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Title	Respiration and the Growth Efficiency in Relation to Crop Productivity
Author(s)	YAMAGUCHI, Junichi
Citation	Journal of the Faculty of Agriculture, Hokkaido University, 59(1), 59-129
Issue Date	1978-11
Doc URL	https://hdl.handle.net/2115/12920
Type	departmental bulletin paper
File Information	59(1)_p59-129.pdf

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RESPIRATION AND THE GROWTH EFFICIENCY IN RELATION TO CROP PRODUCTIVITY

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Received March 16, 1978

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[J. Fac. Agric. Hokkaido Univ., Vol. 59, 59-129, 1978]

Abbreviations

ATP	Adenosine triphosphate
CE	Conversion efficiency on the basis of dry weight
$CE_{(e)}$	Conversion efficiency on the basis of calorie
DW	Dry weight
EMP	Embden-Meyerhof-Parnas glycolytic sequence
GE	Growth efficiency, GR/P'_g or $GR/(GR+R)$
GE_d	Growth efficiency, based on the gain of dry weight of new growing organs and the loss of dry weight of old organs
GE_g	Growth efficiency on the basis of R_g, $GR/(GR+R_g)$
GR	Growth rate
HC	Heat of combustion
IRGA	Infrared gas analyzer
LAI	Leaf area index
M	Mineral
N	Nitrogen
NAD	Nicotinamide adenine dinucleotide
NADH	Nicotinamide adenine dinucleotide reduced
P_g	Gross photosynthesis, P_n+R or P'_g-M
P'_g	Gross photosynthesis including minerals, GR+R or P_g+M
P_n	Net photosynthesis
Q_{10}	Temperature coefficient, (rate at $t+10$°C)/(rate at t°C)
R	Respiration, R_g+R_m
R_g	Growth respiration
r_g	Rate of growth respiration per unit weight
R_m	Maintenance respiration
r_m	Rate of maintenance respiration per unit weight
TCA cycle	Tricarboxylic acid cycle
TDW	Total dry weight

I. INTRODUCTION

Dry matter production of crop plants has been intensively studied during the last few decades, and the results of these studies are contributing to the improvement of crop yield.

Considerable information about two key metabolic processes of the plant —photosynthesis and respiration— has been accumulated. The dry matter

produced by the plant denotes the chemical energy stored in the plant body: The green plant converts the solar energy into the chemical energy through photosynthesis; synthesizes primary photosynthates; liberates energy by expending a part of the primary photosynthates as respiratory substrates; produces various substances from the primary photosynthates by using the energy liberated by the respiration; and composes a new plant body. In this respect the dry matter production is closely related to the bio-energetics of the plant.

Analysis of plant growth through energy metabolism has attracted the attention of many researchers, and several attempts to describe quantitatively the relationship between growth and respiration have been made since the early 1920's.

TERROINE *et al.*[103] proposed a concept of the *material efficiency* to express the efficiency of stored substances in seeds to produce seedlings. The material efficiency was defined as $P/(P_1-P_2)$, where P was the dry weight of the seedlings at a given stage of germination in the dark, and P_1 and P_2 were the dry weight of the seeds at the start and at a given stage, respectively. This concept was succeeded by several investigators[2,19,24,36,53,54,57,98]. These studies demonstrated that the material efficiency of starchy seeds was 50~70 percent, that of oily seeds was even higher, and that the effect of temperatures within a normal range on the efficiency was small.

The energetics of photosynthesizing plants has been discussed in some studies. However, these studies were mostly confined with the plants at juvenile stages because of the difficulty of measuring the CO_2 exchange of large plants. THOMAS and HILL[104] measured daily amounts of photosynthesis and respiration of alfalfa and sugar beet growing in the field, and reported that respiration occupied 35~49 percent and 29~33 percent of the gross photosynthesis for alfalfa and sugar beet, respectively. In an analysis of the net assimilation rate of crop plants, WATSON[111] indicated that the amount of respiration was almost equal to that of net photosynthesis in field-grown plants. MÜLLER[59] reviewed a limited number of available data at that time, and estimated that respiration occupied 20~40 percent of the gross photosynthesis. LOOMIS and WILLIAMS[44] considered that respiration occupied one-third of gross photosynthesis.

