95	1.28						
1/0	1.05	1.34						

rises from the beginning of growth and this rise continues until the death of the leaf. The calcium content of a leaf is highest when the leaf dries. This suggests that the accumulation of calcium is not related with metabolic activity. The rise of calcium content in company with the growth of the leaf is steeper in the case of the lower leaf than in the case of the upper leaf.

Generally speaking, at death, the upper leaf is lower in calcium content than the lower leaf. Namely, the calcium content of 1/0–5/0 is 1.2–1.4% when these leaves dry, that of 6/0–9/0 is about 1.0% and that of 10/0–12/0 is lower than 0.9%.

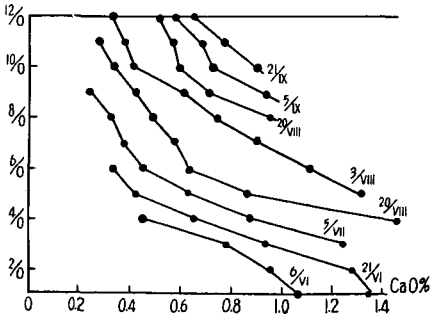


Fig. 14. Calcium content of leaves at various positions on main stem.

Figure 14 shows differences in calcium content among leaves on the main stem at various stages of growth.

At any stage of growth, the calcium content of the upper leaf is lower than that of the lower leaf. In other words, the older leaf is higher in calcium content than the younger leaf. This is quite reasonable because the calcium content of a leaf continues to rise with the growth of the leaf until its death

as described above.

The amounts of calcium in each leaf at successive stages of growth were calculated. The data[44] are given in table 11 and also in figure 15.

TABLE 11. Amount of calcium in each leaf on main stem

(CaO mg per leaf)

Name of leaf	Date of sampling							
	6/VI	21/VI	5/VII	20/VII	3/VIII	20/VIII	5/IX	21/IX
12/0					5.3	20.5	23.9	26.8
11/0				1.6	14.2	28.1	32.8	32.3
10/0				7.8	15.9	22.4	21.6	23.6
9/0			0.17	9.7	16.9	18.9	18.2	
8/0			2.00	8.4	12.4	12.9		
7/0			3.6	7.3	10.3			
6/0		0.77	3.9	5.5	8.0			
5/0		1.02	3.3	4.1	5.1			
4/0	0.27	1.91	2.61	3.2				
3/0	0.94	1.44	1.69					
2/0	0.91	0.69						
1/0	0.42	0.24						

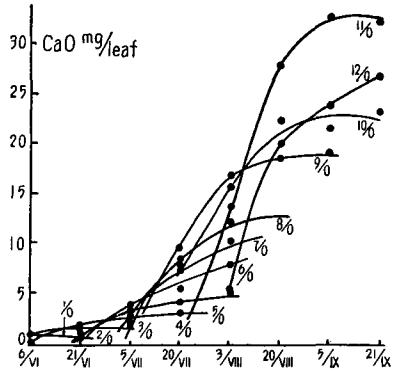


Fig. 15. Amount of calcium in each leaf at successive stages of growth.

The amount of calcium in a leaf continues to increase with the growth of the leaf. The increase continues even after the leaf has started to die at the tip. The calcium in a leaf reaches the maximum amount when the leaf dries completely. This suggests that calcium accumulates through the transpiration stream and it does not flow out after it is accumulated. The lack of mobility of foliar applied calcium has been reported.[45] Calcium accumulation seems to have no relation to the physiological activity of leaves.

Magnesium: Determinations of the magnesium content of leaves on the main stem at various stages of growth were carried out on the same samples on which calcium was determined. The results[44] are given in table 12.

TABLE 12. Magnesium content of each leaf on main stem

(MgO% on dry matter basis)

Name of leaf	Date of sampling							
	6/VI	21/VI	5/VII	20/VII	3/VIII	20/VIII	5/IX	21/IX
12/0					0.23	0.24	0.23	0.21
11/0				0.20	0.25	0.31	0.28	0.24
10/0				0.17	0.28	0.24	0.16	0.15
9/0			0.22	0.26	0.18	0.17	0.12	
8/0			0.23	0.29	0.17	0.15		
7/0			0.26	0.29	1.15			
6/0		0.29	0.30	0.25	0.15			
5/0		0.36	0.33	0.23	0.18			
4/0	0.47	0.35	0.30	0.20				
3/0	0.34	0.30	0.25					
2/0	0.34	0.21						
1/0	0.35	0.15						

Figure 16 shows the fluctuation curves of magnesium content of each leaf on the main stem during growth.

The magnesium content of 1/0 and 2/0 decreases very suddenly after transplanting. The content of 3/0–5/0 also drops continuously until the death of these leaves, although the slope is not so steep as for 1/0 and 2/0. In the cases of leaves whose position is higher than 6/0, the magnesium content goes up slowly at early stages of growth for some time, reaches the maximum, and then drops. The maximum magnesium content of each leaf is about the same, that is about 0.3%. The peak of the magnesium content ranges from the lower leaf to the upper leaf, successively.

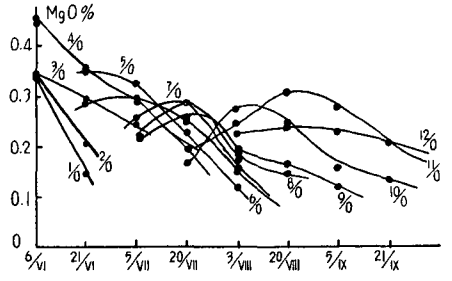


Fig. 16. Magnesium content of each leaf at successive stages of growth.

In figure 17, the differences of magnesium content among leaves on the main stem at various stages of growth are shown.

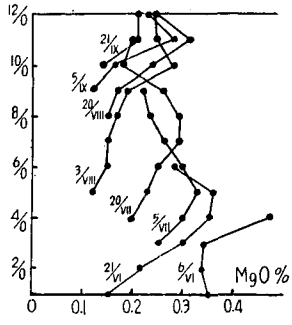


Fig. 17.
Magnesium content of leaves at various positions on main stem.

At transplanting, the higher the position of the leaf, the higher the magnesium conent. However, after this stage, the magnesium content of leaves at the middle position is highest and decreases in leaves above and below. This distribution of magnesium content among leaves on the main stem resembles the distribution of potassium content at later stages of growth.

The amount of magnesium in each leaf was calculated and the data[44] are given in table 13 and figure 18.

The magnesium in a leaf increases with the growth of the leaf. It reaches the maximum amount and then decreases. Accumulation and effluxion of magnesium takes place in the lower leaf first and then in the upper leaf similarly to that of nitrogen and phosphorus. This suggests that magnesium accumulation is related to the activity of the leaf. Magnesium which has been accumulated in the lower leaf flows out of the leaf and translocate into the upper leaf.

TABLE 13. Amount of magnesium in each leaf on main stem

(MgO mg per leaf)

Name of leaf	Date of sampling							
	6/VI	21/VI	5/VII	20/VII	3/VIII	20/VIII	5/IX	21/IX
12/0					3.75	9.48	9.66	8.65
11/0				1.16	9.35	15.56	11.26	8.93
10/0				4.03	10.89	9.12	4.80	3.98
9/0			0.16	6.03	8.99	3.96	2.45	
8/0			1.44	5.05	2.86	2.04		
7/0			2.53	3.71	1.71			
6/0		0.71	2.59	2.20	1.08			
5/0		1.11	1.73	1.10	0.58			
4/0	0.29	1.03	0.90	0.44				
3/0	0.41	0.46	0.34					
2/0	0.33	0.11						
1/0	0.14	0.03						

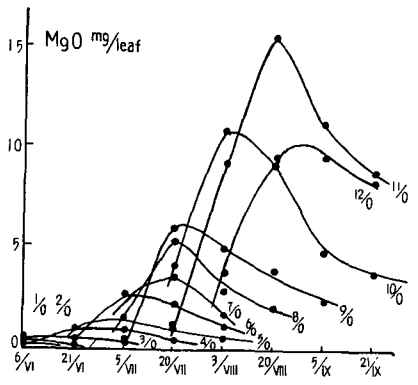


Fig. 18. Amount of magnesium in each leaf at successive stages of growth.

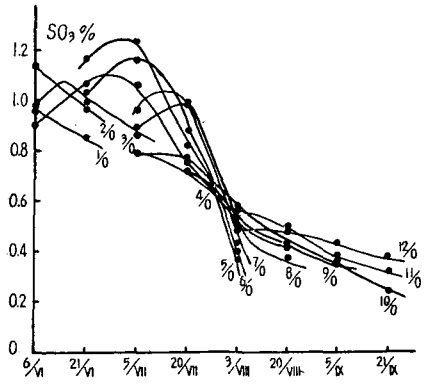


Fig. 19. Sulphur content of each leaf at successive stages of growth.

Sulphur: The sulphur content of each leaf was determined on the samples used for calcium and magnesium determinations and the data[44] are given in table 14.

Figure 19 shows the fluctuation curves of sulphur content of each leaf.

The sulphur content of 1/0 and 2/0 drops after transplanting until these leaves are dry. In the cases of 3/0-9/0, the sulphur content increases at an early stage of growth, reaches a maximum, and then starts to decrease. The

TABLE 14. Sulphur content of each leaf on main stem

(SO_3% on dry matter basis)

Name of leaf	Date of sampling							
	6/VI	21/VI	5/VII	20/VII	3/VIII	20/VIII	5/IX	21/IX
12/0					0.48	0.48	0.43	0.38
11/0				0.68	0.57	0.50	0.39	0.32
10/0				0.72	0.58	0.41	0.36	0.24
9/0			0.80	0.70	0.48	0.43	0.30	
8/0			0.89	0.99	0.48	0.38		
7/0			0.96	0.99	0.48			
6/0		1.03	1.16	0.86	0.42			
5/0		1.16	1.23	0.82	0.42			
4/0	0.90	1.06	1.06	0.75				
3/0	0.96	0.99	0.86					
2/0	1.13	0.96						
1/0	0.95	0.85						

maximum sulphur content of each leaf rises from 3/0 to 5/0 and after 5/0, the maximum goes down. There is no increase in the sulphur content associated with the growth in the leaves in the cases of 10/0–12/0. In the cases of these upper leaves, the sulphur content continues to decrease from the beginning of growth until the death of the leaf. The sulphur content at death is higher in the case of the lower leaf than in the case of the upper leaf. The fluctuation of the sulphur content is more or less the same as that of the nitrogen content. The behavior of sulphur closely resembles to that of nitrogen.

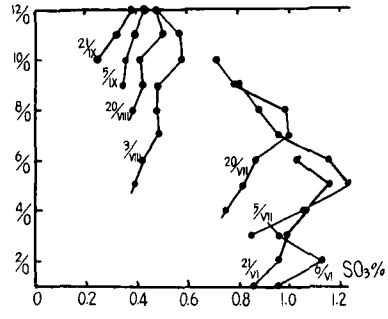


Fig. 20. Sulphur content of leaves at various positions on main stem.

In figure 20, the differences of sulphur content among leaves on the main stem at various stages of growth are shown.

Until the ear-initiation stage, on July 20, the sulphur content of the leaf at the middle position is highest, and after this stage, the difference in sulphur content among leaves becomes smaller. Generally, the sulphur content of the upper leaf is slightly higher than that of the lower leaf.

The amount of sulphur in each leaf at successive stages of growth was calculated and are given in table 15 and figure 21.

TABLE 15. Amount of sulphur in each leaf on main stem

(SO_3 mg per leaf)

Name of leaf	Date of sampling							
	6/VI	21/VI	5/VII	20/VII	3/VIII	20/VIII	5/IX	21/IX
12/0					7.8	14.0	18.0	15.7
11/0					21.3	25.1	18.8	13.6
10/0				17.0	22.6	15.6	10.8	6.4
9/0			0.57	18.3	13.3	10.0	6.0	
8/0			5.57	17.2	8.06	5.17		
7/0			9.35	12.7	5.47			
6/0		2.49	10.02	7.57	3.02			
5/0		3.58	6.45	3.94	1.64			
4/0	0.56	3.12	3.18	1.65				
3/0	1.16	1.51	1.17					
2/0	1.08	0.52						
1/0	0.38	0.15						

Similarly to nitrogen, phosphorus or magnesium, sulphur accumulates in a leaf during the growth, reaches the maximum and then decreases. Accumulation of sulphur seems to be related to metabolic activity. It is clear from these data that sulphur translocates from the older leaf to the younger leaf. Translocation of sulphur from one leaf to other leaves has also been described by several authors.[46][47]

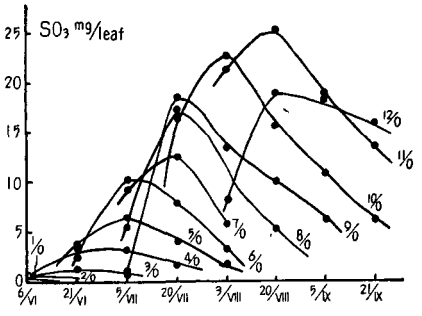


Fig. 21. Amount of sulphur in each leaf at successive stages of growth.

Translocation quotient of elements: Using the dry weight method described on page 16, the translocation quotients of elements of each leaf were calculated[43][44] and are given in table 16 and also in figure 22.

The translocation quotient of nitrogen differs according to the position of leaves. In the cases of 3/0–5/0, it is about 50%, in the cases of 6/0–8/0, it is about 70%, and in the cases of 9/0–12/0, it is as high as 75%. The quotient of 1/0 and 2/0, which are formed during seedling stages, is large. This may be due to the withering of these leaves after transplanting. However, except for these two leaves, the higher the position of leaf, the larger the

TABLE 16. Translocation quotient of elements

Name of leaf	Nitrogen	Phosphorus	Potassium	Calcium	Magnesium	Sulphur
12/0	74	68	23	0	10	17
11/0	77	91	25	0	43	46
10/0	77	93	24	0	63	72
9/0	77	90	24	0	59	67
8/0	71	85	26	0	60	70
7/0	71	82	26	0	54	57
6/0	70	77	35	0	58	70
5/0	61	38	39	0	66	74
4/0	40	33	58	0	57	48
3/0	51	93	76	0	17	23
2/0	60	97	74	31	66	52
1/0	75	100	86	43	79	61
Average	67	79	40	6	53	55

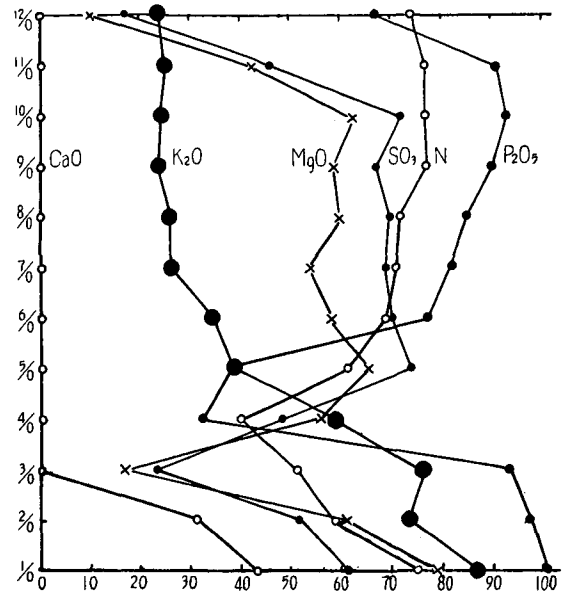


Fig. 22. Translocation quotient of elements.

quotient. In the case of 3/0, when the leaf died the nitrogen amount was one half of the maximum nitrogen amount in the leaf. On the other hand, 9/0–12/0 maintained their activity even when the nitrogen in these leaves decreased to about 20% of the maximum.

The translocation quotient of phosphorus shows almost the same tendency to that of nitrogen. The quotient is very large in the cases of lower leaves, 1/0–3/0. That of 4/0 and 5/0 is small. From 6/0, the higher the position, the larger the quotient, except for the flag leaf.

The quotient for sulphur shows almost the same tendency as that of nitrogen or phosphorus. However, the quotient of 11/0 and 12/0 is extremely small.

The quotient of potassium continues to become smaller from lower to upper leaf.

The quotient of calcium is zero except for 1/0 and 2/0. The 1/0 and 2/0 die and wither rapidly after transplanting, with the results calcium seems to flow from these leaves to the outside of the plant body.

The quotient of magnesium is larger than that of potassium, but is smaller than that of nitrogen, phosphorus or sulphur.

The translocation quotient shows the possibility of the translocation of elements after accumulation from one organ to other organs. This type of

translocation is generally called redistribution. This quotient becomes larger or smaller according to the conditions of the element supply to the plant as will be discussed later. The quotient of an element of each leaf differs according to the position of the leaf. This is partly due to a change of conditions of element supply in the soil during growth processes and partly due to differences of the physiological character of leaves at various positions.

Generally speaking, the translocation quotient of those elements which are constituents of protein, i. e. nitrogen, phosphorus and sulphur, is large and the quotient of phosphorus is the largest. The quotient of magnesium is somewhat smaller than that of nitrogen or sulphur, but larger than that of potassium. The quotient of potassium is smaller than that of the other elements and that of calcium is the smallest.

BUKOVAC et al.[47] classified elements into three groups by their mobility, i. e. mobile, partially mobile and immobile, by using radio-active tracers. Their classification is more or less in agreement with the results obtained here. However, they stated that potassium is more mobile than phosphorus. This difference may be due to the reason that the rice plants on which the quotients were estimated were receiving a sufficient potassium supply.

Increase and decrease of carbohydrates

Sugar: Carbohydrate analyses were made, i. e. total sugar, starch and hemicellulose, of leaves on the main stem at successive stages of growth. The

TABLE 17. Total sugar content of each leaf at successive stages of growth

(% on dry matter basis as glucose)

Name of leaf	Date of sampling							
	6/VI	21/VI	5/VII	20/VII	3/VIII	20/VIII	5/IX	21/IX
12/0					6.9	3.9	2.4	2.0
11/0				5.3	5.4	3.6	2.1	1.1
10/0				6.8	3.6	3.5	1.6	trace
9/0			3.5	8.5	3.3	1.5	0.6	
8/0			4.0	9.0	2.4	0.8		
7/0		3.0	5.6	7.8	1.9			
6/0		3.8	5.9	7.0	1.3			
5/0		4.5	5.0	3.0	1.0			
4/0	3.4	5.8	3.8	1.5				
3/0	4.4	2.5	2.0					
2/0	3.8	1.7						
1/0	1.9	0.6						

same samples were used for calcium, magnesium and sulphur, in the year 1957.[48]

Data of total sugar content are given in table 17 and figure 23.

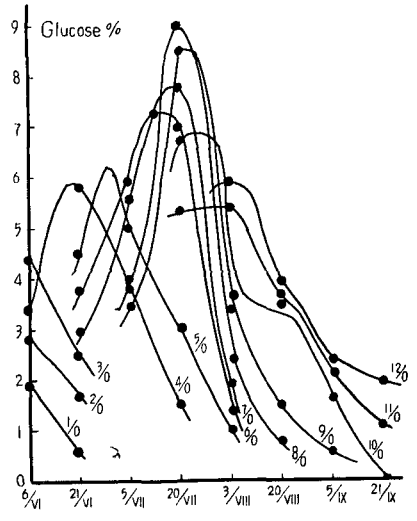


Fig. 23. Sugar content of each leaf at successive stages of growth.

In the cases of 1/0–3/0, the sugar content decreases after transplanting. However, with the other leaves, the sugar content increases with the growth of each leaf, reaches the maximum and then drops. The maximum sugar content of leaves differs according to the position of the leaves.