However, GAASTRA[18] pointed out that the data cited above were not enough to understand the relationship between growth and respiration, and more data of the respiratory rate of various organs throughout the ontogeny of crops in the field were necessary.

With recent improvements of infrared gas analyzers, it became possible

to measure the photosynthesis and respiration of large plants more precisely than used to be possible. MONTEITH[58] reported that the ratio of net photosynthesis to gross photosynthesis (P_n/P_g ratio) of sugar beet grown in the field was 44 percent during the growth cycle. MCCREE and TROUGHTON[50] reported that the P_n/P_g ratio of white clover grown in a growth cabinet was 57~62 percent. The dry matter production of perennial herbs was estimated to be 45~50 percent of gross photosynthesis[28,34].

A concept of the *growth efficiency* (*GE*) has been proposed by TANAKA and YAMAGUCHI[96] to evaluated the significance of respiration in dry matter production. The *GE* is defined as $W/(W+R)$, where W is the amounts of dry matter produced and R is that of substances respired in a given period of plant growth. Thus, the *GE* is the proportion of the amount of growth in a given amount of substrates. They demonstrated that the *GE* of rice plants in the tropics was about 60 percent during active vegetative growth stages and decreased at later stages of growth.

COCK and YOSHIDA[10] reported that the ratio of respiration to gross photosynthesis (R/P_g ratio) was about 40 percent over a wide range of leaf area indices (LAI) of tropical rice, and that there was little difference between tall and short varieties. Studies on the rice plant by SUZUKI and MURATA[86] showed that the P_n/P_g ratio decreased with growth, and the average value from transplanting to harvest was 67 percent. OJIMA[65] reported that the P_n/P_g ratio of soybeans was 53~59 percent before flowering, and after this stage it decreased to 34~40 percent due to respiration in the pods. KOH and KUMURA[40] reported that the R/P_g ratio at successive growth stages of winter wheat was about 15 percent during the initial growth period, about 27 percent before and after flowering, and became more than 200 percent shortly before full maturity. HESLEHURST and WILSON[26] found that the R/P_g ratio of tropical pasture plants was lower in legumes (18~43 percent) than in grasses (37~44 percent).

KIRA[39] described in his review that the P_n/P_g ratio was 50~70 percent in annual plants, 50~55 percent in perennial herbs, and 25~40 percent in forests, but the potential productivities of these ecotypes were similar, since the gross photosynthesis was larger in forests than in annual plants.

The balance between photosynthesis and dry matter production can be estimated by measuring the amount of ^{14}C retained in a plant at a certain period after assimilating ^{14}C. LIAN and TANAKA[43] observed in tropical rice plants that the retention percentage at harvest of ^{14}C assimilated at the maximum tiller number stage and at the milky stage was about 60 and 40 percent, respectively. In barley the retention percentage was reported to be about

40 percent by HOZYO *et al.*[30,31] and RYLE *et al.*[80] HUME and CRISWELL[32] reported that in soybeans it was 30~40 percent during vegetative growth, and was about 65 percent during ripening.

Aerobic respiration is the major energy producing processes in the higher plants, and the energy efficiency in the breakdown of glucose to CO_2 and H_2O by the Embden-Meyerhof-Parnas (EMP) glycolytic sequences and the tricarboxylic acid (TCA) cycle is more than 90 percent[4]. Chemical processes of the bio-synthesis of polysaccarides, lipids, proteins, and other plant constituents have been reasonably well described. However, little information is available as to how respiration as a whole is linked with growth because of the greater complexity of these synthetic processes and the uncertainty of bio-energetics in biomass[42].