In the cases of 4/0 and 5/0, the maximum sugar content is about 6%. The time when the sugar content reaches a maximum comes in the sequence of the position. The maximum increases from 6/0 to 8/0, and reaches as high as 9% in the case of 8/0. The maximum of 9/0 is a little lower than that of 8/0. The maxima of 6/0–9/0 are clearly higher than those of the other leaves. The time when the sugar content of those leaves reaches the maximum comes almost

TABLE 18. Starch content of each leaf at successive stages of growth

(% on dry matter basis as glucose)

Name of leaf	Date of sampling							
	6/VI	21/VI	5/VII	20/VII	3/VIII	20/VIII	5/IX	21/IX
12/0					14.3	11.3	2.7	5.0
11/0				11.3	14.8	18.0	4.8	1.5
10/0				13.8	17.2	15.5	4.0	1.0
9/0			7.8	15.0	18.3	13.3	3.5	
8/0			9.8	14.8	16.3	12.9		
7/0		5.2	11.2	16.0	16.0			
6/0		5.7	13.2	14.3	13.1			
5/0		7.2	14.6	12.5	12.1			
4/0	5.3	10.5	13.8	11.8				
3/0	7.7	13.3	11.8					
2/0	6.0	5.8						
1/0	5.3	3.7						

simultaneously with the ear-initiation stage, and when the development of ear-primordium and elongation of stem begin, the sugar content of these leaves starts to decrease. The maximum sugar contents of the leaves, 10/0–12/0, are lower than those of 6/0–9/0.

Starch: Data of the starch content are given in table 18 and figure 24.

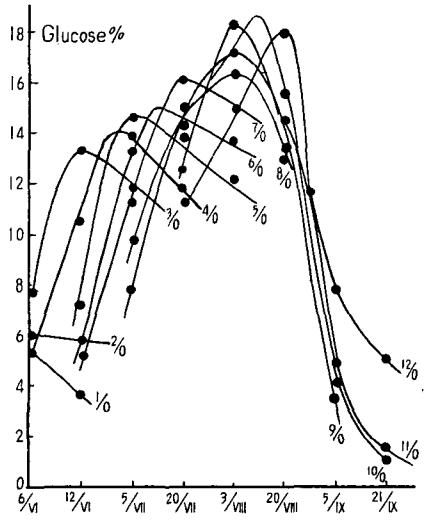


Fig. 24. Starch content of each leaf at successive stages of growth.

The starch content of a leaf increases with the growth of the leaf. It reaches the maximum and then decreases with the ageing of the leaf. The higher the position of a leaf, the higher is the maximum starch content. The maximum starch content of each leaf comes in the sequence of the position of leaves. In the cases of 3/0–8/0, the starch content at death of these leaves is rather high, usually above 10%. However, in the cases of 9/0–12/0, the starch content at death is very low. The content of these leaves remains high until the flowering stage and then decreases very suddenly. These facts suggest that starch, which is stored in these leaves until the flowering, is related to maturing and is translocated from these leaves into ear with ripening.

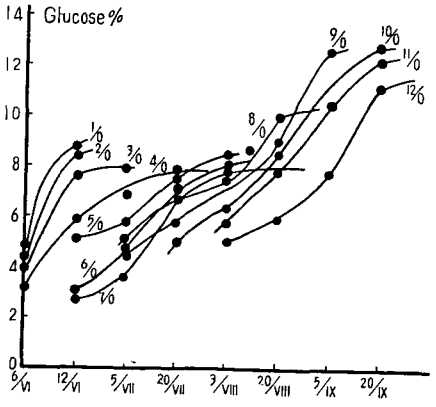


Fig. 25. Hemicellulose content of each leaf at successive stages of growth.

Hemicellulose: Data of hemicellulose are given in table 19 and figure 25.

The behavior of hemicellulose is different from that of sugar or starch. The hemicellulose content of a leaf continues to increase until death of the leaf when it reaches a maximum. The hemicellulose content at death of 1/0–7/0 is between 8–9%. There is little difference in the content among these leaves. However, in the cases of leaves on the position higher than 7/0, the content at death is higher than that of the lower leaves. The hemicellulose content of 9/0–12/0 at their death is about 12%.

TABLE 19. Hemicellulose content of each leaf at successive stages of growth
(% on dry matter basis as glucose)

Name of leaf	Date of sampling							
	6/VI	12/VI	5/VII	20/VII	3/VIII	20/VIII	5/IX	21/IX
12/0					5.0	5.8	7.7	11.1
11/0				3.7	5.8	7.8	10.5	12.2
10/0				5.0	6.3	8.5	11.5	12.8
9/0			3.5	5.8	7.3	10.5	12.6	
8/0			4.0	7.0	7.5	10.0		
7/0		2.8	4.4	6.8	7.9			
6/0		3.0	4.8	7.2	8.1			
5/0		5.1	5.7	7.4	8.5			
4/0	3.1	5.9	6.3	7.9				
3/0	4.0	7.7	7.9					
2/0	4.4	8.5						
1/0	4.8	8.8						

The fact that the hemicellulose content reaches a maximum at death suggests that hemicellulose is a component of the cell-wall which can not be utilized again after it has been deposited.

Sequence of accumulation of leaf components

In the foregoing discussions, it was clearly shown that the accumulation processes of elements are different. For example, phosphorus accumulates in a leaf at the early stages of leaf growth and then flows out of the leaf at later stages of growth. However, calcium accumulation continues until the death of the leaf. To get exact knowledge on accumulation processes of each element and also to have ideas about the mechanism of element accumulation, the growth process of 11/0 is cited for an example. The accumulation process of each element in 11/0 is summarized in figure 26. In this figure, the relative amount of each element is shown at successive stages of growth on the basis of the maximum amount of respective elements in the leaf. Since nitrogen, phosphorus and potassium were determined on plants grown in the year 1952 and calcium, magnesium and sulphur on plants grown in the year 1957, it may be difficult to compare the accumulation processes of all these elements because of possible differences in growing conditions. However, for comparison of this element accumulation, these data are presented in figure 26.

From this figure, it can be stated that the accumulation of elements in 11/0 takes place in the following order; nitrogen, sulphur, phosphorus, potassium,

(dry matter), magnesium and calcium. This order is not always the same. It differs from leaf to leaf to some extent. Generally speaking, the following order exists; (phosphorus, nitrogen, sulphur) (potassium) (magnesium, dry matter) (calcium).

Nitrogen, phosphorus and sulphur are the constituent elements of protein, so these elements accumulate at early stages of growth. Among these three elements, phosphorus is an important component of the cell nucleus. Generally, the accumulation of this element takes place at the earliest stage. These three

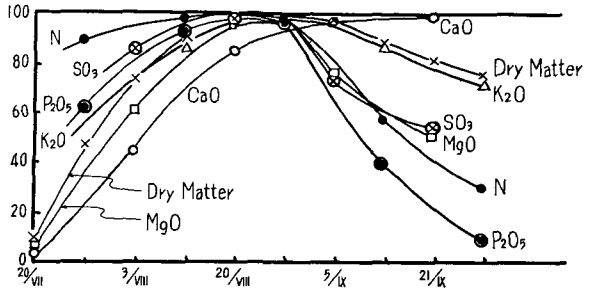


Fig. 26. Accumulation processes of elements in 11/0.

elements start to efflux before the leaf reaches maximum dry weight. Phosphorus starts to flow out first. The accumulation of these elements is rapid when the leaf is very young and is active physiologically. This suggests that the accumulation of these elements is related to metabolic activity. On the contrary, the accumulation of calcium is not so active as other elements at early stages of growth, but it continues to be active until late stages of growth when physiological activity of the leaf becomes weak. This suggests that the accumulation of calcium is not related to metabolic activity. The behavior of potassium and of magnesium is intermediate between the phosphorus group and calcium.

The accumulation of elements is related to metabolic activity. The elements which accumulate at early stages of growth are more intimately related to metabolism than those which accumulate at later stages of growth. MITSUI et al [49] reported that element uptake through the roots is inhibited by inhibitors of aerobic respiration, such as H_2S, NaCN, NaN_3, etc. The inhibition is more serious from the left to the right in the following order; P_2O_5, K_2O, SiO_2, NH_4-N, MnO, H_2O, MgO, CaO. TAKAHASHI et al.[50] also proposed this type of order by studying the effects of temperature on element uptake. Uptake of some elements by the root requires energy which is obtained by aerobic respiration. This type of element uptake is called "metabolic absorption".[51] Since H_2S is an inhibitor of aerobic respiration and respiration is retarded by low

temperature, these orders show the degree of relation between element uptake and aerobic respiration. The order which was proposed by MITSUI et al. and TAKAHASHI et al. is almost the same as the sequence of element accumulation in the leaf which is described above.

The above discussions suggest that the mechanism which governs accumulation of elements in the leaf seems to be very similar to the mechanism of the metabolic absorption.

To make clear the sequence of carbohydrate accumulation, figure 27 was prepared, in which the vertical axis shows the position of the leaves and the horizontal axis shows the content of carbohydrates of each leaf on July 5.

The sugar content increases from 9/0 to 6/0, taking the maximum value at 6/0 and then going down from 6/0 to 3/0. The starch content reaches its

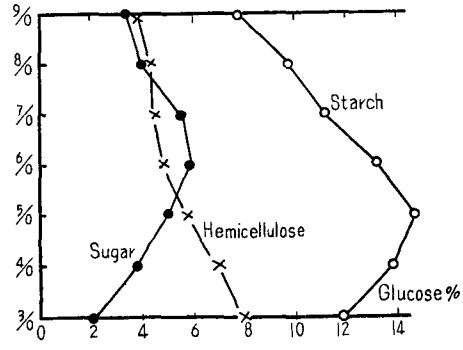


Fig. 27. Content of carbohydrates of various leaves on main stem on July 5.

maximum at 5/0. It decreases at both ends of the scale. The content of hemicellulose is lowest in the top leaf and increases until the lowest leaf. The maximum contents of sugar, starch and hemicellulose are reached at 6/0, 5/0 and 3/0, respectively. The position of the leaf where the maximum percentage is found is higher in the following sequence; sugar, starch and hemicellulose. The higher the position of a leaf, the younger the leaf. So, it can be said that with the growth of a leaf, sugar accumulates first, starch accumulates next and hemicellulose accumulates last. Judging from the accumulation process of elements, it was pointed out that protein accumulates at the earliest stage.

Growth of a leaf starts with accumulation of protein. By means of the protein thus accumulated, the leaf expands and performs carbon-assimilation. With these products, accumulation of sugar and starch takes place. Besides accumulation of protein, sugar and starch, accumulation of hemicellulose is going on from the beginning of growth. After some stage of growth, constituents

of the leaf start to efflux from the leaf except for cell-wall substances, such as cellulose and hemicellulose, which continue to increase until the death.

OOTA[52] distinguished two patterns in the growth of tissue, namely, the accumulation of protoplasmic protein or the PP-pattern, and the accumulation of cell-wall substances or the CW-pattern. It was pointed out that at early stages of growth, both the PP-pattern and the CW-pattern take place, but at later stages of growth, only the CW-pattern goes on. He did not consider storage substances. However, the leaf stores substances for later growth. If the storage substances are taken into consideration, the growth process of the leaf can be classified into the following four phases. The first phase is formation of protoplasmic substances, the second phase is accumulation of storage substances, the third phase is effluxion of storage substances and the fourth phase is decomposition of protoplasm. Cell-wall substances are accumulated from the first phase until the third phase.

CHARACTERISTICS OF LEAVES

Morphological characters of leaves

To characterize the shape of leaves on the main stem, observations were made on the length of leaf-blade and leaf-sheath in the year 1952.

Table 20 shows the length of leaf-blade and leaf-sheath and also the ratio of length of leaf-blade to that of leaf-sheath.

TABLE 20. Length of leaf-blade and leaf-sheath (cm)

Name of leaf	1/0	2/0	3/0	4/0	5/0	6/0	7/0	8/0	9/0	10/0	11/0	12/0
Leaf-blade (a)	1.9	6	9	10	12	17	23	31	34	42	40	29
Leaf-sheath (b)	3.0	5.0	8	8	9	10	13	16	19	22	27	32
a/b	0.6	1.1	1.1	1.2	1.3	1.7	1.8	1.9	1.8	1.9	1.5	0.9

The length of leaf-blade increases from 1/0 to 10/0. After 10/0, it decreases. The length of leaf-blade reflects the environmental conditions under which the leaf was elongated as will be discussed later. However, it can be stated that generally the length of leaf-blade increases progressively from a lower leaf to an upper leaf until a certain position at which it starts to decrease. On the other hand, the length of leaf-sheath continues to increase from 1/0 to 12/0, the flag leaf.

The ratio of length of leaf-blade to that of leaf-sheath is smaller in the cases of 1/0 to 5/0. The ratios of the leaves between 6/0 and 10/0 are greater than those of the leaves in the other positions. After 10/0, the ratio becomes

smaller if the position goes up.

The physiological functions of the leaf-blade and the leaf-sheath differ completely from each other; the leaf-blade being the organ where photosynthesis takes place, but the leaf-sheath being the organ in which products of photosynthesis translocate or are stored. The ratio of leaf-blade length to leaf-sheath length varies according to the positions. This suggests that there are differences in physiological functions among leaves.

In the year 1957, more detailed observations on morphological characteristics of leaf-blades were conducted. The results are given in table 21 and figure 28.

TABLE 21. Morphological characteristics of leaf-blade of leaves on main stem

Name of leaf	Length (cm) a	Breadth (cm) b	a/b	Area (cm^2)	Weight (g)	Weight per unit area (mg/cm^2)
12/0	29.3	0.84	348	24.6	0.420	17.1
11/0	41.0	0.79	518	32.4	0.512	15.8
10/0	35.3	0.72	490	25.4	0.401	15.8
9/0	28.7	0.69	416	19.8	0.277	14.0
8/0	25.7	0.64	401	15.2	0.174	11.6
7/0	21.6	0.57	379	12.4	0.128	10.3
6/0	18.8	0.52	361	9.78	0.086	8.79
5/0	13.3	0.48	277	6.38	0.0524	8.21
4/0	10.2	0.45	227	4.59	0.0360	7.84
3/0	7.6	0.34	223	2.74	0.0153	5.58
2/0	6.0	0.26	223	1.43	0.0096	6.71
1/0	2.4	0.17	141	0.41	0.0040	9.75

This year, the leaf-blade of 11/0 is the longest. However, the general tendency of leaf-blade length is more or less the same as that observed in the year 1952. The breadth of leaf-blade continues to increase from the lower leaf up to the flag leaf. Ratio of length to breadth becomes greater from 1/0 to 11/0, meaning that the upper leaf is more slender. However, the flag leaf is rather round. The area and weight increase also from 1/0 to 11/0 and those of 12/0 are smaller than those of 11/0. This tendency is just the same as the length of leaf-blade. Weight per unit area which shows the thickness was calculated by dividing the weight by the area. The results are also given in table 22. The thickness of the leaf increases from the lower to the upper leaf until the flag leaf is reached.

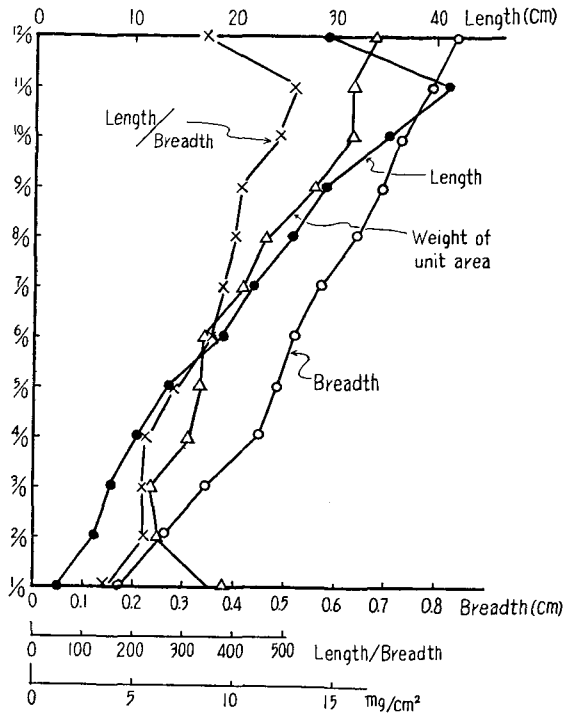


Fig. 28. Morphological characteristics of leaf-blade.

These data show that each leaf has morphological characteristics according to the position on the stem. This suggests that each leaf has certain physiological characteristics and functions corresponding to its position on the stem.

Characteristics of physiological conditions

The morphological observations suggest that each leaf seems to have physiological characteristics according to its position on the stem.

To characterize this, a comparison between the lower leaves and the upper leaves was made. The 4/0 and 11/0 were taken as representatives of the lower leaves and the upper leaves, respectively. Since the leaf-blade and the leaf-sheath differ, these organs were treated separately.

In the year 1953, the growth process of 4/0 and 11/0 were studied.[53] Table 22 and figure 29 shows the growth process of these leaves.

The leaf-blade of 4/0 elongates with elongation of the leaf-sheath of 3/0 and it stops elongation after completion of 3/0. The leaf-sheath of 4/0 starts to elongate after its leaf-blade finishes elongation. The weight of leaf-blade and leaf-sheath increases as they grow longer and even after the morphological

enlargement ends. The weight of these organs decreases very slightly after reaching the maximum.

TABLE 22. Length, weight and nitrogen content of 4/0 and 11/0 at successive stages of growth

4/0

Date of sampling		4/VI	9/VI	16/VI	22/VI	26/VI	30/VI	7/VII	14/VII	21/VII
Length (cm)	blade	4.2	10.5	11.7	12.8	12.5	12.8	12.5	12.4	12.4
	sheath			3.9	7.3	7.7	7.9	8.0	7.9	8.0
Dry weight (mg/leaf)	blade	1.17	5.07	10.5	15.0	17.0	18.2	20.5	20.0	19.2
	sheath			3.2	11.5	15.0	18.6	22.8	23.4	21.4
Dry matter %	blade	16.8	18.2	25.6	32.4	33.0	34.7	35.7	35.8	40.3
	sheath			12.8	18.6	18.6	20.6	25.9	23.0	24.0
Nitrogen content(N%)	blade	6.10	5.00	3.87	3.55	3.61	3.96	3.30	2.49	2.20
	sheath			4.04	1.93	1.62	1.36	1.24	1.24	1.00

11/0

Date of sampling		26/VII	1/VIII	7/VIII	15/VIII	21/VIII	26/VIII	2/IX	15/IX
Length (cm)	blade	17.5	31.8	31.6	32.0	32.0	32.0	32.0	32.0
	sheath	1.2	12.4	26.6	26.8	27.0	27.0	27.0	27.0
Dry weigth (mg/leaf)	blade	19.5	104	156	202	228	203	160	145
	sheath		54	210	293	337	329	250	220
Dry matter %	blade	14.2	27.3	31.8	36.9	40.0	43.2	45.3	48.0
	sheath		15.5	17.7	31.0	35.0	36.0	36.5	37.8
Nitrogen content (N%)	blade	7.15	2.34	2.09	2.49	2.61	2.30	1.75	1.02
	sheath		1.70	1.06	0.84	0.89	0.81	0.77	0.56

The growth process of 11/0 shows more or less the same pattern to that of 4/0. However, some differences can be pointed out. In the case of 4/0, the weight of leaf-blade and that of leaf-sheath are almost the same, but in the case of 11/0, the leaf-sheath is far heavier than the leaf-blade. Another great difference is that for 4/0, the decrease of weight after attaining the maximum is very slight, but in the case of 11/0, the decrease is remarkable. Since the leaf-sheath is considered to have some function as a reservoir and greater decrease of weight suggests greater effluxion of reserved materials, it is evident that 11/0 has more importance as a reserving organ than 4/0.

Generally speaking, the dry matter percentage of 11/0 is higher than that of 4/0 as is shown in table 22.

In figure 30, the nitrogen content of leaf-blade and leaf-sheath at successive stages of growth of 4/0 and 11/0 is shown.