Nevertheless, on the basis of up-to-date knowledges of biochemical pathways and their energetics, PENNING DE VRIES[70,71,73] and PENNING DE VRIES *et al.*[74] have made theoretical estimations of the *production value*, which is defined as the amount of a certain compound synthesized from a unit amount of substrate required for carbon skeletons and energy production. He concluded that his calculations corresponded well with observed values in juvenile plants under controlled conditions: 70~80 percent of primary photosynthates was converted into the plant constituents.

The energy metabolism of domestic animals has been intensively investigated since the 19th century to establish efficient feeding methods[6,7,46,51,62]: Various experiments have revealed that the efficiency of conversion of the metabolizable (net) energy is 50~60 percent for fattening, and 60~70 percent for milk production, although it varies with the level of feed and the kind of animal.

The energy budget of the food-animal population chain in the natural ecosystem has been studied by zoologists[63,66,84]: The ratio of calories retained in products to those used for the production is evaluated through the *net yield efficiency* or the *assimilation efficiency*, which is estimated to be 62 percent at its maximum in mollusks.

In microorganisms or plant cell culture, the relation between energy consumption and the production of organisms or byproducts has been studied[3,17,37,68,82]: 55~65 percent of substrate carbon is generally incorporated into organisms during actively growing stages, while RAVEN[78] has suggested that higher values can be obtained for photolithotrophic growth of unicellular algae because of direct use of photo-produced cofactors.

In nutrition of animals[7,46,51] as well as of microorganisms[75], respiration is classified into several categories; growth, production, maintenance, and work.

There have also been attempts to classify the respiration of plants (R) into two components, *i. e.*, growth respiration (R_g) and maintenance respiration (R_m)[21,27,45,48,49,52,55,71,72,81,91,105,116]. McCREE[48,49] defined the R_m as the efflux of CO_2 from the plant after more than 48 hours in the dark. He found that the rates of R_g and R_m per unit weight (r_g and r_m) were dependent on gross photosynthesis (P_g) and plant dry weight (DW), respectively: $R = r_g \cdot P_g + r_m \cdot DW$, and estimated that r_m were 15 and 5.4 mg glucose$\cdot g^{-1}DW \cdot day^{-1}$ in white clover and sorghum, respectively. RYLE *et al.*[81] described the total respiratory efflux of $^{14}CO_2$ in terms of two main components: an intense efflux characterized by a half-life of 4~8 hours, which was identified with the biosynthesis of new tissue (R_g); and a much less intense efflux characterized by a half-life of 26~120 hours, which was identified with the maintenance of metabolic activity (R_m).

From the above mentioned information, available in the literature, it is clear that respiration is essential to the plant growth and occupies a considerable fraction of gross photosynthesis, but the quantitative relationship between growth and respiration is not yet fully understood.

The purpose of this paper is to elucidate the energy metabolism of plant growth through the *GE* to make a quantitative analysis of dry matter production. For this purpose rice (C_3 plant) and maize (C_4 plant), whose grains are rich in carbohydrates, and soybeans (C_3 plant), whose seeds are rich in lipids and proteins, are dealt with.

In Chapter III the *GE* of seedlings germinating in the dark for various durations at different temperatures is discussed to demonstrate the effect of chemical compositions of seeds, availability of substrates, and germination temperatures on the *GE*. In Chapter IV the *GE* of plants which are performing photosynthesis under natural light conditions is described. As a plant is composed of various organs, which have their own characteristic functions, the respiratory rate and the *GE* of each organ, especially that of the reproductive organs are treated. In Chapter V the effects of light and nutritional status on the *GE* are discussed by using the plants growing actively in the light to elucidate the nature of respiration. In Chapter VI the results obtained in these studies are discussed to evaluate the significance of respiration to the plant growth quantitatively and a balance sheet of photosynthesis and respiration during growth, and the potential productivity of various crops are presented through the concept of bio-energetics in the plant.

Acknowledgement

The author wishes to express his gratitude to Dr. Akira TANAKA, Professor, Faculty of Agriculture, Hokkaido University for his encouragement and helpful discussion throughout the work. Most of the seed materials were supplied by the courtesy of the Hokkaido National Agricultural Experiment Station and the Takikawa Breeder's Stock Farm, Hokkaido Central Agricultural Experiment Station.