The nitrogen content of the leaf-blade goes down quickly as it grows, reaches the minimum, and then goes up again for some period. After reaching

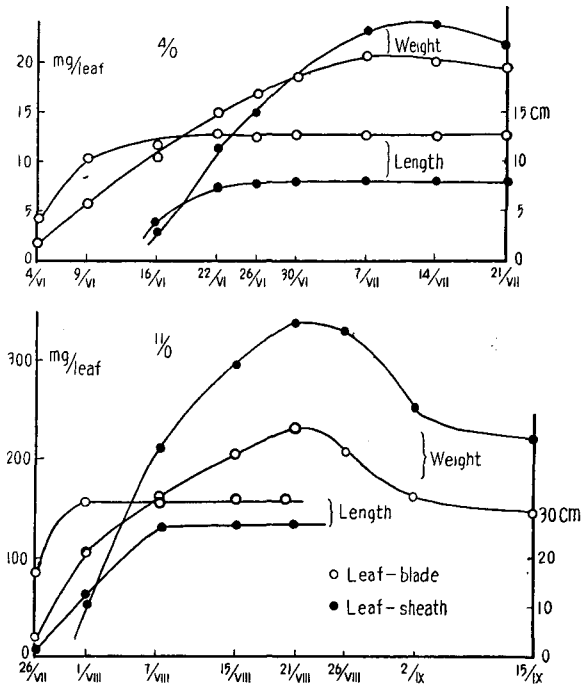


Fig. 29. *Growth process of 4/0 and 11/0.*

the second maximum, it starts to drop again. The time when the minimum nitrogen content is reached is at the end of morphological elongation. Until this stage, the leaf seems to be receiving substances from lower leaves. After reaching the minimum nitrogen content, the dry weight and also the nitrogen content increase. At this phase of growth the leaf seems to discharge its characteristic functions by its own physiological activities. This increase of nitrogen content is more remarkable in the case of 11/0 than in the case of 4/0, suggesting that 11/0 has more capacity to store nitrogen within the leaf-blade. The nitrogen content of leaf-sheath continues to decrease from the beginning to the end of its growth.

On the basis of above discussions, it can be stated that a leaf discharges its characteristic functions most actively at the growth stage when nitrogen content of the leaf reaches its second maximum. The maximum value of 4/0 is about 3.5%, whereas that of 11/0 is 2.0%. It may be said that 4/0 performs its characteristic functions under high nitrogen content, while 11/0 performs its characteristic functions under rather low nitrogen content.

From figure 4 and 7, the contents of nitrogen and phosphorus of each leaf

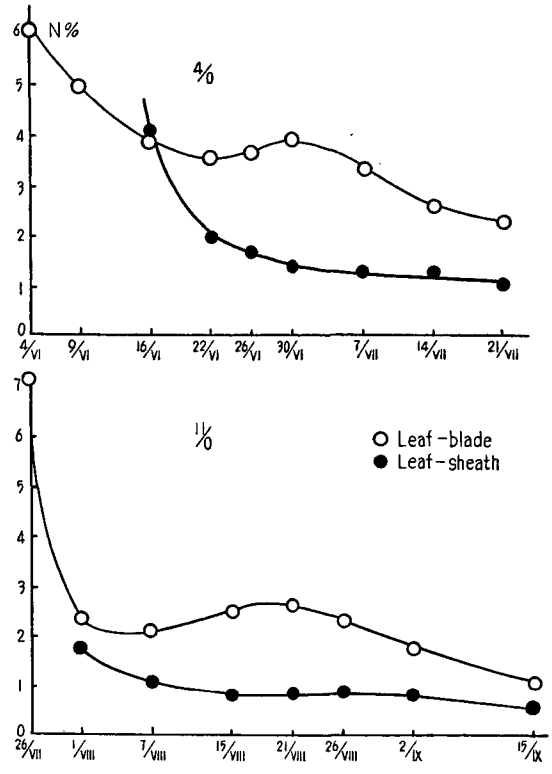


Fig. 30. Fluctuation of nitrogen content of 4/0 and 11/0.

at the time when the leaf discharges its characteristic functions were estimated approximately and these contents are shown in figure 31.

The content of nitrogen and phosphorus of 1/0 and 2/0 continues to go down after transplanting until the death, so these leaves do not have as great a nitrogen and phosphorus content as that described above for either 4/0 or 11/0. In the cases of lower leaves, 4/0–7/0, these leaves discharge their characteristic functions under high nitrogen and low phosphorus conditions. On the other hand, in the cases of upper leaves, 10/0–12/0, these leaves discharge their characteristic functions under high phosphorus and low nitrogen conditions. The leaves, 8/0 and 9/0, are transitional between these two

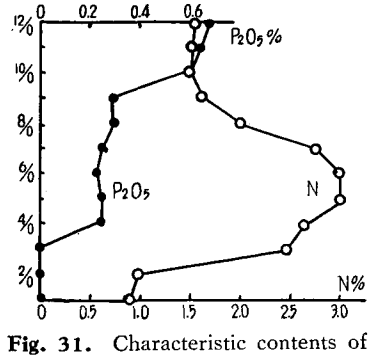


Fig. 31. Characteristic contents of nitrogen and phosphorus of leaves at functioning.

groups.

On the other hand, regarding carbohydrate metabolism, the leaves on the main stem can be classified into three groups, on the basis of figure 23 and 24, that is:

3/0–5/0: The accumulation of sugar and starch in these leaves takes place in sequence from lower leaf to upper leaf. The maximum percentage of sugar and starch of these leaves is lower than that of leaves in a higher position.

6/0–9/0: Sugar and starch accumulate in these leaves with growth. The maximum amount of sugar is attained at the ear-initiation stage. The maximum sugar percentage of these leaves is higher than that of other leaves.

10/0–12/0: Amount of starch in these leaves reaches its maximum at the time of flowering, after which it decreases. The maximum percentage of starch of these leaves is higher than that of lower leaves.

To characterize the physiological conditions of lower leaves and upper leaves, the activity of some enzymes which are related to carbohydrate metabolism is estimated at 35°C by using leaf-blades of 4/0 and 11/0 just after their expansion. The results are given in table 23.

Catalase activity of 11/0 is stronger than that of 4/0. Activities of phosphorylase and phosphatase are also stronger in 11/0 than in 4/0. Amylase and invertase are more active in the case of 4/0 than in the case of 11/0.

Generally, lower leaves are stronger in hydrolitic enzymes and upper leaves are stronger in condensation enzymes.

TABLE 23. Activity of several enzymes in 4/0 and 11/0

Name of leaf		4/0	11/0
Catalase	1)	8.8	25.15
Phosphorylase	2)	0.20	0.35
Phosphatase	3)	0.31	0.99
Amylase	4)	2.2	2.0
Invertase	5)	5.8	3.8

1) Volume (ml) of O_2 evolved from 3% H_2O_2 by 2 ml leaf sap.[a)]

2) 3) mg of phosphorus (P_2O_5) released from 0.1 M cori-ester or 1% glycerophosphate by 0.5 ml leaf sap.[b)]

4) 5) Volume of N/100 $KMnO_4$ equivalent to the reducing power of sugar released from 1% starch or 1% sucrose by 5 ml leaf sap.[a)]

a) 2 g of fresh sample is mashed with 10 ml pH 6.8, 1.25 M phosphate buffer solution and made up to 100 ml.

b) 10 g of fresh sample is mashed with 30 ml H_2O and pressed through cheese cloth.

ISHIZUKA and the author,[16] pointed out that at early stages of growth of rice plants, protein synthesis is the main feature of physiological functions and at later stages, accumulation of carbohydrates is the main character. FUJIWARA et al.[14] distinguished two phases of growth, i.e. the early stage is the nitrogen phase and the later stage is the carbon phase.

The results obtained here suggest that lower leaves which are formed during early stages of growth, discharge their functions under high nitrogen and low sugar conditions. On the other hand, upper leaves which are formed at later stages of growth discharge their functions under low nitrogen and high carbohydrate conditions.

The protein synthesis at early stages of growth is related to the high nitrogen and low carbohydrate content and also the strong activity of hydrolytic enzymes of lower leaves. However, the accumulation of carbohydrate at later stages of growth is related to the low nitrogen and high starch content and also to the strong activity of condensation enzymes in the upper leaves.

The physiological conditions which characterize each leaf are quite similar to the characteristic conditions of the rice plant at the growth stage under which these leaves are formed.

Characteristics of functions

In the previous sections, it was pointed out that each leaf has morphological and physiological characteristics according to its position. These findings suggest that each leaf has characteristic functions.

To study the predominant functions of each leaf in the whole plant which understandably is constructed from these leaves, an experiment was conducted in the year 1952. In this experiment, the leaf-blades at various positions were cut off at various stages of growth, and observations of the influence of this cutting were made on the rice plant at harvest, especially on the yield components.

Table 24 shows an outline of the growth process of the rice plants on which the experiment was conducted.

Figure 32 is the experimental scheme which shows conditions of leaves on the main stem and also positions of leaves which were cut off at each treatment. The leaves of the tillers were also cut off in the same way as those on the main stem. The conditions of leaves on the tillers were more or less the same as the respective synchronous leaves on the main stem as shown in figure 1.

Name of treatments in figure 32 suggest date and degree of cutting. For example, the treatment III-II means that the leaves which were existing at the growth stage II were cut off at the growth stage III. Number I, II, III, IV,

TABLE 24. Outline of growth

No.	Date	Stage of growth
I	June 10	Transplanting
II	23	Establishing
III	July 7	Tillering
IV	21	Ear-initiation
V	Aug. 6	Elongation
VI	20	Flowering
VII	Sept. 3	Milky stage
VIII	17	Maturing

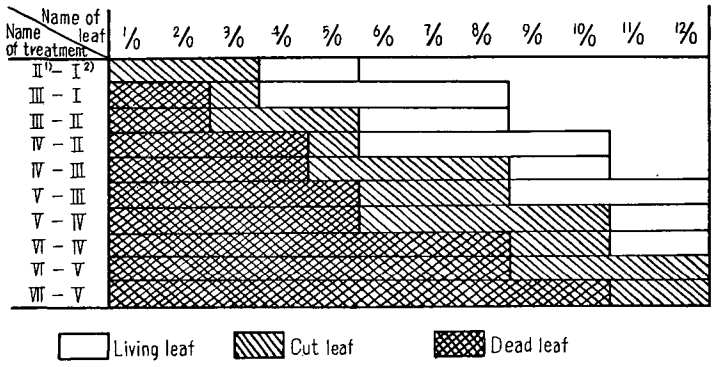


Fig. 32. Diagram of developmental condition of leaves on main stem at each treatment and of position of cut leaves.
Column 1) shows the time of treatments.
Column 2) shows the time when treated leaves developed.
The numbers in these columns correspond to the numbers which suggest the growth stages in table 24.

V, VI and VII suggest growth stages of transplanting, establishing, tillering, ear-initiation, elongation, flowering, and milky stage, respectively.

The rice plants which received these treatments were harvested after maturing and observations were made on the effects of such treatments on the top-length, weight of ear, weight of straw, number of tillers, number of ears per plant, number of grains per ear and 1000 grain weight. The data[54] of these observations are given in table 25.

The data of the dry weight of ear and straw are shown in figure 33.

The weight of ear as well as straw of the treatment II–I is very small, suggesting the importance of the leaves formed in the nursery bed for establishment. The weight of ear and straw of the treatment III–I is almost the same

TABLE 25. Effects of leaf cutting on rice plants at harvest

Treatment	Top-length (cm)	Number of ears	Dry weight (g/plant) Straw	Ear	Weight of one ear (g)	Number of grains per ear	Weight of 1000 grain (g)
II–I	104	13.3	21.3	22.7	1.70	69	23.3
III–I	110	14.7	26.0	28.3	1.93	70	23.8
III–II	110	13.3	25.7	26.8	2.02	74	25.2
IV–II	110	14.0	24.7	26.5	1.89	70	23.9
IV–III	105	12.3	24.0	25.3	2.05	74	24.3
V–III	104	15.3	24.7	24.5	1.68	60	23.6
V–IV	99	15.7	24.2	24.0	1.53	52	23.3
VI–IV	108	15.3	24.3	27.7	1.81	67	24.2
VI–V	108	15.3	24.7	19.3	1.26	65	18.9
VII–V	109	15.3	24.0	27.7	1.81	67	25.0
Control	109	15.3	24.7	29.0	1.90	68	26.0

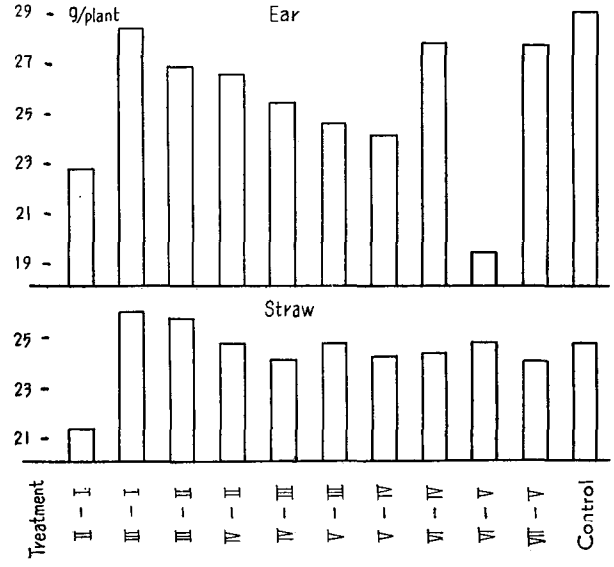


Fig. 33. Dry weight of ears and straw.

as those of the control, suggesting that the leaves grown in nursery bed have no meaning for tillering. Until the flowering stage, the later the cutting or the greater the cutting is, the smaller the yield is. If the leaves which are formed during elongation are cut at the flowering stage, remarkable decrease of yield takes place. However, after flowering, there is no noticeable decrease

in yield.

The yield is the product of ear number per plant multiplied by average ear weight. Ear weight is the product of grain number per ear multiplied by average grain weight. For this reason, ear number per plant, grain number per ear and 1000 grain weight are called the yield components.

Data of the yield components are shown in figure 34.

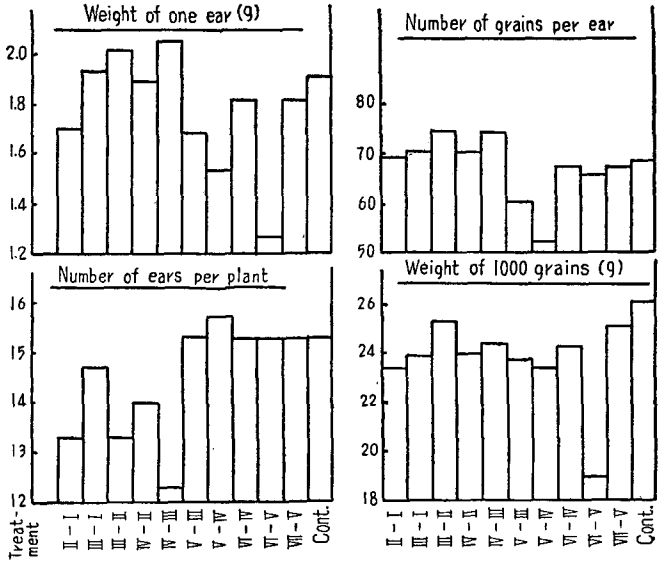


Fig. 34. Effect of leaf cutting on the yield components.

Number of ears per plant is very small in the cases of treatments in which the leaves formed during the growth stages between establishment and the tillering stage were cut off at the growth stages between the tillering stage and the ear-initiation stage. On the other hand, if the leaves formed during the growth stages between ear-initiation and elongation were cut off at the stages of elongation or flowering, the weight of one ear decreases very remarkably. Number of grains per ear decreases remarkably if the leaves formed during the growth stages between the tillering stage and the ear-initiation stage were cut off at the elongation stage. 1000 grain weight becomes very small if the leaves grown at the elongation stage were cut at the flowering stage.

From these results, it can be stated that each leaf has its characteristic functions.

The leaves on the main stem can be classified by their functions into the following four groups.

The leaves (1/0-2/0) which emerged at seedling stage influence the power of revival from damage by transplanting. Those (3/0-5/0) emerging at the period of recovery from damage by transplanting, affect the number of tillers. Those (6/0-9/0) which emerged during the tillering phase affect elongation of the stem and the formation of spikelets, and those (10/0-12/0) emerging during the elongation phase have influence upon the degree of ripening.

The predominant function of each leaf is diagramaticaly shown in figure 35.

From these facts, it may be said, generally, that the growth during any stage is chiefly influenced by the leaves which emerged in the previous stage and the leaves which are formed at one stage contribute to the growth of the next stage. In this way, rice plant develops phase by phase.

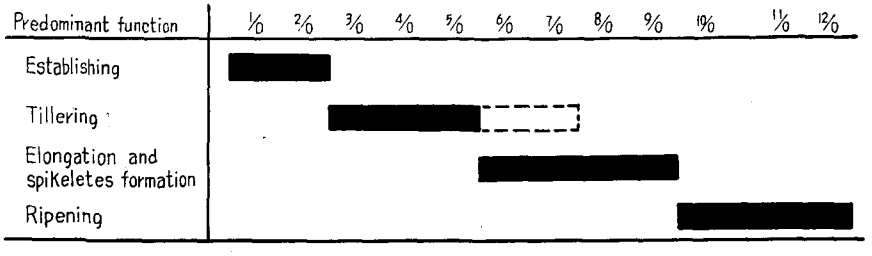


Fig. 35. Diagram of the characteristic predominant function of each leaf on main stem.

THE ACTIVE CENTER LEAF AND ITS RELATION TO THE WHOLE PLANT

Physiological significance of the active center leaf

The dry weight of a leaf increases with the growth of the leaf. After reaching the maximum dry weight, it decreases. The time when a leaf reaches the maximum dry weight comes in sequence from lower leaf to upper leaf. Lower leaves grow first and then the upper ones grow, successively. From this fact, it is suggested that active leaf goes up from lower position to upper position in company with growth of a whole plant.

The dry weight of a leaf increases with its growth. The increase in dry weight of a leaf is due to the accumulation of substances in the leaf. While the decrease in the dry weight is due to the efflux from or the consumption of substances by the leaf. At a given stage of growth of a rice plant, one leaf is at its maximum weight and other leaves are increasing or decreasing their weight. It seems that a leaf discharges its greatest function at the growth stage when the leaf takes its maximum dry weight. A leaf at maximum weight

seems to discharge the greatest physiological functions of all leaves at that stage. So, a leaf at maximum dry weight can be called the "active center leaf". This is the concept of the "active center leaf" proposed by the author.

To get ideas on the physiological meaning of the active center leaf, some studies were carried out, in which the physiological conditions of leaves at various positions on the main stem were compared.

Photosynthesis: It was pointed out that the photosynthetic activity of a leaf becomes greater in company with growth until it reaches the maximum and then becomes smaller.[55] This means that a young leaf is weak in photosynthesis, a middle-aged leaf is strongest, and an old leaf is again weak.

To find out the position-assimilation relationship, measurements of the photosynthetic activity of each leaf were carried out in the year 1957. Rice plants were grown under pot conditions. The pots used contained 2 kg soil. N, P_2O_5 and K_2O were given to each pot at the level of 0.7 g/pot as ammonium sulphate, superphosphate and potassium sulphate. Three seedlings were transplanted to each pot on May 23. On June 28, July 27 and September 4, measurements of the photosynthetic activity of each leaf on the main stem were carried out. The dates of these estimations are the tillering stage, the elongation stage and the milky stage, respectively. Measurements of photosynthetic activity were made by measuring the reduction of CO_2 concentration of the air which was passed through a glass tube in which the leaf under study is placed. The leaf is kept attached to plant. Three replicate measurements were made on each leaf, because there were rather great variations among obtained data on the same leaf. The author is indebted to Mr. A. OSHIMA, at the Hokkaido Agricultural Experiment Station, who carried out the meassurements.

The data are given in table 26. These are expressed on the basis of leaf area.

On June 28, the leaf-blade of 7/0 has just finished its morphological expansion. The photosynthetic activity of 7/0 is the weakest among all leaves. The 6/0 which has completed its morphological formation some time before, and is increasing its weight, is rather great in photosynthetic activity. The activity of 5/0 which is at its maximum weight, is the greatest among the leaves. On July 27, the activity of 9/0 is the strongest. The difference of photosynthetic activity among leaves is more or less the same as at the previous stage. On September 4, the flag leaf, 12/0, was long past its morphological formation and this leaf was the greatest in photosynthetic activity.

Comparison of photosynthetic activity among leaves was carried out farther by using C^{14}.

Two rice plants which were growing in a pot under normal water culture

TABLE 26. Photosynthetic activity of leaves at various positions on main stem

Date of measurement	Name of leaf	Area (cm^2)	CO_2 uptake ($mg/100^2\ cm^2/hr$)
28/VI	7/0	8.72	13.0
	6/0	9.56	36.6
	5/0	5.19	58.7
	4/0	4.62	15.0
27/VII	10/0	9.18	18.3
	9/0	20.52	26.6
	8/0	15.36	20.3
	7/0	10.77	14.1
4/IX	12/0	24.6	11.1
	11/0	30.7	6.1

conditions were placed in a glass box as shown in figure 36.

Two mg of $BaC^{14}O_3$ (ca. 100 μc) was placed in a beaker which is hunging from ceiling of the box. After the rice plants were placed in the box, 10% $HClO_4$ was introduced from a separating funnel to generate $C^{14}O_2$. Thirty minutes after $C^{14}O_2$ generation, the rice plants were removed from the box, one was uprooted and the other was kept under ordinary conditions for further studies. The uprooted plant was separated into each organs. The leaves from the main stem were dried by using electric iron and were arranged to take radio-autograph. After drying at ca. 80°C, each organ was powdered and then 10 mg of powdered samples were taken for estimation of radio-activity using ordinary Geiger-Muller counter. Since the energy of β-rays from C^{14} is weak, ordinary G.M. counter is not suitable. However, the data obtained by this instrument can be used for comparison of relative activities. To avoid geometrical error, three replicate estimations were made on each sample.

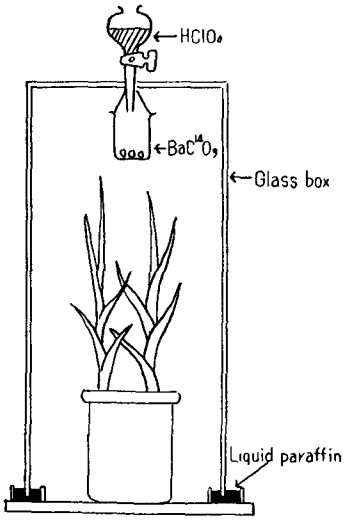


Fig. 36. Apparatus used for $C^{14}O_2$ assimilation.

The experiments were conducted on July 20 and August 21.

Figure 37 shows the radio-autograph which shows photosynthetic activity

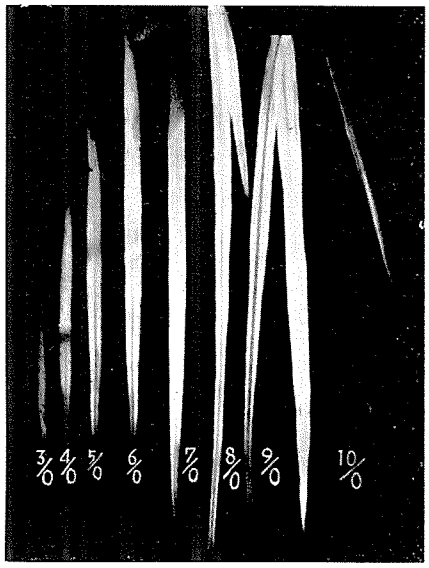


Fig. 37. Radio-autograph which shows photosynthetic activity of leaves on main stem on July 20.

of leaves on the main stem on July 20. In table 27, the data[56] on that date were also given.

The radio-activity of the leaf-sheaths, stem and roots is far smaller than that of the leaf-blades. This suggests that the photosynthetic activity of the leaf-blade is strong, while the activity of the leaf-sheath is extremely weak. Also it suggests that the translocation of photosynthetic products from the leaf-blade to other organs is very small during a 30 minutes period. So, under these experimental conditions, C^{14} which is assimilated by a leaf-blade during $C^{14}O_2$ exposure, remains in it. Radio-activity of each leaf-blade shows relative activity of photosynthesis of the leaf-blade. These activities are expressed on the basis of dry weight and also of leaf area.

Radio-activity per unit weight of 9/0 is the greatest. The activity of 10/0 is far smaller. The leaf-blade of 10/0 was under elongation and was rolled up. It can be seen from figure 37 that the part of 10/0 which was exposed to $C^{14}O_2$ directly, assimilated C^{14} considerably. However, the inside part of the rolled leaf shows almost no radio-activity. 11/0 just started to elongate and radio-activity of the leaf is extremely small. The activity of 8/0–6/0 is as great as that of 9/0. The activity becomes smaller below 6/0 to a remarkable degree. Radio-activity per unit area shows more or less the same tendency as that per unit weight. In this case, the activity of 8/0 is the strongest.

TABLE 27. Photosynthetic activity of each organ on July 20

Name of organ	Position	Area	Dry weight (mg)	cpm/10 mg	cpm/cm²
Leaf-blade	11/0	·	20	82	—
	10/0	10.7	60	1998	1008
	9/0	26.4	150	5710	3244
	8/0	15.4	98	5562	3540
	7/0	10.8	64	5562	3296
	6/0	9.4	48	5334	3724
	5/0	5.8	26	4482	2010
	4/0	3.9	16	4106	1684
	3/0	1.5	9	2372	1422
Leaf-sheath	10/0	-	23	96	—
	9/0	- -	86	376	—
	8/0	--	103	246	—
	7/0	—	70	212	—
	6/0	·	35	130	—
	5/0	-	28	130	—
	4/0		12	130	—
	3/0	—	6	130	—
Stem	--	·	55	82	-
Roots	-		270	32	—

In talbe 28, the data obtained on August 21 are given.

At this stage, the flag leaf is the greatest in photosynthetic activity on a dry weight basis as well as on an area basis. If position of a leaf goes down, the activity becomes smaller. C^{14} in spikelets is very small, so it can be said that photosynthetic activity of spikelets is extremely small. The activity of peduncle or leaf-sheaths is greater than that of spikelets, though it is far smaller than that of leaf-blades. The activity of internodes is negligible. These data suggest that carbohydrates which accumulate in grains are mostly the products of photosynthesis at leaf-blades.

From these data, it can be stated that photosynthetic activity of a leaf is very small until its full expansion. It is the greatest at some time after the morphological completion of the leaf and it becomes smaller as the leaf ages. The active center leaf is that leaf among leaves on the stem which is the greatest in photosynthetic activity.

Respiration: At various stages of growth, activities of respiration of each organ were estimated. Respiratory activity was expressed by the amount of

TABLE 28. Photosynthetic activity of each organ on August 21

Name of organ	Position	Area (cm^2)	Dry weight (mg)	cpm/10 mg	cpm/cm^2
Spikelets	—	—	330	23	—
Peduncle	—	—	89	126	—
Leaf-blade	12/0	24.6	130	1668	882
	11/0	35.3	180	1060	540
	10/0	36.6	203	960	532
	9/0	32.4	135	814	350
	8/0	18.1	85	762	358
Leaf-sheath	12/0	—	155	118	—
	11/0	—	178	144	—
	10/0	—	167	168	—
	9/0	—	163	88	—
	8/0	—	110	50	—
Internode	Ear–12/0 green part	—	45	38	—
	Ear–12/0 yellow part	—	78	10	—
	12/0–11/0	—	198	10	—
	11/0–10/0	—	260	10	—
	10/0– 9/0	—	210	10	—
Roots	—	—	350	—	—

oxygen uptake on the basis of fresh weight. The estimations were carried out by using the WARBURG's manometric method. Rice plants were grown under the same pot conditions as that for the measurement of photosynthetic activity. Three hundreds mg of fresh matter of each organ was placed in a measuring vessel and the uptake of O_2 during 30 minutes was estimated.

The results are given in table 29.

At the tillering stage, on June 25, the leaf-blade of 7/0 and the leaf-sheath of 6/0 were undergoing vigorous growth. Among leaf-blades, 7/0 is the strongest in respiration. The activity of 6/0–4/0 are more or less the same. The leaf-blade of 2/0 has started to dry up and it is weak in respiration. The respiratory activity of the leaf-sheath of 6/0 was the greatest among leaf-sheaths. The activity of leaf-sheaths of other leaves are more or less the same. Generally speaking, respiration of leaf-sheaths seems to be weaker than that of leaf-blades on respective positions. At the ear-initiation stage, on July 20, the same tendency as the previous stage is observed among organs, though respiration

TABLE 29. Activity of respiration of organs on main stem

(O_2 uptake (μl/g))

Date of estimation	Position	Name of organs		
		Leaf-blade	Leaf-sheath	Internode
25/VI	7/0	64	—	—
	6/0	53	53	—
	5/0	59	29	—
	4/0	57	32	—
	3/0	47	27	—
	2/0	40	28	—
20/VII	12/0	50	—	—
	11/0	29	46	—
	10/0	32	18	—
	9/0	27	14	—
	8/0	24	13	—
	7/0	24	15	—
23/VIII	Ear	18	—	} 7
	12/0	51	13	
	11/0	44	12	} 2
	10/0	48	8	} 2
	9/0	30	7	} 3
	8/0	34	5	

of each organ at this stage seems to be weaker than that of at the tillering stage. At the maturing stage, on August 23, the respiration of the leaf-blades is rather strong. At this stage, the upper leaf is more active in respiration than the lower leaf, as at previous stages.

Respiration of the leaf-sheaths and internodes is rather weak at this stage, though the upper ones are somewhat stronger than the lower ones.

Generally speaking, the leaf-blade which is under elongation is strong in respiration, but it is not active in photosynthesis. After finishing the elongation, the activity of respiration in the leaf-blade is almost constant, but the activity of photosynthesis becomes greater with increase of dry weight. After reaching the maximum dry weight, both respiration and photosynthesis of the leaf-blade become weaker with ageing of the leaf-blade.

The uppermost leaf is strong in respiration, the next leaf, which has just finished its morphological formation, is not so strong in respiration as in

photosynthesis. The leaf, which has finished its formation some time back and is at the maximum dry weight, is strong in photosynthesis but not as active in respiration as the uppermost leaf. The leaves which are losing their weight are weak in both respiration and photosynthesis.

The uppermost leaf is strong in respiration. However, this activity depends upon the products of photosynthesis from leaves in the lower positions. The leaf, which is at its maximum weight, is strong in photosynthesis and the activity of respiration of the leaf is also fairly strong. This leaf of maximum weight is active with its own ability. In this sense, the leaf can be called the active center leaf.

Accumulation of elements and physiological activity

Accumulation of elements in a leaf takes place in company with growth of the leaf, after reaching the maximum amount, effluxion of elements from the leaf takes place. To know the relation between the accumulation of elements in a leaf and the physiological activity of the leaf, some experiments were carried out. In these experiments, P^{32} and Ca^{45} were used.

As described previously, the behavior of phosphorus and of calcium is entirely different. Phosphorus is an element which accumulates very quickly in the leaf as it grows, and after reaching the maximum amount, it flows out from the leaf significantly. On the other hand, calcium is an element which accumulates very slowly and it does not flow out after it is accumulated. Accumulation of phosphorus is related to physiological activity and that of calcium is not related to the activity. Since physiological activity differs among leaves, the distribution of phosphorus and calcium among leaves is not uniform. It is affected by the difference in physiological activity among leaves.

Rice plants were grown under water culture conditions. P^{32} or Ca^{45} were supplied to the plants from roots at different stages of growth. One or two days after the applications, observations on the distribution of these radio-active isotopes among leaves were made.

Application of P^{32} was made by the following method. Rice plants were grown under normal water culture conditions in the year 1954. On June 28, July 15 and August 1, the tillering stage, the ear-initiation stage and the milky stage respectively, P^{32} was given to these rice plants. At each application, three plants were shifted to 250 ml of culture solution which contains P^{32} (ca. 250 μc as H_3PO_4) and no phosphorus as carrier. After 24 hours, the plants were removed from the culture solution. The plants were separated into individual leaves and after ashing, the radio-activity of each leaf was estimated by using G. M. counter. The results[57] are given in table 30 and figure 38.

At any stage of growth, the accumulation of P^{32} in the uppermost leaf is very great. The accumulation in leaves just below the top leaf is rather small and if the position goes down, it becomes greater. The second peak of accumulation comes at the third of fourth leaf from the top. Then the accumulation becomes smaller if the position goes down farther.

From this characteristic distribution pattern, it may be considered that the accumulation of P^{32} is governed by two physiological activities. Since the

TABLE 30. Distribution of P^{32} absorbed from roots

(cpm/10 mg)

Date of P^{32} application	28/VI	15/VII	1/VIII
Ear	—	322	27
12/0	—	129	17
11/0	—	234	28
10/0	2532	243	28
9/0	1462	265	26
8/0	1811	243	26
7/0	2007	190	—
6/0	1222	150	—
5/0	1022	130	—
4/0	980	—	—
Stem	—	—	49

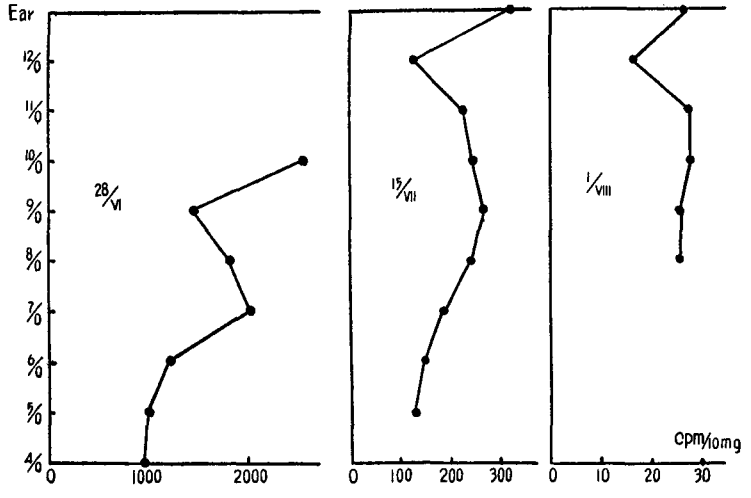


Fig. 38. Distribution of P^{32} absorbed from roots.

uppermost leaf is active in accumulating P^{32} and this leaf is also active in respiration, the accumulation of P^{32} is related to respiration. The third or fourth leaf from the top is active in accumulating P^{32} and this leaf is active in photosynthesis, so accumulation of P^{32} seems to be related to photosynthetic activity. 7/0 on June 28, 9/0 on July 15 and 11/0 on August 1, are the leaves which seem to be most active in photosynthesis and also in accumulating P^{32}. These leaves are the active center leaves at respective growth stages.

It has been reported that accumulation of P^{32} is related to metabolic activity.[58)59)] The results obtained here are in agreement with these reports. However, it was pointed out here that the accumulation is related not only to respiration but also to photosynthesis. Although no report has come out which points out the relation between photosynthesis and accumulation of P^{32}, the relation is quite possible, because phosphorus takes a very important place in photosynthesis.[60)] To ascertain the relation between photosynthesis and phosphorus accumulation, an experiment was conducted. A part of a leaf of a water cultured rice plant was covered with tin-paper to keep it dark for two days; then P^{32} was added to the culture solution. After 24 hours, a radio-autograph of the plant was taken. Figure 39 shows the radio-autograph.

It is very clear from the radio-autograph that the part which was darkened by tin-paper is very weak in radio-activity. This suggest that the accumulation of P^{32} is related to photosynthesis. The accumulation of P^{32} is accelerated by

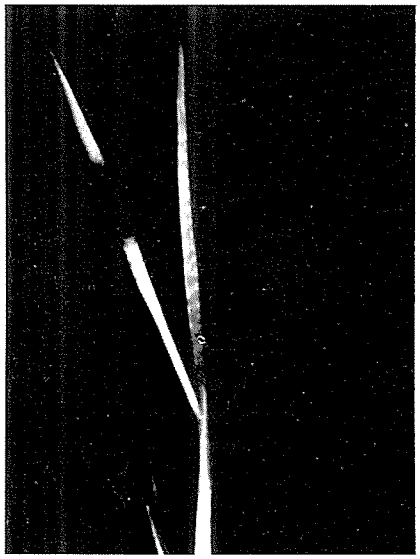


Fig. 39. Effect of darkening on distribution of P^{32}.

photosynthesis. However, from this experiment, it is not clear whether photosynthesis effects the accumulation directly or the accumulation is caused by the products of photosynthesis.

The above mentioned experiments show that the active center leaf has special importance in accumulating phosphorus.

In the year 1955, applications of Ca^{45} to rice plants were made on July 5, July 23 and August 15, the tillering stage, the ear-initiation stage and the flowering stage respectively. To apply Ca^{45}, rice plants were shifted to a culture solution containing Ca^{45} (ca. 40 μc/4l, as $CaCl_2$, specific activity 3.34 mc/g). Three days after the applications, rice plants were uprooted and separated into each leaf. Determinations of radio-activity were made after ashing. The results are given in table 31 and figure 40.

TABLE 31. Distribution of Ca^{45} absorbed from roots

(cpm/50 mg)

Date of Ca^{45} application	5/VII	23/VII	15/VIII
Date of estimation	8/VII	26/VII	18/VIII
Ear			464
12/0		225	803
11/0		1262	775
10/0		1095	668
9/0	507	891	1503
8/0	1296	924	1413
7/0	1096	1447	—
6/0	1016	1624	—
5/0	816	1888	—
4/0	930	—	—
3/0	760	—	—

The distribution pattern of Ca^{45} is quite different from that of P^{32}. On July 8, 9/0 started to elongate. Accumulation of Ca^{45} in this leaf is very small and that in 8/0 is the greatest. On July 26, 12/0 is growing vigorously. The accumulation in 12/0 is extremely small, that in leaves in the positions between the third and fifth from the top is rather small, but it becomes greater from 8/0 to 5/0. On August 18, the accumulation in 12/0–10/0 is far smaller than that in 9/0 or 8/0.

Generally speaking, the accumulation of Ca^{45} in growing leaves, where the active accumulation of P^{32} takes place, is very weak, that in leaves just after

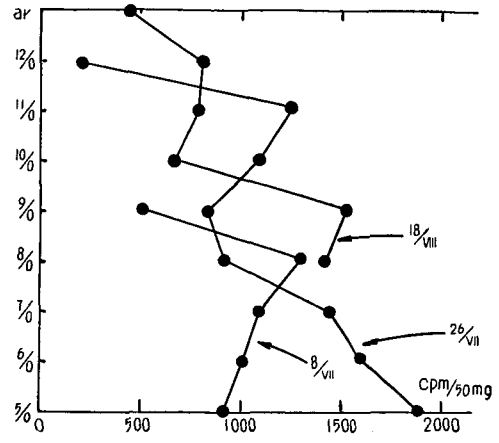


Fig. 40. Distribution of Ca^{45} absorbed from roots.

morphological expansion is rather active. However, the active center leaf is not so active in accumulating Ca^{45}. In the leaves below the active center leaf, rather active accumulation of Ca^{45} takes place. This general tendency of Ca^{45} distribution is quite contrary to that of P^{32} distribution. Distribution of Ca^{45} seems to be governed by neither respiration nor photosynthesis. It may have some relation to transpiration.

The active center leaf is active in photosynthesis. As described previously, the accumulation of some elements, such as phosphorus, nitrogen etc., are more intimately related to metabolic activity than the other elements such as calcium. The elements whose accumulation is related to metabolic activity are distributed in the active center leaf in greater amount than in the other leaves.

Relation between growth of individual leaves and that of whole plant

By ISHIZUKA and the author, growth of a whole rice plant was divided into three phases, i.e. the vegetative phase, the reproductive phase and the maturing phase. This fact suggests that growth of a whole rice plant must be understood as a phasal development.

Leaves on the main stem come out one after another from lower leaf to upper leaf and the active center leaf goes up from a lower position to an upper position in company with the growth of a rice plant which is constructed from these leaves.

If the growth of a whole plant has characteristics of phasal development, as described above, there should be some characteristic change in the mode of position shift of the active center leaf during growth in relation to the phasal development.

As nitrogen is one of the most important constituents of protein which constructs protoplasm, the physiological condition of plants reflects remarkably in the behavior of nitrogen. Accumulation and effluxion of nitrogen in or from a leaf is intimately related to the activity of the leaf. So, the process of accumulation and effluxion of nitrogen in or from each leaf supply knowledges on vicissitude of activity of each leaf with the growth of a whole plant. To visualize the mode of fluctuation of nitrogen in each leaf on the main stem, figure 41 was prepared from table 5. In this figure, the relative amount of nitrogen in a leaf at successive stages of growth on the basis of the maximum amount of nitrogen in the leaf was shown on the vertical axis and growth stages on the horizontal axis.