II. MATERIALS AND METHODS

Materials

Rice (*Oriza sativa*), maize (*Zea mays*), and soybeans (*Glycine max*) were used. The cultivars of rice and soybeans used were 'Yūkara' and 'Kitamishiro', respectively, which are commercial medium-late varieties in Hokkaido. Three cultivars of maize, Wisconsin Hybrid Corn No. 95, Fukko No. 8 [(W23 × W28) × (A357 × Oh40B)], and D403 × D405, were used depending upon the purpose of the experiments, the availability of seeds, and the genetic variability within a cultivar. Wisconsin Hybrid Corn No. 95 and Fukko No. 8 are commerical medium-late varieties, and D403 × D405 is a single cross as a parent of a double cross variety.

Culture Methods

For studies during germination in the dark, uniform seeds were germinated either of vermiculite or on quartz sand contained in small pots (640 ml) supplied with demineralized water in a temperature-control cabinet. The numbers of seeds used were 200, 25, and 50 per pot, for rice, maize, and soybeans, respectively.

For studies during juvenile growth stages in the light, seedlings were grown on vermiculite contained in small pots supplied with a standard culture solution (Table 1) in a glass-house or in a net-house. The number of plants grown was 25 to three per pot depending upon the duration of the experiments.

For studies during vegetative growth stages, plants were grown in pots containing soil mixed throughly with a given amount of fertilizers. The size of the pots used depended upon the object of the experiments. Combinations of the pot size, the amount of soil, and the amount of fertilizers are shown in Table 2. The number of plants was 10 to one per pot depending upon the duration of the experiments. Tap water was irrigated from the bottoms of the pots to maintain an adequate moisture condition of the soil.

TABLE 1. Composition of the standard culture solution for rice and maize plants.

Element	Concentration (ppm)		Salts used
	Rice	Maize	
N*	30	100	NH_4NO_3, $NaNO_3$, $(NH_4)_2SO_4$
P	10	20	$NaH_2PO_4 \cdot 2H_2O$
K	30	60	KCl/K_2SO_4
Ca	30	20	$CaCl_2 \cdot 2H_2O$
Mg	20	20	$MgSO_4 \cdot 7H_2O$
Fe	2	3	$FeSO_4 \cdot 7H_2O$
Mn	0.5	1	$MnSO_4 \cdot 4H_2O$
(pH)	(4.5–5.0)	(5.5)	

* Rice: NH_4NO_3 alone, or $NH_4NO_3 : (NH_4)_2SO_4 = 3:1$ as N,
Maize: $NH_4NO_3 : NaNO_3 = 5:2$ as N.

TABLE 2. Combinations of size of pots, amount of soil, and amount of fertilizer elements for soil-pot culture.

Crop		Maize		Soybeans	
Pot size (liter)		4	14	4	14
Soil* ($kg \cdot pot^{-1}$)		3	10	3	9
Fertilizer element** ($g \cdot pot^{-1}$)	N	2	4	0.5	1
	P_2O_5	2	4	1	3
	K_2O	2	4	1	3

* Air-dried soil taken from a field of Hokkaido University (an alluvium).
** Fertilizers used were ammonium sulfate, superphosphate, and potassium sulfate, respectively.

TABLE 3. Standard culture conditions of field experiments.

Crop		Rice	Maize	Soybeans
Hill spacing (cm×cm)		30×15	40×40	40×40
Number of plants per hill		2	1	2
Amount of fertiizer* ($kg \cdot ha^{-1}$)	N	80+40**	150+(50~100)**	20
	P_2O_5	100	150	100
	K_2O	100	150	100

* Fertilizers used were ammonium sulfate, superphosphate, and potassium sulfate, respectively.
** Top dressing from the middle to the end of July.