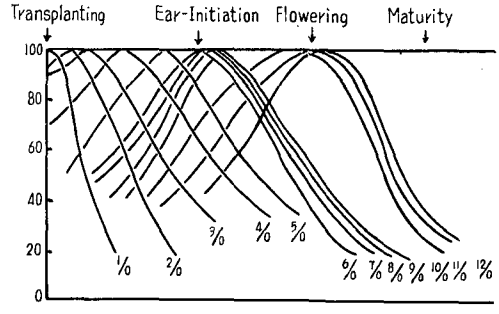


Fig. 41. Fluctuation curves of nitrogen in each leaf.

From this figure, it is evident that intervals between two successive peaks of nitrogen fluctuation curves are not constant throughout the growth process. Between 3/0 and 5/0, the intervals are more or less constant. The peak of 3/0 comes first, that of 4/0 comes some time after that of 3/0. The interval of the peaks between 4/0 and 5/0 is almost the same as that between 3/0 and 4/0. Between 6/0 and 9/0, nitrogen accumulate from lower leaf to upper leaf, but it does not flow out from these leaves until the ear-initiation stage. When this stage comes, nitrogen in all these leaves starts to flow out all at once and the accumulation of nitrogen in the stem and the young ear takes place simultaneously. Between 10/0 and 12/0, the accumulation of nitrogen in these leaves takes place from lower leaf to upper leaf. Nitrogen in these leaves does not efflux until the flowering stage and after the stage, nitrogen in these leaves flows out and nitrogen in ear increases synchronously.

From the facts mentioned above, leaves on the main stem can be classified into three groups, namely, 3/0–5/0, 6/0–9/0 and 10/0–12/0. These three groups can be correlated with the vegetative phase, the reproductive phase and the maturing phase. Namely, it seems that 3/0–5/0 discharge their function during

the vegetative phase, 6/0–9/0 have special importance to formation of ear and stem elongation and the function of 10/0–12/0 is connected with maturing.

By using the same method which was employed to prepare the nitrogen fluctuation curves, fluctuation curves of sugar and starch were made from the data in table 17 and 18. These curves are given in figure 42.

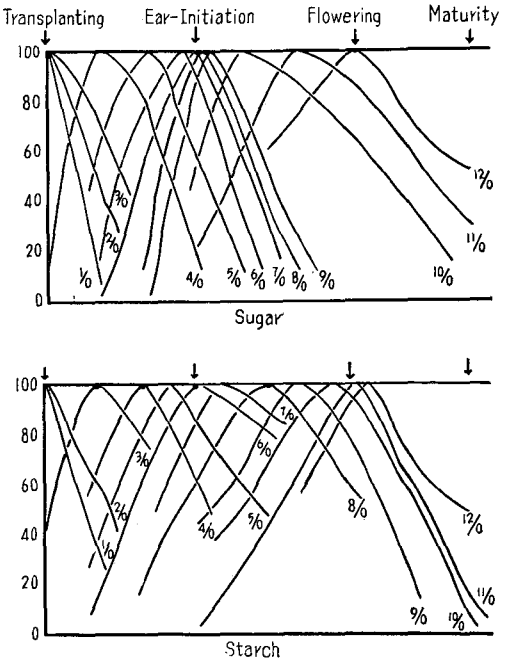


Fig. 42. Fluctuation curves of sugar and starch.

The increase and decrease of sugar take place successively from lower leaf to upper leaf until 5/0. After 6/0, increase of sugar takes place from lower leaf to upper leaf, but no decrease takes place until the ear-initiation stage. When the stage comes, decrease of sugar in 6/0–9/0 starts suddenly. After the ear-initiation stage, increase and decrease of sugar take place from 10/0 to 12/0 successively.

The increase and decrease of starch take place successively from lower leaf to upper leaf until 9/0. However, after 10/0, starch in 10/0–12/0 increase from lower leaf to upper leaf, but it does not decrease until the flowering stage. After the flowering stage, starch starts to disappear from these leaves quickly. The decrease of starch from 12/0 is somewhat slower than in the cases of 10/0 and 11/0.

From the above discussions, leaves on the main stem can be classified into

three groups. The first group is 3/0-5/0 which are related to tillering. These leaves are formed during the growth stages between transplanting and establishment. Nitrogen accumulates and flows in or from these leaves from lower leaf to upper leaf, successively. The second group is 6/0-9/0. These leaves seems to be related to spikelet formation and elongation of stem. The accumulation of nitrogen and sugar takes place from lower leaf to upper leaf. The nitrogen or sugar translocate or disappear rapidly from these leaves after the ear-initiation stage. The third group is 10/0-12/0. These leaves seem to have a special connection with ripening. Nitrogen and starch accumulate in these leaves from lower leaf to upper leaf. The flowing out or disappearance of these substances from these leaves take place rapidly after the flowering stage.

This classification of leaves on the main stem is quite in agreement with the classification described in figure 35. Leaves on the main stem can be classified into three groups and these three groups are correlated with the three growth phases of a whole plant.

The active center leaf at a given growth stage goes up from lower position to upper position in company with growth. This acropetal transition of the active center leaf seems to be retained at two stages of growth, i.e. the ear-initiation stage and the flowering stage.

The transition between 6/0-9/0 is retained at the ear-initiation stage. When the stage comes, the retention is removed and the active center leaf goes up beyond 9/0. The transition of the active center leaf between 10/0-12/0 is retained again at the flowering stage. After this stage, nitrogen and starch in these leaves start to flow out or disappear simulataneously.

MUTUAL RELATION AMONG LEAVES

In the previous discussions, it was pointed out that each leaf on the main stem has its physiological characteristics and also characteristic functions corresponding to its position. However, no attention has been paid so far, on the relationship among leaves.

Young leaves and roots depend upon old leaves by receiving assimilation products and also elements. Growing points of shoot and roots receive assimilation products from leaves which are active in photosynthesis. Some elements in old organs translocate to younger organs. Moreover, the main stem has several primary tillers, these primary tillers also have secondary tillers and the main stem as well as the tillers have many leaves. Rice plants have such a complicated construction that to have an idea of a whole rice plant, knowledge of individual leaves is not sufficient. Knowledge of the mutual relation among leaves is as important as that of individual leaves.

Relationship among leaves on the main stem

To know the relationship among leaves on the main stem, the translocation of substances among leaves was studied. For this purpose, P^{32} or C^{14} was given to leaves on the main stem at various positions and the movement of these isotopes among leaves was traced.

In the year 1955, P^{32} was introduced to the active center leaf and translocation of P^{32} to other leaves was traced. Rice plants which were grown under normal water culture conditions were used. P^{32} was supplied to these plants at 7/0 on June 28, at 9/0 on July 15 and at 11/0 on July 31. To supply P^{32}, the tip of these leaves were cut off by 2 cm and the cut end was dipped into 10 ml of no phosphorus culture solution containing P^{32} (ca. 10 μc). After 48 hours, the distribution of P^{32} among organs on the main stem was estimated. The results are given in table 32.

P^{32} which is taken up from 7/0 on June 28, translocates into 10/0 most actively. 10/0 is the leaf which was growing at that stage. P^{32} which is taken up from 9/0 on July 15, translocates predominantly to the ear-primordium and stem. Since the rice plant was at the ear-initiation stage and the ear and stem were growing actively at that stage, the result is quite reasonable. P^{32} which is taken up from 11/0 at the flowering stage translocates to ear most actively.

TABLE 32. Distribution of P^{32} introduced to the active center leaves at successive stages of growth (cpm)

Name of organ	Date of application		
	28/VI	15/VII	31/VII
Ear	—	60	96
12/0	—	12	6
11/0	—	26	5582
10/0	80	14	12
9/0	26	10336	0
8/0	16	6	0
7/0	1594	0	—
6/0	62	0	—
5/0	0	—	—
Stem	—	35	28
Roots	48	62	36

A great amount of P^{32} was distributed in roots at all these stages. The radio-autograph showed that P^{32} in the roots is accumulated at the root tips.

The fact that phosphorus translocates from shoot to root has been reported by several authors.[61]

From these data, it can be stated that P^{32} which is taken into the plant body from the active center leaf translocates most actively to the organs which are growing vigorously at that stage. The active center leaf is most intimately related to the growing points.

By using the same method described above, the introduction of P^{32} was made from leaves at various positions on the main stem. On July 5, P^{32} was given at 5/0, 7/0 or 9/0. After 48 hours, the distribution of P^{32} was estimated. At this stage, 10/0 was growing vigorously and 7/0 was the active center leaf. The results are given in table 33.

TABLE 33. Distribution of P^{32} introduced from 5/0, 7/0 or 9/0 on July 5 (cpm)

Name of organ	P^{32} was introduced at		
	5/0	7/0	9/0
10/0	3	80	113
9/0	13	104	2155
8/0	28	51	300
7/0	27	356	79
6/0	25	12	29
5/0	97	9	6
4/0	12	3	0
7-tiller	12	27	28
6-tiller	15	77	38
5-tiller	96	38	46
4-tiller	31	36	53

If P^{32} is introduced at 5/0, great activity is found in 5-tiller. P^{32} introduced at 7/0, translocates to 10/0 and 9/0 which are growing at that stage. If P^{32} is introduced at 9/0 which is growing, it is taken into the leaf itself most actively.

The results obtained here suggest that the active center leaf is intimately related to the growing point of the stem as described above. The leaves whose positions are lower than the active center leaf are related to the tillers. The upper leaves which are under growth utilize substances in itself. It is evident from these facts that there is division of activities among leaves.

The same type of experiments were conducted by using C^{14} in the year 1957. On July 27, either 11/0, 9/0 or 7/0 was exposed to $C^{14}O_2$ and the

distribution of C^{14} after 24 hours was estimated. To expose these leaves to $C^{14}O_2$, the leaf was enclosed in a glass tube by using a rubber stopper. In the glass tube, a small glass dish which contained 0.5 mg $BaC^{14}O_3$ (ca. 5 μc), was placed as shown in figure 43. The rice plant was covered with black cloth except for the leaf where C^{14} was assimilated. Then, 2 ml of 10% $HClO_4$ was

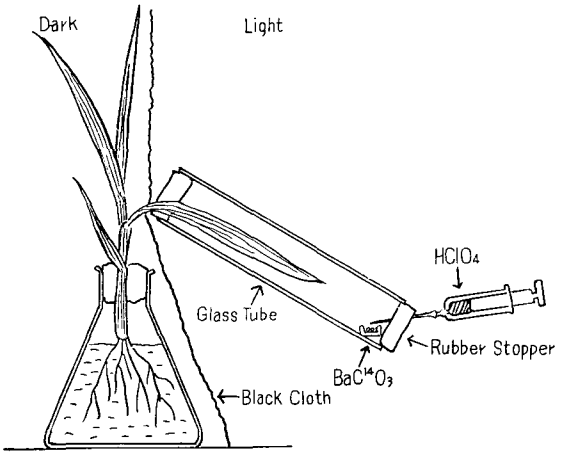


Fig. 43. Apparatus to expose leaf to $C^{14}O_2$.

put into the dish by using an injection apparatus through the rubber stopper. After 24 hours, the plant was sampled and each organ was separated. After taking a radio-autograph, these were powdered and determinations of radio-activity were made on these powdered samples by using G. M. counter as de-scrived before.

The results[56] are given in table 34 and the radio-autographs are shown in figure 44.

At this stage, 10/0 or 11/0 was the active center leaf. The C^{14} assimi-lated at 7/0 translocated vigorously to roots and tillers. The C^{14} assimilated at 9/0 translocated actively to 12/0, to the ear-primordium and to the elongating stem. Considerable amount of C^{14} translocated to tillers and also roots. The C^{14} assimilated at 11/0 entered very actively into 12/0, ear and elongating stem. In this case, the translocation to tillers or to roots was very small. These data are in agreement with the radio-autographs in figure 44.

From these data, it can be stated that the lower leaves which have no elongated internode are related to roots and tillers, on the other hand, the upper leaves whose internode is elongated are related to the growing organs of the stem at that stage.

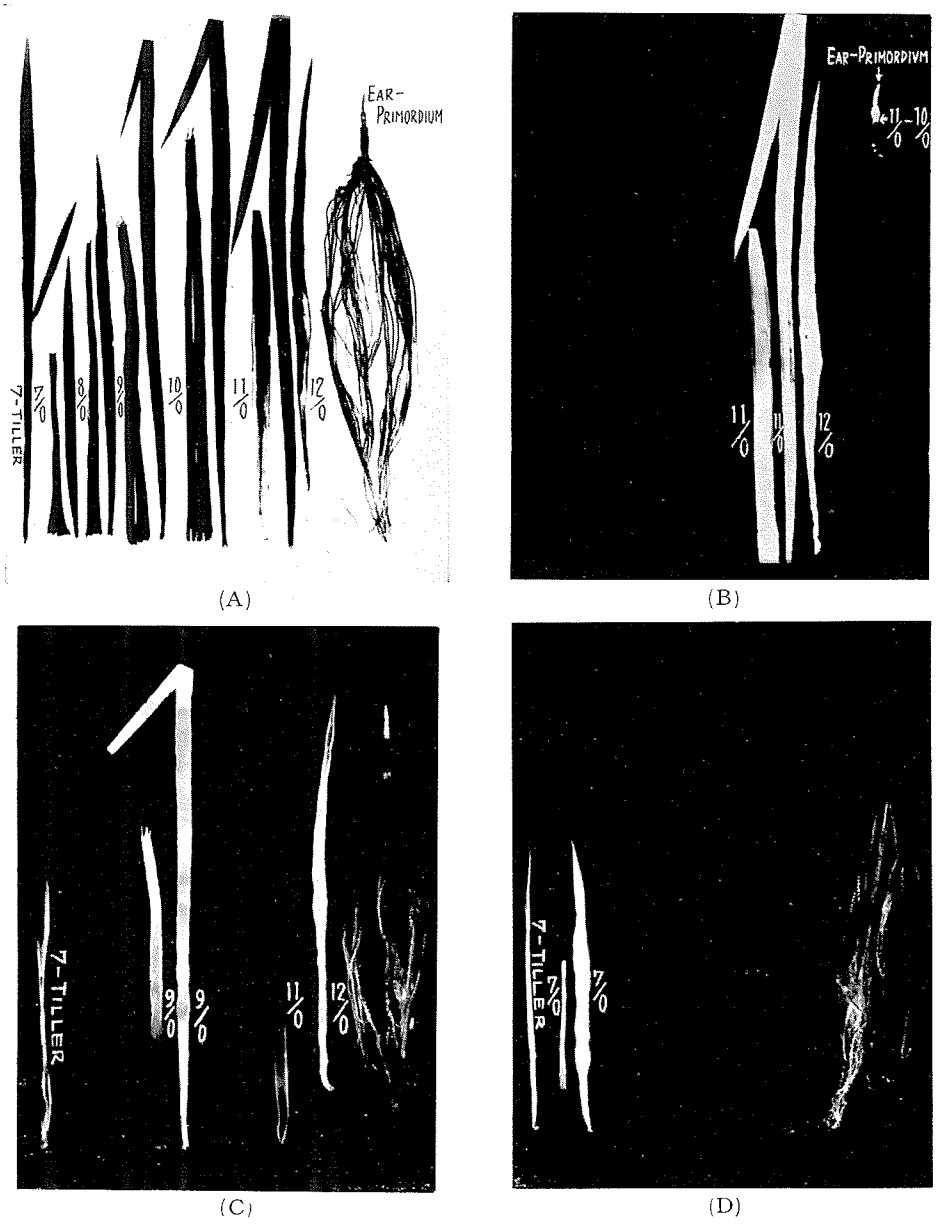


Fig. 44. Distribution of C^{14} assimilated at 11/0, 9/0 or 7/0 on July 27.
(A) Condition of rice plant on July 27.
(B) Radio-autograph showing distribution of C^{14} assimilated at 11/0.
(C) " 9/0.
(D) " 7/0.

TABLE 34. Distribution of C^{14} assimilated at 11/0, 9/0 or 7/0 on July 27

(cpm/10 mg)

Organ		Dry weight (mg)	C^{14} was assimilated at		
			7/0	9/0	11/0
Ear-primordium		4	30	1585	2665
Leaf-blade	12/0	52	169	7333	14004
	11/0	194	77	240	9121
	10/0	143	50	41	50
	9/0	102	25	23427	12
	8/0	50	20	22	14
	7/0	28	38126	10	26
Leaf-sheath	11/0	96	31	345	8869
	10/0	180	81	33	63
	9/0	178	32	921	27
	8/0	69	20	30	37
	7/0	33	2103	45	26
Stem above	10/0	5.5	72	564	5052
Stem below	9/0	24	89	116	224
Stem base	—	63	110	52	47
Roots	—	368	623	325	209
6-tiller	—	103	2209	1757	41
Tillers (except 6-tiller)	—	3130	107	62	23

The same type of experiment was conducted on August 21, at the milky stage. C^{14} was assimilated at 12/0, 10/0 or 8/0. 12/0 was the flag leaf. The results[56] are given in table 35 and figure 45.

The C^{14} assimilated at 8/0 translocates actively to stem base and roots. However, it does not enter appreciably into upper leaves, stem and ear. On the other hand, the C^{14} assimilated at 12/0 actively enters into ear. In this case, no translocation to roots and leaves occurs below 11/0. The behavior of C^{14} assimilated at 10/0 is intermediate between the cases of 8/0 and 12/0.

During the maturing phase, assimilation products in the flag leaf or the next leaf, enter into ear, but these do not move downward. The assimilation products in the lower leaves which have no elongated internode enter into stem base and roots, but not into upper organs.

From these results, it is evident that after the beginning of internode

TABLE 35. Distribution of C^{14} assimilated at 12/0, 10/0 or 8/0 on August 21

(cpm/10 mg)

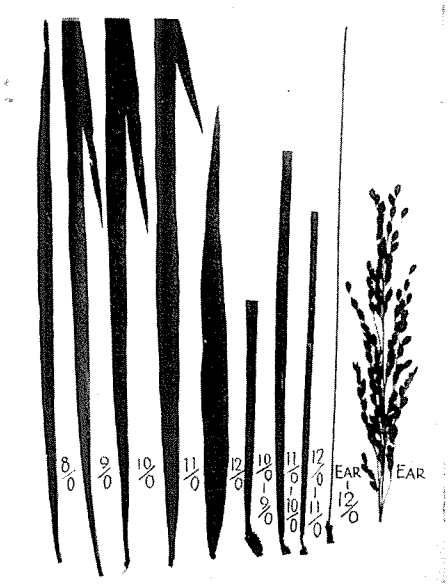
Organ		Dry weight (mg)	C^{14} was assimilated at		
			8/0	10/0	12/0
Ear		505	60	370	2562
Leaf-blade	12/0	140	106	106	36124
	11/0	210	66	130	0
	10/0	190	50	26560	0
	9/0	120	40	34	0
	8/0	70	51360	0	0
Leaf-sheath	12/0	140	52	100	2974
	11/0	155	76	80	0
	10/0	170	42	4170	0
	9/0	140	30	0	0
	8/0	90	4188	0	0
Internode	Ear-12/0	140	114	240	620
	12/0–11/0	260	112	70	376
	11/0–10/0	290	40	70	24
	10/0– 9/0	240	40	70	16
Stem base		60	322	0	0
Roots		500	444	0	0

elongation, there is a division of activities among leaves. The upper leaves which have elongated internode are intimately related to the growing point of the stem on which the leaf emerges. The lower leaves which have no elongated internode are intimately related to roots of the stem and also to tillers.

The assimilation products of the lower leaves translocate to roots, and are consumed there by respiration. This respiration promotes absorption of elements by roots. The elements, thus absorbed, translocate to the active center leaves and also the growing points of the shoot. The assimilation products of the active center leaf translocate to the growing point, where they are taken into constituents of the growing organs.

In this way, each leaf discharges its characteristic functions corresponding to its position.

However, the division of activites among leaves is not so clear during early stages of growth. At these stages, photosynthetic products of the active



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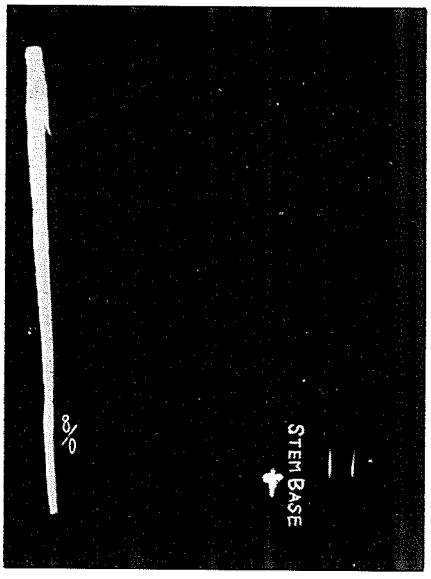

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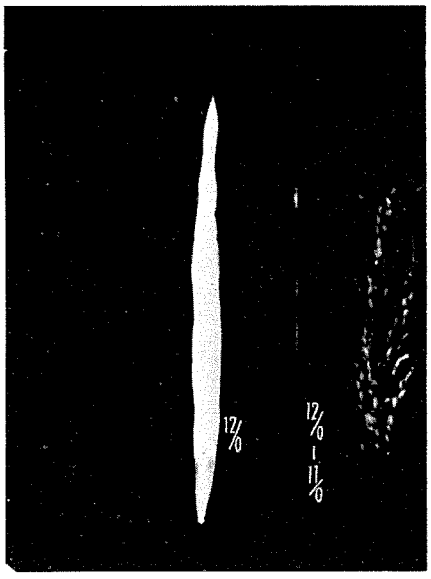

(C)

Fig. 45. Distribution of C^{14} assimilated at 12/0, or 8/ on August 22.
(A) Condition of rice plant on August 22.
(B) Radio-autograph showing distribution of C^{14} assimilated at 8/0.
(C) " 12/0.

center leaf goes into growing leaves as well as roots as shown in figure 47.

Relation between the main stem and tillers

Tillers are sprouts which emerge from the nodes of the mother stem. These sprouts grow with help from the mother stem at early stages of growth, but later many leaves and roots are formed on these sprouts and these grow independently of the mother stem. To clarify the relation between the mother stem and the tillers, the growth process of a tiller was studied in the year 1953.

The dry weight and the content of nitrogen, phosphorus and potassium of 4-tiller were determined during growth of the tiller. The results are given in table 36 and figure 46.

TABLE 36. Growth process of 4-tiller

Date of sampling	26/VI	30/VI	7/VII	14/VII	21/VII	6/VIII
Dry weight (mg)	0.6	12.1	59.4	158	508	1520
Nitrogen content (N%)	5.28	4.68	3.45	2.69	3.38	1.90
Phosphorus content (P_2O_5%)	1.85	1.04	0.69	0.50	0.58	0.60
Potassium content (K_2O%)	5.30	3.60	3.00	2.55	2.80	2.41

In associated with the growth of the tiller, leaves and roots emerge from the tiller. The increase of dry weight is slow at early stages of growth but later it becomes vigorous. The tiller has three leaves when the vigorous increase in dry weight begins. The content of nitrogen, phosphorus and potassium

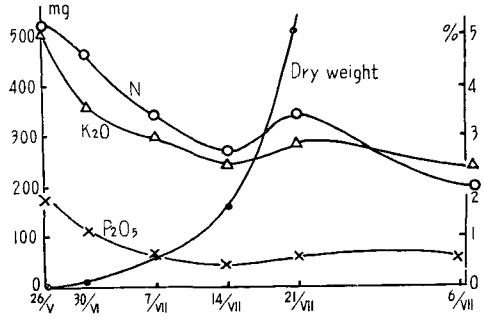

Fig. 46. Growth process of 4-tiller.

decreases at the early stages of growth until the vigorous growth starts. However, after this initial stage, the content of these elements increases for a while. The content begins to decrease after reaching maximum. From the fluctuation of the contents of these elements, two phases can be distinguished in the growth

process of a tiller. The first phase is the heterotrophic phase and the second is the autotrophic phase. During the first phase, the tiller receives substances from mother stem. This supply of substances from mother stem to the tiller is not so vigorous that the content of elements in the tiller drops and the increase of dry weight is not rapid. During this phase, three leaves and three or four roots are formed on the tiller. When the second phase begins, absorption of elements by its own roots begins, and the content of elements rises for a while. The photosynthesis of the leaves on the tiller also becomes active, and the increase of dry weight becomes active. Due to the active accumulation of assimilation products in the tiller, the content of elements of the tiller drops again. In this way, the tiller becomes independent of the mother stem.

From the above discussions, it can be said that a tiller is independent from the mother stem when the tiller possesses more than three leaves. To ascertain this point, an experiment was conducted by using radio-active tracers.

On June 22, 1957, C^{14} was assimilated at 5/0 by the same method described on page 67. After 24 hours, the distribution of C^{14} was studied. The results[56] are given in table 37 and figure 47.

From the data, it is evident that the C^{14} which is taken into the plant body at 5/0 translocates to 6/0, 2/2 and 1/3, actively. At this stage of growth, 6/0 was under elongation. 6/0, 3/1, 2/2 and 1/3 are synchronous leaves each other. Thus, the C^{14} assimilated at 5/0 seems to translocate to growing synchronous leaves except 3/1.

TABLE 37. Distribution of C^{14} assimilated at 5/0 on June 22

(cpm/organ)

Name of leaf	cpm	Name of leaf	cpm	Name of leaf	cpm	Name of leaf	cpm
6/0	6812	3/1	150	2/2	3442	1/3	2913
5/0	28300	2/1	146	1/2	335		
4/0	630	1/1	63				
3/0	316						
2/0	90						
1/0	21						

The elongating leaf of 1-tiller at that stage is 3/1. The leaf receives the assimilation products from the leaves on 1-tiller, i.e. 1/1 and 2/1, but it does not receive much of the products from leaves on the main stem. This suggests that 1-tiller is almost independent from the main stem. However, 2/2 or 1/3 receive abundantly assimilation products from the main stem. The 2-tiller and 3-tiller receive and are dependent on assimilation products from the main stem.

(A) (B)

Fig. 47. Distribution of C^{14} assimilated at 5/0 on June 22.
(A) Condition of rice plant on June 22.
(B) Radio-autograph which shows distribution of C^{14} assimilated at 5/0.

From these facts, it can be concluded that a tiller seems to be almost independent from mother stem when it develops three leaves.

Morphologically, tillers are always connected with mother stem.

Figure 48 shows the cross section of the base of stem. This figure suggests that the junction of the younger tiller with the main stem is broader than that of the older tiller. However, it is very clear that even the older tiller is connected with the main stem.

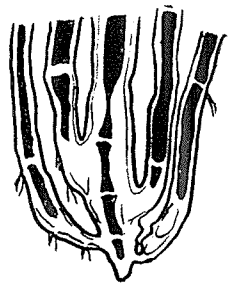

Fig. 48. Cross section of stem base.

Since there is a junction, there may be some mutual relation even between the old tiller and the main stem.

Concerning this point, experiments were conducted using P^{32}.

Two similar rice plants were selected at the flowering stage. All tillers were removed from the main stem except 7-tiller which is at the highest position.

By using these two rice plants, translocation of P^{32} between the main stem and 7-tiller was traced. At this stage, 7-tiller had four leaves. The roots were cut off from the main stem of one plant and from 7-tiller of

the other plant. After roots removed, an application of P^{32} was made by dipping the remaining roots into a culture solution containing P^{32}. In this case, the cut ends of roots on the main stem or 7-tiller were excluded from the solution to avoid P^{32} penetration from the cut ends. After 24 hours, the P^{32} in the main stem and 7-tiller was determined. The results[57] are given in table 38.

TABLE 38. P^{32} in main stem and 7-tiller

Treatment	Roots on main stem	+	+	−
	Roots on 7-tiller	+	−	+
P^{32} (cpm)	Main stem	1800	2706	107
	7-tiller	1383	684	3073

+ : not treated. − : removed.

The P^{32} which is absorbed by the roots on the main stem translocates in appreciable amounts to 7-tiller. The P^{32} which is absorbed by the roots on 7-tiller also translocates to the main stem, though the amount is not so great as in the previous case.

Generally, translocation can take place from the main stem to tiller and also from tiller to the main stem in both directions. Translocation from the main stem to tiller is more active than from tiller to the main stem.

In the next experiment, a rice plant at the flowering stage was selected. Roots on all tillers were removed and only roots on the main stem were kept intact. P^{32} was supplied from the remaining roots on the main stem and the distribution of P^{32} among tillers after 24 hours was determined. The results[57] are given in table 39.

TABLE 39. Distribution of P^{32} among tillers which is absorbed by roots on main stem (cpm)

7-tiller	105
6-tiller	73
5-tiller	45
4-tiller	40
Main stem	265

It is clear from the data that the P^{32} which is absorbed by the roots on the main stem most actively enters into the main stem, but the P^{32} goes also into tillers.

Since, at this stage, all these tillers possessed more than four leaves, these

were almost independent from the mother stem. However, substances were translocated from the mother stem to these tillers to some extent. Translocation to younger tillers is more active than to older tillers.

Generally, if a tiller could possess more than three leaves, the tiller becomes effective and if a tiller fails to possess more than three leaves, it becomes ineffective.

If environmental conditions are not suitable for tillering, translocation of substances from the mother stem to the ineffective tiller stops before the tiller forms three leaves due to a scarcity of substances in the mother stem which are necessary for the growth of the tiller. Nitrogen is one of the most important factors for tillering.[62] Thus, scarcity of nitrogen in the main stem causes ineffective tillers.

Passways of subtances between mother stem and ineffective tiller remain open. Thus, substances in ineffective tillers can translocate back to mother stem as has been pointed out by several authors.[63][64] In this way, some substances in ineffective tiller can be utilized again by mother stem.

EFFECT OF ENVIRONMENTAL CONDITIONS ON NUMBER, SIZE AND ACTIVITY OF LEAVES

The number of leaves on the main stem and the size and activity of these leaves can be changed by environmental conditions. Each leaf has its own characteristic functions as described previously. If the number of leaves which are related to some function could be increased by some way, the function would be emphasized. If the size of a leaf could be expanded, the function which is governed by the leaf would be activated. If a leaf could be activated, the function which is related to the leaf is increased.

From these considerations, it is necessary to make clear the relations between environmental conditions and number, size and activity of leaves.

The discussions which have been made before were limited to those plants which were grown under normal conditions. The meaning of normal conditions is that during the growth of the plants, no element is insufficient and none of the other environmental conditions, such as temperature and quality and quantity of light etc., was measurably limiting to normal yield. Under such normal conditions, the rice plants, variety *Chuseieiko*, possess twelve leaves on the main stem. These leaves have three characteristic functions, that is, some leaves are related to tillering, some are related to formation of ear-primordium and elongation of stem, and the others are related to ripening.

In the previous discussions, the relation between position and function of leaves was expressed by the following manner. For example, 9/0 is related to

ear formation and elongation of stem, but the main function of 12/0 is to ripen the ear. However, if environmental conditions are not normal, the number of leaves on the main stem changes. If 9/0 is the flag leaf under some conditions, the main function of the leaf is to help ripening, though the function is related to ear formation and elongation of stem under normal conditions. In this way, the expressions employed above seem not always to apply. In this connection, there should be some other method to classify leaves on the main stem to correlate position and functions of leaves. For this purpose, it must be clarified how the number of leaves is changed by environmental conditions and also how the functions of a leaf on some position changes with the change in the number of leaves.

Effect of nutrient elements on number and size of leaves

Rice plants were grown under water culture conditions in the year 1957. A complete culture solution was given for one week after transplanting and then these plants were shifted to culture solutions which were deficient in one element, such as nitrogen, phosphorus, potassium, calcium, magnesium or sulphur. Observations on the number and size of leaves on the main stem were made. The results are given in table 40.

TABLE 40. Leaf-blade length of leaves on main stem of rice plants grown under nutrient deficient conditions (cm)

Name of leaf	Cultural condition						
	Normal	-N	-P	-K	-Ca	-Mg	-S
13/0	—	—	—	—	—	27	—
12/0	24	—	—	15	13	45	—
11/0	40	—	—	26	31	52	25
10/0	52	23	15	31	37	47	36
9/0	44	30	21	32	41	43	40
8/0	34	29	24	25	33	33	34
7/0	24	19	18	21	24	23	22
6/0	20	14	15	19	19	18	18
5/0	15	11	12	15	15	15	15

(In all cases, 4/0=11, 3/0=7, 2/0=4, 1/0=1.2).

From the data, it is evident that the number of leaves on the main stem is changed by nutrient conditions. If nitrogen, phosphorus or sulphur are deficient, the number decreases. Nitrogen, phosphorus and sulphur are essential elements for protein. So, it can be said that if one of the elements which

are necessary for protein is deficient, the number of leaves decreases. On the other hand, if magnesium is deficient, the leaf number increases.

The length of leaf-blade becomes shorter, if a plant is deficient in some elements. However, if magnesium is deficient, the leaf length becomes longer.

If the number of leaves on the main stem is increased, the number of leaves on the node where tiller emerges, increases. So, by increasing the number of leaves on the main stem, generally, the number of tillers can be increased. Therefore, nitrogen, phosphorus and sulphur are important to the increase of tiller number.

Relation between time of nitrogen application and number and size of leaves

To know the effects of nutritional conditions on the number of leaves on the main stem and also on the size of each leaf, the following experiment was conducted in the year 1954.

Since nitrogen affects both the number and size of leaves most prominently, this element was chosen as the variable. By differentiating the time of nitrogen application, 26 treatments were made as shown in figure 49. Each pot contains four liters of culture solution which was renewed once every five days. Two uniform plants were grown in each pot.

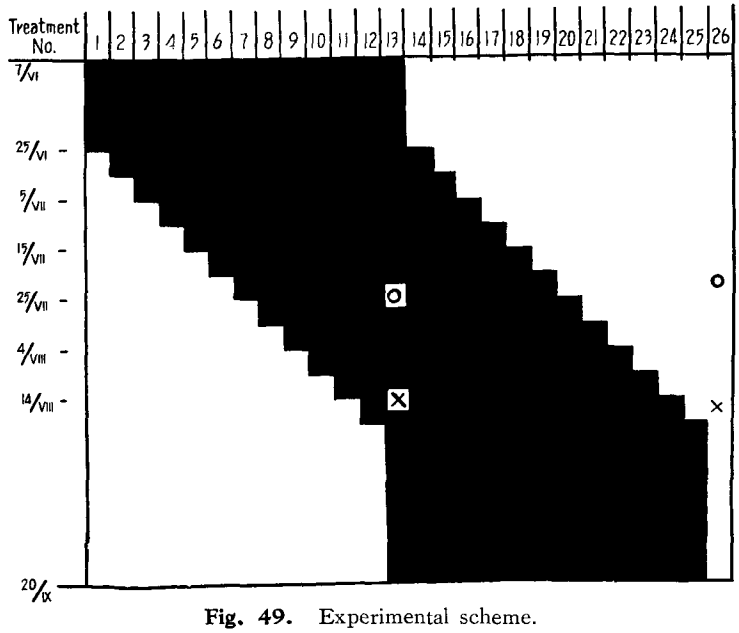

Fig. 49. Experimental scheme.

■ Nitrogen supply at 60 ppm N. ○ Ear initiation. × Ear emergence.

Observations were made on the leaf-blade length of leaves on the main stem. The results[65] are given in table 41 and figure 50.

The number of leaves on the main stem changes by time of the nitrogen supply. The flag leaf of No. 1 and No. 2 treatments is 10/0, that of No. 3 – No. 6 treatments is 11/0 and that of No. 7 –No. 13 treatments is 12/0. 12/0 is the flag leaf of treatments No. 14 –No. 16. In treatments between No. 16 and No. 19, the position of the flag leaf drops one by one and for treatments between No. 19 and No. 26, 9/0 is the flag leaf. From the data described here, it can be concluded that the shorter the duration of the nitrogen supply, the smaller the number of leaves on the main stem.

TABLE 41. Length of leaf-blade (cm)

Name of leaf	No. of treatment												
	1	2	3	4	5	6	7	8	9	10	11	12	13
12/0	—	—	—	—	—	—	14	21	28	28	28	28	28
11/0	—	—	13	15	18	25	31	41	47	47	47	47	47
10/0	19	20	22	25	30	43	43	43	43	43	43	43	43
9/0	21	22	23	31	36	36	36	36	36	36	36	36	36
8/0	21	25	30	32	32	32	32	32	32	32	32	32	32
7/0	22	24	26	26	26	26	26	26	26	26	26	26	26
6/0	19	19	19	19	19	19	19	19	19	19	19	19	19
5/0	16	16	16	16	16	16	16	16	16	16	16	16	16

Name of leaf	No. of treatment												
	14	15	16	17	18	19	20	21	22	23	24	25	26
12/0	28	29	30	—	—	—	—	—	—	—	—	—	—
11/0	47	49	49	31	—	—	—	—	—	—	—	—	—
10/0	44	50	50	45	25	—	—	—	—	—	—	—	—
9/0	37	39	43	45	39	26	15	11	9	9	9	9	9
8/0	32	33	35	37	32	19	15	15	15	15	15	15	15
7/0	27	28	27	23	15	15	15	15	15	15	15	15	15
6/0	22	20	16	14	14	14	14	14	14	14	14	14	14
5/0	12	12	12	12	12	12	12	12	12	12	12	12	12

(In all cases, 4/0=11, 3/0=8, 2/0=4, 1/0=1.5)

The length of leaves is also changed by the duration of the nitrogen supply. Between No. 1 and No. 2, 10/0 is the flag leaf and the leaf-blade of 10/0–7/0 is longer in the case of No. 2 than in the case of No. 1. Between No. 3 and No. 6, 11/0 is the flag leaf and the leaf-blade of 11/0–9/0 becomes shorter

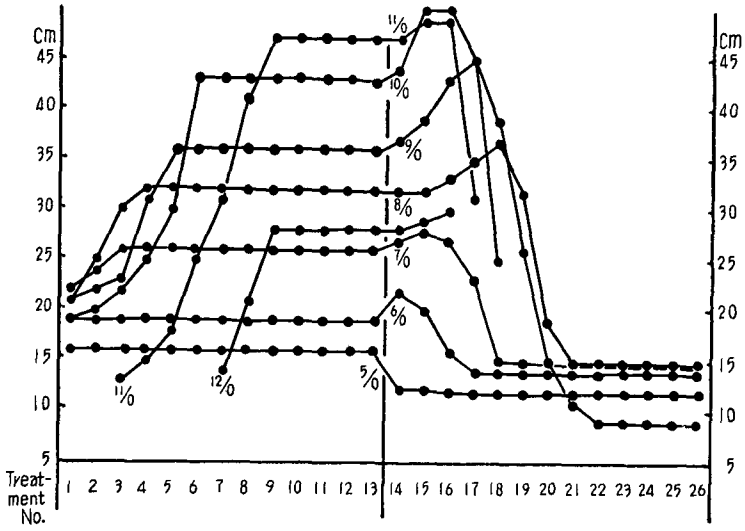

Fig. 50. Length of leaf-blade.

by shortening the duration of the nitrogen supply. Between No. 7 and No. 13, 12/0 is the flag leaf. Between No. 6 and No. 9, the length becomes shorter in association with shortening the duration of the nitrogen supply. However, between No. 9 and No. 13, the length of 12/0 remained constant. Between No. 14 and No. 16, 12/0 is the flag leaf, and here, the length of leaf-blades between 12/0 and 8/0 becomes a little longer by delaying the starting of the nitrogen supply. After No. 17, the number of leaves decreases and the size of leaves becomes remarkably smaller by shortening the duration of the nitrogen supply. However, after No. 20, no change takes place in the number and size of leaves.

From these data, it can be said that the longer the duration of the nitrogen supply, the longer the leaf-blade.

Each leaf has characteristic functions corresponding to its position on the stem. By their characteristic functions, leaves on the main stem were classified into three groups; that is, leaves which are related to tillering; leaves which are related to differentiation of ear-primordium and elongation of stem; and leaves which are related to ripening. In the case of the normal rice plant, these three groups are 3/0–5/0, 6/0–9/0 and 10/0–12/0. However, the number of leaves on the main stem is changed by conditions of nutrient supply. Because of this change in leaf number, defining the leaf function becomes more complicated.