For studies during later growth stages, plants were grown according to standard commercial practices in Hokkaido: For rice one-month old seedlings were transplanted to a paddy field of Hokkaido University by the end of May, and for maize and soybeans seeds were sown in a field of Hokkaido University in the middle of May. Hill spacing, number of plants per hill and level of fertilizers are shown in Table 3. Harvesting was done from late September to early October.

In the case of solution cultures, seeds were germinated on a nylon-screen bed floating on water contained in an enameled tray, the seedlings were transferred to pots which contained 12 liters of the standard culture solution, and the plants were grown in a glass-house. The solution was renewed every 7 to 10 days.

Measurements

The respiratory rate and the dry weight were measured at a given time on all of the plants of a pot or plants of four neighbouring hills in the field. Most of the measurments were duplicated.

Respiratory Rate of the Shoot: The chamber method described elsewhere[112,117] was used. The intact plant(s) was placed in a chamber (A) and the rate of CO_2 release from the shoot(s) in the dark was estimated by measuring the difference of CO_2 concentration of the air between the inlet

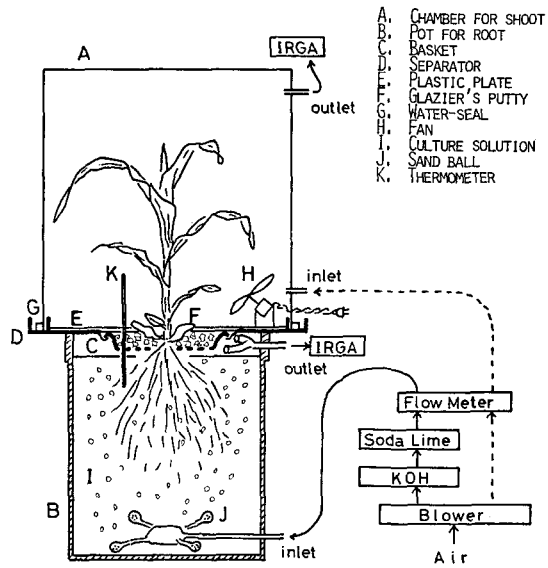

Fig. 1. Illustration of the set-up for measuring the respiratory rates of shoot and root of the intact plant, separately.

and the outlet of the chamber and the rate of air flow through the chamber (upper portion of Fig. 1).

The chamber was made of a transparent colorless plastic film or plate. The size of the chamber was selected to minimize dead space in the chamber during measurement; the smallest was $20 \times 20 \times 30$ cm^3 for seedlings grown in a small pot and the largest was $80 \times 80 \times 250$ cm^3 for maize plants at late growth stages in the field. An air-mixing fan (H) was installed inside the chamber to make the CO_2 concentration in the chamber uniform.

Atmospheric air was taken at 6 m above the ground, mixed in a room (app. 8 m^3) to make it uniform, and sent into the chamber with a blower. The rate of air flow was adjusted to one to 200 liters per minute depending upon the rate of respiration of sample plants to make the difference of CO_2 concentration between the inlet and the outlet below 30 ppm in general. The flow rate was measured by several types of flow meters; a manometer (0.5~4 $l \cdot min^{-1}$), a liquid type gas meter (Kinmon MFG., 0.5~10 $l \cdot min^{-1}$), a gas meter (Kinmon MFG., Model T-3, 1~50 $l \cdot min^{-1}$), or an orifice-type flow meter (Motoyama MFG., 20~80 $l \cdot min^{-1}$ and 60~250 $l \cdot min^{-1}$).

The difference of CO_2 concentration between the inlet and the outlet of the chamber was continuously monitored by a differential-type infrared gas analyzer (IRGA, Hitachi-Horiba MFG., Model LIA-2), which was generally adjusted to read differences smaller than 50 ppm CO_2 with a 0.5 ppm sensitivity. Another IRGA (Hitachi-Horiba MFG., Model EIA-1), which was adjusted to read concentrations between 0 and 600 ppm CO_2, was used to measure the absolute concentration of CO_2 in the air.