For example, if 12/0 is the flag leaf, 9/0 is the leaf which is intimately related to differentiation of ear-primordium and elongation of stem, on the other hand, if 10/0 is the flag leaf, 9/0 is the leaf which is related to ripening. By

this way, the function of a leaf which is on a definite position, changes in accordance with number of leaves on the main stem.

A rice plant is constructed from many leaves, internodes and tillers.

Main stems can be defined as the repetition of units which are constructed from three organs, i.e. leaf, internode and tiller. These three organs construct a unit by the arrangement as shown in figure 51.

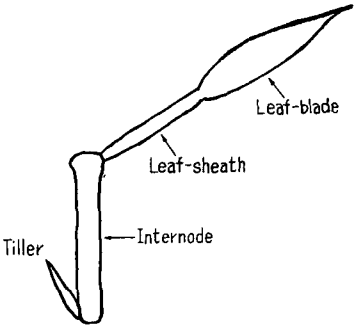

Fig. 51. Constitution of a unit of rice plant.

In some cases, the internode fails to elongate, with the result, that the unit seems to be constructed only from leaf and tiller. Also in some cases, the tiller fails to grow, with the result, that the unit seems to be constructed from leaf and internode. In other cases, both the tiller and internode fail to develop. Accordingly, the units are classified into three types: the first type is constructed from leaf and tiller; the second type is constructed from only leaf; and the third type is constructed from leaf and internode.

To know the relation between type of unit and position on the main stem, observations were made on positions of tillers and also on positions of elongated internodes by using the rice plants grown under the conditions described in figure 49. The results[65] are given in figure 52.

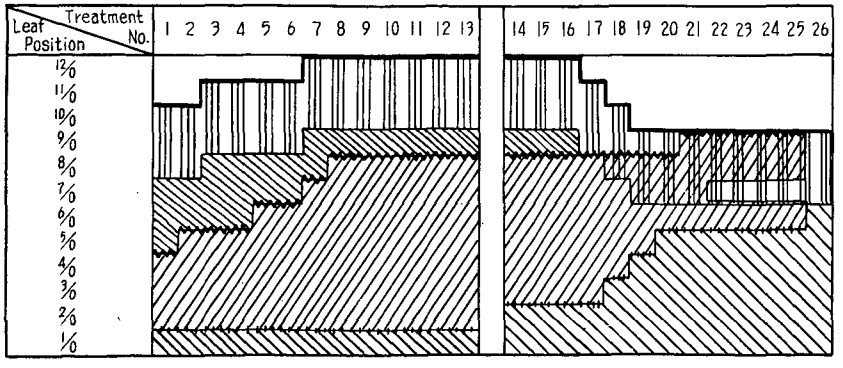

Fig. 52. Position of units of various types on main stem.

- Position of the flag leaf.
- Position of the highest tiller.
- Position of the lowest tiller.
- Units having tiller.
- Units having neither tiller nor elongated internode.
- Units having elongated internode.

Between No. 1 and No. 8, the position of the highest tiller rises by increasing the duration of the nitrogen supply. It is kept at 8/0 in the case of treatments between No. 8 and No. 13. It is kept also at 8/0 between No. 14 and No. 20. It rises to 9/0 by starting the nitrogen supply at very late stages of growth. By delaying the starting of the nitrogen supply, the position of the lowest tiller rises. The discussions on the position of the flag leaf were made earlier. Three internodes elongate regardless of the duration of the nitrogen supply. A few units have neither tiller nor elongated internode.

Under normal nutrient conditions, the units of the first type are at 2/0–7/0 (or 8/0), the units of the second type are at 8/0 and 9/0, and the units of the third type are at 10/0–12/0. This classification of leaves on the main stem is almost the same as that which is given in figure 35.

Tillering is main function of the leaves which belong to the first type of units. Such leaves can be called the "leaf for vegetative growth". The leaves which belong to the third type of units are related to maturing. Such leaves can be called the "leaf for reproductive growth". The leaves which belong to the second type of units are the "transitional leaf".

The leaf number of the first type of units decreases or increases corresponding to a shorter or longer duration of the nitrogen supply. The leaf number of the third type of units is always three. The leaf number of the second type of units changes remarkably. If the nitrogen supply is stopped at early stages of growth, the leaf number is more than three. On the other hand, if the nitrogen supply is started at a late stage of growth, the leaf number decreases. Sometimes, the leaf number becomes negative, because some units have a tiller as well as an elongated internode.

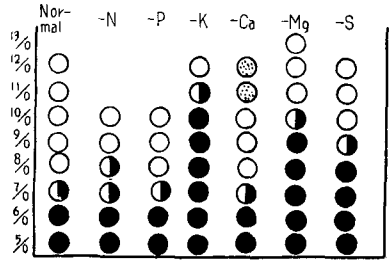

Fig. 53. Condition of leaves on main stem of rice plants which are deficient in some element.

○ Healthy leaves.
◑ Partially dead leaves.
● Dead leaves.
⊛ Leaves showing calcium deficiency.

Relation between photosynthetic activity and element content of leaves

Many experiments have been conducted to determine the relation between photosynthetic activity and nutrient condition of plants. These experiments have pointed out generally that if a plant is deficient in some element, photosynthetic activity of the plant is low. For example, GREGORY et al.[66] reported that if barley is deficient in nitrogen or potassium, photosynthetic activity becomes low. ISHIZUKA also showed that wheat plants which are deficient in potassium, calcium, magnesium or sulphur are weak in photosynthetic activity. However, there are very few reports on the effect of elements on the leaf area which is effective for photosynthesis and the effect of element content of leaf on photosynthetic activity per unit area of the leaf. Photosynthetic activity of a leaf is a function of leaf area and photosynthetic activity per unit area of the leaf. Even if the size of a leaf is great, if photosynthetic activity per unit area is low, the activity of the leaf can not be great.

In order to study the relation between photosynthetic activity per unit leaf area and the nutrient condition, observations were made in 1957 on rice plants grown where various elements were deficient.

Figure 53 shows the condition of leaves on the main stem of rice plants grown under various conditions at the flowering stage. At flowering, there are five healthy leaves on the main stem of normal rice plants. If some element is insufficient, death of lower leaves takes place. Nitrogen deficient plants have only two healthy leaves on the main stem. If phosphorus or sulphur is deficient, there are three healthy leaves. Potassium deficient plants have only one healthy leaf due to the death of lower leaves. Magnesium deficient plants have more leaves on the main stem. However, the death of lower leaves is so serious that only three leaves are alive at the flowering stage. Calcium deficient plants have five live leaves, but the flag leaf and the second leaf from the top show calcium deficient symptomes. Generally speaking, the death of lower leaves is serious, if the translocation quotient of the deficient element is high and the death is slight, if the quotient is low. From these facts, it is evident that leaf size shows only one part of photosynthetic activity. When there is death of the lower leaves, the photosynthetic leaf area is far smaller than the total leaf area. Moreover, the lower leaves which are partially dead seems to be low in photosynthetic activity.

On July 21, 1957, estimations were made of photosynthetic activity of each leaf on the main stem of rice plants which were grown under deficient conditions in various elements. Seven rice plants, each for normal, nitrogen deficient, phosphorus deificient, potassium difficient, calcium deficient, magnesium deficient and sulphur deficient plants, were shifted to 200 ml Erlenmayer flasks

which contained appropriate culture solutions. These plants were placed in a glass box. Then, $C^{14}O_2$ was generated in the box by introducing 10% $HClO_4$ solution into a beaker containing $BaC^{14}O_3$ (ca. 100 μc) which is hanging from ceiling of the glass box as shown in figure 36. Thirty minutes after the generation of $C^{14}O_2$, plants were taken out, leaves on the main stem were separated. After measuring leaf area, these leaves were dried, weighed and powdered. Determination of assimilated C^{14} was made on 10 mg of powdered samples using G. M. counter. The results[67] are given in table 42.

TABLE 42. Photosynthetic activity of leaves of rice plants which are deficient in various elements

(cpm/10 mg)

Name of leaf	Condition of rice plants						
	Normal	-N	-P	-K	-Ca	-Mg	-S
8/0	2444	2290	1576	1468	2284	1424	1548
7/0	2610	2088	1308	2002	2962	1568	960
6/0	2396	1326	1388	2210	2732	1462	584
5/0	2160	778	908	1368	2516	690	422
4/0	1964	344	30	74	2160	300	312

The activity expressed on an area basis shows almost same tendency as that expressed on a dry matter basis. From these data, it is evident that photosynthetic activity of the leaves of a plant which is deficient in some element is less than that of normal plants. The activity of the lower leaves are extremely low. This seems to be related with partial death of lower leaves. However, the activity of the calcium deficient plant seems to be higher than for the normal plant.

The activity of leaves varies according to their position on stem. Element content of these leaves also varies according to the leaf position. Therefore, there should be some relation between photosynthetic activity and element content of these leaves. To find out this relation, the element contents of each leaf were estimated. The results are given in table 43.

From these data, the graphs whicn show the relation between element content and photosynthetic activity of each leaf were prepared in figure 54.

Regarding nitrogen, the higher the nitrogen content, the higher the photosynthetic activity. Between 4% and 2%, the activity is decreased by the decrease in nitrogen content. If the nitrogen content decreases below 2%, the photosynthetic activity becomes remarkably low. The activity is almost negligible, if nitrogen content is lower than 0.7%.

TABLE 43. Element content of leaves on main stem

(% on dry matter basis)

Condition of plant	Position of leaf	Element					
		N	P_2O_5	K_2O	CaO	MgO	SO_3
Normal	8/0	3.76	0.72	2.43	0.30	0.56	1.05
	7/0	3.76	0.77	2.63	0.30	0.58	1.12
	6/0	3.72	0.64	2.42	0.38	0.62	1.18
	5/0	2.86	0.61	1.50	0.56	0.43	0.95
	4/0	2.56	0.59	1.30	0.72	0.38	0.83
Deficient in respective element	8/0	2.76	0.47	0.96	0.14	0.38	0.48
	7/0	2.36	0.40	0.92	0.18	0.25	0.40
	6/0	1.26	0.37	0.86	0.26	0.18	0.25
	5/0	1.02	0.30	0.56	0.34	0.09	0.23
	4/0	0.92	0.20	0.38	0.39	0.07	0.23

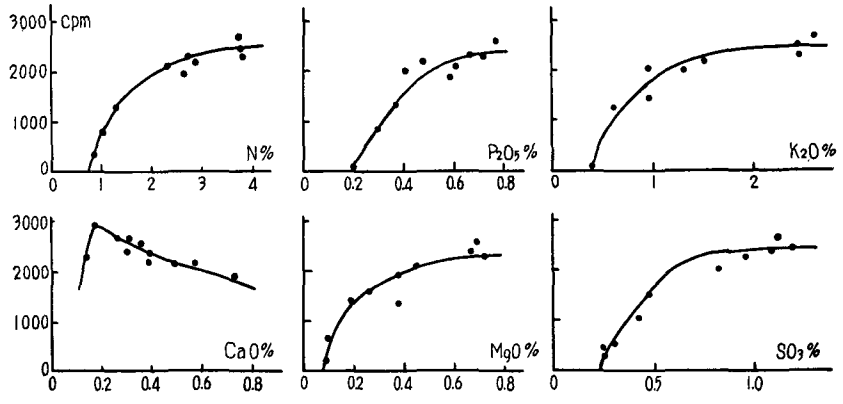

Fig. 54. Relation between element content and photosynthetic activity of leaves.

The higher the phosphorus content, the greater the photosynthetic activity. However, increasing the phosphorus content higher than 0.5%, does not increase the activity of photosynthesis remarkably. The photosynthetic activity decreases remarkably with a decrease of phosphorus content below 0.5%. It becomes negligible, when the phosphorus content goes down below 0.2%.

If the potassium content is higher than 1.5%, no change in photosynthetic activity is produced by changing the potassium content. Below 1.5%, the photosynthetic activity decreases with the decrease of potassium content until it reaches 0.4% where the activity is almost nil.

The relation between calcium content and photosynthetic activity is somewhat different from the other cases. The activity becomes higher by decrease of calcium content until it reaches 0.2%. However, if the calcium content decreases below 0.2%, the activity becomes remarkably lower.

In association with a decrease of magnesium content, photosynthetic activity decreases. The decrease of photosynthetic activity is very slow until 0.4%, but it becomes very steep when it decreases below this level. The activity reaches almost negligible at 0.1%.

There is almost no relation between sulphur content and photosynthetic activity, if the sulphur content is above 0.7%. If the content of sulphur is below 0.7%, the activity is decreased remarkably by the decrease of sulphur content to 0.3% where the activity is negligible.

As described above, the photosynthetic activity is intimately related to the content of elements. To accelerate some function, it is not enough to increase size of those leaves related to that function, but also it is necessary to maintain the element content of these leaves at suitable level when these leaves are discharging their characteristic functions.

TRANSLOCATION OF SUBSTANCES

The growth process of organs is a process of substance accumulation. Organs are constructed from organic substances and also from various elements. These substances which accumulate in the growing organs, are translocated from those leaves where photosynthesis is taking place, from the roots where uptake of elements is going on, and also from older organs in which these substances have been stored.

In order to increase the size of some organ, it is necessary to favor the accumulation of these essential substances in that organ. For this purpose, there is two methods. The one is to activativate photosynthesis or uptake of elements at the critical growth stage, and the other is to provide an abundance of stored substances in older organs.

To make this possible, detail behavior of the translocation of various substances must be clarified.

Translocation of assimilation products

ISHIZUKA and the author[68] studied translocation of carbohydrates and protein from straw to grain during the ripening phase. It was reported that starch or protein which are stored in straw, translocate to grain as non-reducing sugars or as amino acids. The carbohydrates which accumulate in grain are primarilly those assimilation products produced during the ripening phase. The percentage

of carbohydrates, which are stored in the straw until the flowering stage and then are translocated into the grain, is almost 10% of the total carbohydrates in grain at the time of harvest.

MURAYAMA and YOSHINO[36] also studied the translocation of carbohydrates from straw to grain and reported almost the same conclusions. However, they reported as much as 30% of the total carbohydrates in the grain at harvest are those once stored in the straw. They pointed out that these carbohydrates (later translocated) are mainly stored in leaf-sheaths and in internodes. They studied farther[69] on this point under various environmental conditions and pointed out that storage of carbohydrates in straw is greater with lower nitrogen level and also with longer duration of growth.

However, translocation of organic substances is very difficult to study, because organic substances are formed or decomposed easily and quickly, and the change of the amount of these organic substances in each organ does not show an exact pattern of translocation among organs.

TABLE 44. Distribution of C^{14}, assimilated on July 26, on August 1

Name of organ	Position	Dry weight (mg)	cpm/10mg
Leaf-blade	12/0	41	216
	11/0	156	640
	10/0	208	1240
	9/0	154	856
	8/0	104	572
	7/0	43	324
	6/0	27	392
Leaf-sheath	12/0	8	212
	11/0	63	200
	10/0	253	936
	9/0	233	384
	8/0	143	224
	7/0	63	192
	6/0	28	152
Ear primordium	—	6	156
Stem	—	54	62
Stem base	—	113	30
Roots	—	300	30

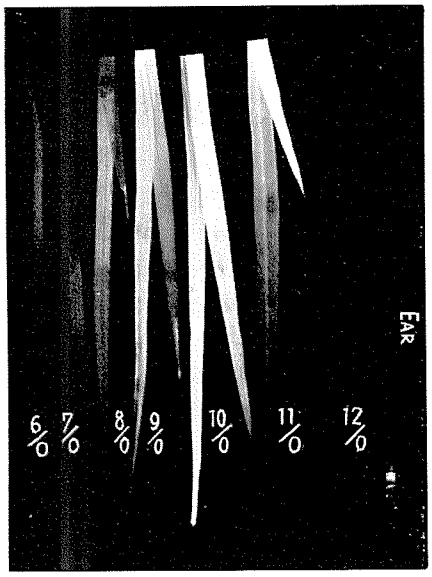

Fig. 55. Distribution of C^{14}, assimilated on July 20, on August 1.

Studies in which C^{14} is used are more precise for the study of this problem. Translocation of assimilation products from organs where assimilation is taking place and also translocation from organs where these are accumulated by primary translocation was traced by using C^{14}.

Two rice plants which had been grown under normal water culture conditions were exposed to $C^{14}O_2$ on July 20. One of these rice plants was uprooted at 30 minutes after exposure to $C^{14}O_2$ and the C^{14} in each organ was estimated. The data are given in table 27 and in figure 37. The other rice plant was kept under normal conditions for another 12 days. The C^{14} in each organ on August 1 was estimated. The results are given in table 44. Figure 55 is the radio-autograph which shows distribution of the C^{14} in each organ.

The data show that C^{14} is most abundant in the leaf-blade and leaf-sheath of 10/0. From the radio-autograph given in figure 55, it can be seen that C^{14} is higher in the base of leaf-blade of 10/0 than in the tip of the leaf. In the tip of 11/0, remarkable amounts of C^{14} are located.

Figure 37 shows the distribution of C^{14} on July 20 when the C^{14} was assimilated. At that time, the tip of 10/0 had been completed, the base of the leaf was growing and the tip of 11/0 started to grow. The base of 11/0 leaf-blade, the 12/0, the stem and the ear grew after July 20. Not much C^{14} is located in these organs.

From figure 37 and figure 55, it is very clear that assimilation products were translocated to these organs which were growing when these were assimilated. They were formed into constituents of the organs and lost their ability to re-translocate.

By the same method described above, distribution of C^{14} which was assimilated on August 21, was studied on September 1. Table 45 shows the results.

TABLE 45. Distribution of C^{14}, assimilated on August 21, on September 1

Name of organ	Position	Dry weight (mg)	cpm/10 mg
Grains	—	1204	120
Husks	—	177	110
Peduncle	—	63	114
Leaf-blade	12/0	146	122
	11/0	229	114
	10/0	225	102
	9/0	148	76
	8/0	64	64
Leaf-sheath	12/0	190	36
	11/0	213	50
	10/0	170	32
	9/0	166	50
	8/0	101	32
Internode	Ear–12/0	149	220
	12/0–11/0	300	190
	11/0–10/0	439	122
	10/0– 9/0	312	94
Stem base	—	130	34
Roots	—	393	36

On August 21, the rice plants were at the milky stage. On September 1, the grains, the internode between ear and 12/0 and also the internode between 12/0 and 11/0 are higher in C^{14} than in other organs. This means that C^{14} assimilated at the milky stage, translocates to the grains through the internodes.

To study the behavior of assimilation products in greater details, $C^{14}O_2$ was given to rice plant on June 15. At this stage, active photosynthesis was

taking place at 4/0 and 6/0 was under elongation. Fractionations of C^{14} were made on 4/0 just after C^{14} assimilation and also on 4/0 and 6/0, 10 days after assimilation, in which the C^{14} was divided into three fractions, i.e. the alcohol soluble, the NaOH soluble and the residual fractions. The data, expressed on the basis of total C^{14}, are given in table 46.

TABLE 46. C^{14} in various fractions

Fraction	Name of leaf		
	4/0 (on June 15)	4/0 (on June 25)	6/0 (on June 25)
Alcohol soluble[1)]	63	46	22
NaOH soluble[2)]	28	45	49
Residue	9	9	29

1) 80% alcohol extract. 2) N NaOH extract.

This table shows that just after assimilation, more than 60% of the assimilated C^{14} is in the alcohol soluble fraction and about 30% is in the NaOH soluble fraction. After 10 days, the alcohol soluble fraction decreases and the NaOH soluble fraction increases. This means that assimilation products are translocated as the alcohol soluble fraction. In the case of 6/0, the alcohol soluble fraction is only 20%. The NaOH soluble fraction and the residual fraction are greater than in the case of 4/0. This suggests that assimilation products enter into growing organs as the alcohol soluble fraction and these are taken into the NaOH soluble or the residual fractions, i.e. protein, cellulose etc.

The alcohol soluble fraction of 4/0 on June 15 was developed by two dimention paper-chromatography by using butanol : acetic acid : water and phenol : water, and radio-autograph of the paper chromatogram was made. This paper-chromatogram shows that sucrose is the most predominant radio-active substance. Glucose, fructose and an unknown substance also show some radio-activity. This is almost in agreement with the results obtained by VERNON et al.[70] SWANSON et al.[71] stated that sucrose is the translocation form of sugars.

From these data, it can be concluded that $C^{14}O_2$ is primarily formed into sucrose at the leaf where photosynthesis is taking place, it is translocated to growing organs, and there it is converted into protein, cellulose, etc. After it is converted into these compounds, re-translocation of the carbon decreases.

In conclusion, in order to increase the size of some organ, it is necessary to provide a high activity of photosynthesis at that stage when the organ is growing. Growth of an organ seems not to depend greatly upon stored organic substances in older organs.

Translocation of elements

The process of accumulation and outflow of elements to or out of leaves of those rice plants grown under normal conditions has been discussed previously. At that time, it was pointed out that some elements translocate more easily than others. Nitrogen and phosphorus are the elements which are very mobile. On the other hand, calcium once deposited is very difficult to translocate.

Here, behavior of elements under various conditions were studied to get clearer ideas on accumulation and translocation of these elements. Through this study, methods to increase the accumulation of essential elements in growing organs will be studied. In this experiment, phosphorus and calcium were chosen, because these elements have respective radio-active isotopes and the former characterizes elements which have high mobility and the later represents element which have low mobility.

Rice plants were grown under normal water culture conditions in the year 1953. On July 13, these plants were shifted to a culture solution without phosphorus. Determination of phosphorus in each organ were carried out at the day when the rice plants were shifted to the zero phosphorus culture solution and also 5 and 10 days after the shifting. The rice plants showed phosphorus deficienct symptomes 10 days after stoppage of the phosphorus supply.

Table 47 shows changes in the content and amount of phosphorus in each organ after the shifting.[72] As shown in figure 56, the phosphorus content of each leaf decreases after the stoppage of phosphorus supply. This is more remarkable in the cases of the lower leaves than the upper leaves. The phosphorus content of the uppermost leaf remains fairly high even 10 days after the stoppage. However, the content of the lower leaves, 4/0 and 3/0, is extremely low, and these leaves had started to die. These results suggest that after the stoppage of phosphorus supply, phosphorus in the lower leaves is translocated to the upper leaves. This is clearly shown in figure 56 in which the amount of phosphorus in each leaf at successive stages are shown. Due to this translocation, the lower leaves die, while, the upper leaves continues to grow. By this way, phosphorus stored in the lower leaves is re-utilized by the upper leaves.

Regarding tillers, the amount of phosphorus in the lower tiller remained fairly constant. Since these lower tillers are old enough to be independent at that stage, only small amounts of phosphorus translocation take place between the main stem and these tillers. However, the upper tillers, i.e. the 4- and 5-tiller, were not independent when the phosphorus supply was stopped, as these tillers were receiving phosphorus from the main stem even after the stoppage of phosphorus supply.

TABLE 47. Content and amount of phosphorus in each organ at or after stoppage of phosphorus supply

Name of organ	Number of days after stoppage					
	0	5	10	0	5	10
	P_2O_5%			P_2O_5 (mg/2 leaves)		
11/0	—	—	1.15	—	—	0.21
10/0	—	1.07	0.61	—	0.07	1.59
9/0	2.10	0.84	0.43	0.67	1.60	1.81
8/0	1.08	0.52	0.38	2.38	2.27	1.20
7/0	1.06	0.43	0.33	2.31	1.19	0.98
6/0	1.01	0.48	0.34	1.68	0.77	0.62
5/0	0.93	0.51	0.33	0.81	0.52	0.34
4/0	0.98	0.35	0.18	0.57	0.18	0.08
3/0	0.95	0.31	0.20	0.24	0.08	0.04
Stem	1.83	0.78	0.62	0.87	0.64	0.69
Roots	1.05	0.61	0.43	3.75	4.03	4.63
5-tiller	1.75	0.80	0.62	1.09	1.49	1.57
4-tiller	1.22	0.68	0.62	2.55	2.92	3.65
3-tiller	1.05	0.60	0.47	4.35	4.71	4.72
2-tiller	0.90	0.54	0.42	6.38	6.42	6.30

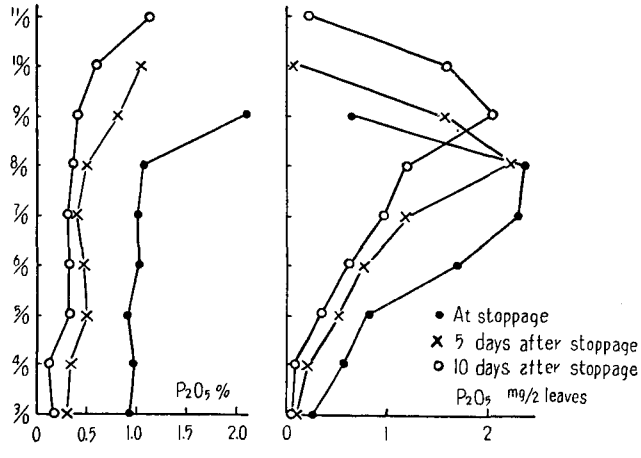

Fig. 56. Phosphorus content of each leaf at or after stoppage of phosphorus supply.

In a companion experiment, rice plants were grown in a culture solution deficient in phosphorus. On July 13, these were shifted to a complete culture solution. The phosphorus content of each leaf is determined at the time of shifting and also 5 and 10 days after starting of the phosphorus supply.

Table 48 and figure 57 show the results.[72]

TABLE 48. Phosphorus content of each leaf at or after starting of phosphorus supply

(P_2O_5%)

Name of leaf	Days after starting		
	0	5	10
10/0	—	—	2.38
9/0	—	2.39	2.09
8/0	0.82	2.00	1.97
7/0	0.35	1.52	1.95
6/0	0.21	0.76	1.51
5/0	0.18	0.53	1.24
4/0	0.23	0.30	0.33
3/0	0.32	0.32	0.29

Five days after the starting of phosphorus supply, the phosphorus content of upper leaves rose remarkably, but that of the lower leaves remained rather low. However, after 10 days, the content of upper leaves remained at almost the same level as the content after 5 days, but that of the lower leaves increased remarkably. No change in phosphorus content occurred at 3/0 and 4/0, these leaves were dead at that time.

These results suggest that if a phosphorus deficient plant absorbs phosphorus, it goes into growing point first and after saturating the growing point, the phosphorus starts to enter into the lower leaves.

There should be some difference of behavior between the phosphorus which is absorbed at an early stage and that which is absorbed at a late stage. It is also expected that mobility of posphorus in plant body is affected by conditions of the phosphorus supply to the plant.

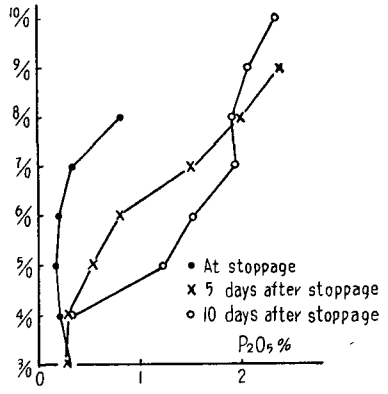

Fig. 57. Phosphorus content of each leaf at or after strting of phosphorus supply.

To clarify these problems, an experiment was conducted by using P^{32} in the year 1953. P^{32} was supplied to water cultured rice plants on June 7. Then, these rice plants were grown with or without phosphorus. On July 1, the rice plants which had been receiving a complete culture solution were shifted to a zero phosphorus culture solution and the rice plants which had been receiving a zero phosphorus culture solution were shifted to a complete culture solution. At or 3 and 10 days after the changes of composition of culture solution, analyses were made on the content of total phosphorus and P^{32} in each leaf of these rice plants.

Table 49 shows the results on the rice plant to which the posphorus supply was discontinued on July 1. In this case, P^{32} represents the phosphorus which is absorbed at early stage and total phosphorus represents the phosphorus absorbed at late stage.

TABLE 49. Content of total phosphorus and P^{32} at or after stoppage of phosphorus supply

Name of leaf	Number of days after stoppage					
	0	5	10	0	5	10
	P_2O_5%			P^{32}*		
11/0	—		1.40	—	—	165
10/0	—	1.30	0.75	—	39	58
9/0	1.40	1.10	0.60	46	45	48
8/0	1.30	1.10	0.55	54	63	67
7/0	1.00	1.00	0.50	66	77	86
6/0	1.00	1.00	0.50	138	160	134
5/0	1.00	1.10	0.40	188	215	145

* The activity is expressed on the basis of the average cpm of all leaves.

The data on total phosphorus are in good agreement with the results which were given in table 47. However, the behavior of P^{32} is completely different from that of total phosphorus.

When the phosphorus supply was stopped, the lower the position of leaf, the higher the P^{32} content. This means that phosphorus absorbed at an early stage is located more in the lower leaves than in the upper leaves and that phosphorus absorbed at the late stage is located more in the upper leaves. Three days after discontinuation of the phosphorus supply, the difference of P^{32} contents among leaves becomes greater, though the content of total phosphorus in the upper leaves is higher than in the lower leaves. This means that after discontinuation of the phosphorus supply, phosphorus absorbed at the late stage

translocates to growing leaves more actively than phosphorus absorbed at the early stage. However, 10 days after the stoppage, when rice plants started to suffer from phosphorus deficiency, growing leaves contain rather high level of P^{32}. This means that phosphorus absorbed at either late stage or early stage translocates to growing point rather actively, if the plant is in phosphorus deficient condition.

Table 50 gives the results on the rice plants which were shifted from the zero phosphorus culture solution to the complete nutrient on July 1. In the phosphorus deficient plants, both total phosphorus and P^{32} are distributed in the upper leaves more than in the lower leaves. Three days after the starting of phosphorus supply, the upper leaves contain more total phosphorus as well as more P^{32} than the lower leaves. Phosphorus absorbed during these 3 days enters into young leaves and at the same time phosphorus in the lower leaves translocates to young leaves. The mobility of phosphorus in the plant was kept high at this stage. However, 10 days after the phosphorus supply began, the content of total phosphorus is higher in the growing leaves than in the lower leaves, but the P^{32} content of the upper leaves is not so high as that of the lower leaves. This means that at this stage, the plants become sufficient in phosphorus and phosphorus in the lower leaves become stable and only a little translocation takes place from the lower to upper leaves. Under such conditions, only the phosphorus absorbed at this stage actively enters into the growing leaves.

TABLE 50. Content of total phosphorus and P^{32} at or after starting phosphorus supply

Name of leaf	Number of days after starting					
	0	5	10	0	5	10
	P_2O_5%			P^{32}*		
10/0	—	—	1.30	—	—	49
9/0	—	1.50	1.30	—	243	59
8/0	1.00	0.75	1.10	212	108	164
7/0	0.40	0.56	1.00	86	55	97
6/0	0.24	0.56	1.00	55	57	91
5/0	0.24	0.57	0.90	47	35	100

* The activity is expressed on the basis of the average cpm of all leaves.

Generally speaking, when a plant is sufficient in phosphorus, phosphorus in that plant is rather stable, and only small amounts translocate to the growing point. However, if a plant is deficient in phosphorus, phosphorus in that plant

becomes mobile and larger quantities translocate to the growing points.

Calcium is an element which is very difficult to efflux, once it is deposited in an organ. To study the behavior of calcium more in detail, an experiment was carried out by using Ca^{45}.

The Ca^{45} was given to rice plant on July 5, when 9/0 is started to grow. After this treatment, some plants were grown with a complete nutrient and the other plants were grown with a zero calcium nutrient. On September 15, Ca^{45} in each leaf was determined and the data are given in table 51. This table shows very clearly that the translocation of calcium from the lower to upper leaves is extremely minute. The translocation is slightly more active under calcium deficient condition than under calcium sufficient condition.

TABLE 51. Distribution of Ca^{45} which was absorbed on July 5, on Sept. 15, in each leaf

(cpm/g)

Name of leaf	Cultural condition	
	Complete	No calcium
12/0	2	5
11/0	2	6
10/0	5	10
9/0	9	31
8/0	319	332
7/0	360	315

Generally, mobile elements such as phosphorus, nitrogen or sulphur in the lower leaves translocate to the upper growing organs to maintain the growth, if the supply of these elements from the roots is stopped. Due to this translocation, the content of these elements in the lower leaves decreases remarkably and finaly these lower leaves die. Those elements stored in the lower leaves translocate to the growing leaves where they are re-utilized. If the storage of an element in the lower leaves is great, the growth of the rice plants can be kept active for some time even after discontinuation of supply of this element. The content of this element in the lower leaves decreases with the translocation and finally the element in these leaves is exhausted. Photosynthetic activity of these lower leaves becomes lower due to this translocation. In this way, accumulation of the limiting element as well as the product of photosynthesis in the growing point decreases. The organs which grow under such conditions become smaller.

If the limiting element is given to those rice plants which are deficient in

the element, this element enters into the growing organs first. Thus, some time (may be more than 5 days) is required for this element to enter into the lower leaves. The photosynthetic activity of these lower leaves can be activated only after this deficient element enters into these leaves. Unless these lower leaves are active in photosynthesis, the growing organs can not receive assimilation products sufficiently.

These results suggest that to make some organ large, it is not sufficient to supply the required elements to the organ when it is growing, but it is also necessary to keep the content of these elements of lower leaves at suitable level under which active photosynthesis can be carried on. The amount of these elements in rice plants must be kept at that level to maintain an optimum supply of these elements to the growing points and also to maintain in adequate for photosynthesis in the lower leaves. In the cases of these mobile elements, the total amount in the plant body is of importance, however, the time when these elements are absorbed is not so important. On the other hand, the elements which are not mobile, such as calcium, are very difficult to be re-utilized. These elements must be absorbed from roots at the time when these are required. In the cases of these elements, the total amount in plant body is not important, however, the time when these elements are absorbed is of importance.

ABSTRACTS

1: In the studies on the nutrio-physiology of the rice plant, in the past, the rice plant has been treated as a whole plant. But it is the author's opinion that attention must be paid to the fact that a whole plant consists of many tillers and these tillers are constructed from many leaves. At any growth stage of a whole plant, some leaves are young and are increasing in weight, while some are old and are decreasing in weight. So, if it is desired to know quantitatively the physiological condition of the rice plant at any stage of growth, analytical studies are necessary in which each of the many organs that make up the whole plant is dealt with. These present studies are to ascertain the characteristics of the physiological conditions; the functions of the leaf at a definite position; and the mechanism through which a tiller is constructed of many leaves; and a whole plant is constructed of many tillers.

2: These studies were performed by using the variety *Chuseieiko*, medium duration variety of rice plant in Hokkaido. It was grown in the fields at the Hokkaido Agricultural Experiment Station or under water culture conditions in the glass-house at Hokkaido University during the years 1952–'57.

3: During the growth process of a leaf, accumulation of inorganic elements in it takes place in the following order:

Phosphorus, nitrogen, sulphur, potassium, magnesium and calcium.
A predominant motive power of element accumulation in leaf seems to be the metabolic activity of the leaf. The elements which accumulate at early stage of growth are related to metabolism more intimately than those which accumulate at late stage. Mobility of an element from a leaf after accumulation in the leaf is expressed by the translocation quotient which is the percentage of translocated amount of the element from the leaf to its amount when the maximum is reached in the leaf. The translocation quotients decrease from left to right in the following order:

Phosphorus, nitrogen, sulphur, magnesium, potassium and calcium.

4: When a leaf developes, sugar accumulate in the leaf first, starch the next, and then hemicellulose is deposited. Sugar and starch decrease after having reached their maximum amount in the leaf, however, hemicellulose does not decrease.

5: The growth of a rice plant is a chain of leafing processes. The components of a unit of the chain are leaf-blade, leaf-sheath, tiller and internode. Development of these parts takes place in that sequence. Under normal condititions, if the tiller in a unit developes, the internode in the unit does not elongate and if the internode elongates, the tiller does not develope.

6: Leaves on tillers can be represented by their synchronous leaves on the main stem; because synchronous leaves develope under approximately the same conditions, these have almost the same physiological conditions and functions.

7: Leaves on the main stem are classified into three types by the construction of the unit of the chain in which the leaf is included.

First type: The unit to which the leaves of this type belong is composed of leaf-blade, leaf-sheath, and tiller. There is no elongated internode in the unit. The leaves of this type are called the "leaf for vegetative growth".

Second type: The unit to which leaves of this type belong comprise leaf-blade and leaf-sheath. Neither tiller nor elongated internode exists in the unit. Leaves of this type are the "transitional leaf".

Third type: The unit in which leaves of this type are included is composed of leaf-blade, leaf-sheath and elongated internode. There is no tiller in the unit. Leaves of this type are called the "leaf for reproductive growth".

8: Under normal condition, *Chuseieiko* possessed twelve leaves on the main stem. These are classified into the following groups by their function:

1/0 and 2/0: These leaves perform their function during the period from the transplanting to the establishment. The longevity of these leaves is very short.

3/0–5/0 : These leaves are classified into the 1st type. The predominant function of these leaves is to affect tillering. The longevity of these leaves is also short.

6/0–9/0 : These leaves are the 2nd type, though 6/0 and 7/0 possess weak tiller. The main function of these leaves is to affect elongation of internode and development of ear-primordium.

10/0–12/0 : These leaves are the 3rd type. They contribute to maturity. The longevity of these leaves is greater than that of other leaves.

9 : Judging from the metabolism of nitrogen and carbohydrates, leaves on the main stem are characterized as follows;

3/0–5/0 : Accumulation and effluxion of nitrogen and carbohydrate take place in sequence from lower leaf to upper leaf. The time when the maximum amount of nitrogen and carbohydrate in a leaf is attained comes in sequence from lower leaf to upper leaf.

6/0–9/0 : In these leaves, nitrogen and sugar accumulate in lower leaf first and then in upper one, but these constituents do not flow out from these leaves until the ear-initiation stage. Accompanying with the internode elongation, nitrogen and sugar in these leaves decrease.

10/0–12/0 : Nitrogen and starch accumulate in these leaves from lower leaf to upper leaf. These constituents reach the maximum amount at the flowering stage. After flowering, they efflux quickly.

10 : Lower leaf, whose predominant function is tillering, discharges its characteristic function under the physiological condition characterized by high water, high nitrogen, high sulphur, low phosphorus and low carbohydrate contents. Activity of amylase and invertase in the leaf is great when it is functioning. Upper leaf, whose predominant function is maturing, discharges its characteristic function under the conditions characterized by high phosphorus, high starch, low water, low nitrogen and low sulphur content. Phosphorylase and phosphatase in these leaves are active when it is functioning.

11 : At any growth stage of a whole plant, the physiological activity of a leaf which has just completed its formation at that stage is greatest. This leaf is called the "active center leaf". The physiological activity of leaves under development or that of leaves at a position lower than the active center leaf is smaller than that of the active center leaf itself. Accompanying with the growth of rice plant, the active center leaf goes up from lower position to upper position.

12 : The number of leaves on the main stem changes according to the growth condition. Type of the unit of chain which includes a leaf at a definite position changes if the number of leaves on the main stem changes.

Accordingly, the function of the leaf depends upon the type of the unit in which the leaf is included.

13: The size of an organ depends upon the physiological conditions of the plant when the organ developes. To make an organ larger, it is necessary to accelerate the photosynthetic activity of the active center leaf at the growth stage when the organ is developing, to make the plant sufficient in elements which are easily translocated within plant body, such as phosphorus, nitrogen, etc. and to cause absorption, from the roots at that growth stage, of those elements, which do not easily translocate, such as calcium.

14: There is a division of functions among leaves. At early stage of growth, the division is not clear. Photosynthetic products of a leaf translocate into elongating leaves on the main stem and into tillers which are synchronous with each other. When internode elongation starts, the division of functions comes into existence. The photosynthetic products of the leaves which can be classified into the third type enter into the growth point of the stem, such as upper elongating leaves, internode or ear-primordium, those of the leaves of the first type translocate into roots or tillers and those of the leaves of the second type translocate both into the growth point of the stem and roots and tillers.

15: A tiller accepts substances, which are indispensable to its growth, from mother stem until the tiller possesses three leaves. A tiller which has less than three leaves is heterotrophic. When a tiller possesses more than three leaves, it synthesises organic substances by means of its own leaves and absorbs nutrient elements by its own roots. The tiller at this stage is autotrophic. It can be said that a whole rice plant is a colony which is composed of several tillers, some of which are depending upon the mother stem and the others are almost independent individuals.

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