Generally, it took about $V/F \times (3\sim5)$ minutes after the start of air flow at a rate of F $l \cdot min^{-1}$ through a chamber having a volume of V liter for the CO_2 concentration at the outlet to become stable. In case there was a measurable release of CO_2 from the growth medium its amount was subtracted from the total CO_2 released in the chamber. Measurements were made in the dark at night or a few hours after shifting sample plants in the sunlight to a dark room[115].

Respiratory rate is generally expressed as mgCO_2 released per gram dry weight per hour ($mgCO_2 \cdot g^{-1} \cdot hr^{-1}$) at the mean temperature between two successive measurements during the growth, assuming that the temperature coefficient (Q_{10}) was two.

Respiratory Rate of the Root: Measurement was made by a set-up illustrated in the lower portion of Fig. 1. A basket (C), on which a plant was growing with the standard culture solution, was hung on a metal separator (D), which was fixed on the top of a pot (B). The upper surface

of the basket and the separator were covered with a plastic plate (E) and the space between the base of the shoot and the plate was sealed with a glazier's putty (F). CO_2-free air, which was obtained by passing the atmospheric air through KOH solution and granular soda lime, was bubbled into the culture solution (I) from the bottom of the pot through a set of sand balls or vinyl tube with small holes (J). The air passed through the culture solution was exhausted to the atmosphere through the outlet, and a portion was sampled by the IRGA.

The size of pots used for measurements was chosen depending upon the size of roots; 0.5, 2, 3, 5, and 14 liters. The pot was kept in a large waterpool to make the temperature of the solution constant during measurements.

At the beginning of measurement the culture solution was aerated with CO_2-free air to purge the CO_2 in the solution until the CO_2 concentration of the air at the outlet reached a low equilibrium (a). Then the plant was placed as described above as quickly as possible, and the rate of air flow was adjusted to a certain level. The CO_2 concentration at the outlet was continuously monitored. When the CO_2 concentration at the outlet reached a new equilibrium with a given flow rate, the CO_2 concentration (b) was measured. After removing the sample plant, the CO_2-free air was passed through the culture solution again and the equilibrated CO_2 concentration (c) was measured. The rate of CO_2 release from the root was calculated by the following fomula: $(b-(a+c)/2)\times F$, where F is the flow rate. As the value of (a) and (c) was fluctuated from 0 to 10 ppmCO_2 by the nature of culture solutions because of unknown reasons, the rate of air flow was adjusted as slowly as possible to minimize experimental error by making the value of (b) large.

The method of respiratory measurement of the intact root described above is reasonably accurate, but tedious. For example, the time required to reach an apparent equilibrium of CO_2 concentration was $V/F\times(5\sim7)$ minutes after the start of air flow (V: volume of culture solution, liter; F: rate of air flow, $l\cdot min^{-1}$). This was about twice the time required for the respiratory measurement of a shoot. Although a higher flow rate could possibly shorten the time-requirement, it would result in physical damages to the root. Thus, it took generally 1.5 to 4.5 hours to complete one measurement.

The respiratory rate measured by this method was constant at least for a few hours and was not affected by the rate of air flow. The temperature coefficient (Q_{10}) of the respiration of the roots was 2.28 ± 0.55 between 13 and 30°C[117].

Dry Weight: Plant samples were washed, separated into various organs if necessary, dried in a air-forced oven at 70~80°C for two days, and weighed. Dried samples were ground with a mill and stored for chemical analyses.

Calculation of Growth Efficiency

In the case of seedlings germinating in the dark, the growth efficiency (*GE*) during a given period between t_1 and t_2 after sowing was calculated by the following formula;

$$GE=(W_2-W_1)/(S_1-S_2), \qquad (1)$$

where W_1 and W_2, and S_1 and S_2 are the dry weight of the seedlings and that of the seeds at t_1 and t_2, respectively. The *GE* was generally expressed as a percentage.

The *GE* of the plants growing in the light was calculated by the following formula;

$$GE=GR/(GR+R), \qquad (2)$$

where $GR=(W_2-W_1)/(t_2-t_1)$, in which W_1 and W_2 were the dry weight of the plant at t_1 and t_2, respectively, and was expressed as $g\cdot plant^{-1}\cdot day^{-1}$, and $R=(R_1+R_2)/2$, in which R_1 and R_2 were the respiratory rate at t_1 and t_2, respectively, and expressed as $g\ CH_2O\cdot plant^{-1}\cdot day^{-1}$, assuming that the respiratory rate in the light was the same as that in the dark. The *GE* in the light was also worked out GR/P'_g, where P'_g was the gross photosynthetic rate including minerals ($g\cdot plant^{-1}\cdot day^{-1}$) and was estimated as $GR+R$.

It should be remembered in relation to these calculation methods that (i) dry matter of the plant is composed not only of organic substances derived from photosynthates but also of mineral elements absorbed by the roots, (ii) the ratio of C : H : O of organic substances in plant is not necessarily 1 : 2 : 1[110], (iii) the photorespiration is not taken into consideration, and (iv) it is uncertain whether dominant substrates for respiration are derived from current photosynthates or from former photosynthates.

Chemical Analyses

The percentage of crude proteins was worked out by multiplying 6.25 with nitrogen percentage determined by the micro-Kjeldahl method (Kjeldahl-N), except for matured grains of rice and soybeans which were figured by multiplying 5.95 and 5.71, respectively[16]. The percentage of crude lipids was determined as the ethylether-extractable matter. The percentage of crude ash was determined as the residue after combustion at 550°C. The percentage of nitrogen free extract was estimated by subtracting the percentages of crude proteins, crude lipids, and crude ash from a unit dry

weight of the plant materials.

The combustion heat was determined by a bomb-calorie meter (Ogawa-seiki MFG., Model OSK-150), based on the calorific value of benzoic acid (6321 $cal \cdot g^{-1}$) as the reference standard.

Various fractions of nitrogen were determined by the method described by MURAYAMA[61] with some modifications: Total nitrogen (T-N) by the Ganning's method or as the sum of the nitrate-N (NO_3-N) and the Kjeldahl-N; soluble-N (Sol-N) by water extraction at 85°C; insoluble-N (Insol-N) as the Kjeldahl-N of the Sol-N free residue or by subtracting the Sol-N from T-N. Various types of nitrogen in the hot water extract (Sol-N) were analyzed: Soluble-protein-N (Sol-prot-N) by the micro-Kjeldahl method after precipitating with lead acetate, ammonium-N (NH_4-N) by the micro-diffusion method of CONWAY[12], amide-N as NH_4-N after hydrolysis with 6N H_2SO_4, amino-N by the colorimetry using α-amino acid ninhydrin reaction with L-leucine as the standard[11], and NO_3-N as NH_4-N by reduction with Devarda's alloy or by the colorimetry of the phenoldisulphonic acid method.

Sugars and starch were determined by the method of McCREADY *et al.*[47]: Sugars were extracted with 80% ethyl alcohol and starch in the sugar-free residue was extracted with 52% $HClO_4$. These were then determined by the colorimetry using the sugar-anthrone-sulfuric acid reaction with glucose as the standard.

III. GROWTH EFFICIENCY OF SEEDLINGS GERMINATING IN THE DARK

Comparison of Growth Efficiency of Seedlings among Rice, Maize, and Soybeans

Seeds of rice, maize (Wisconsin Hybrid Corn No. 95), and soybeans were germinated in the dark at 25±1°C, samplings were made during germination, the dry weights of seedlings (shoot and root) and seeds were measured, and the *GE* values at successive stages were worked out by the formula (1).

In all species, the dry weight of seeds decreased and that of seedlings increased with germination, and the growth rate was slower in rice than in others (Fig. 2). The increase of seedling weight became smaller when the decrease of seed weight became smaller, and then the dry weight of seedlings started to decrease gradually when the decrease of seed weight became negligible.

The utilization percentage of stored substances in the seeds was defined as (A-B)/A, where A and B were the initial weight and the final weight

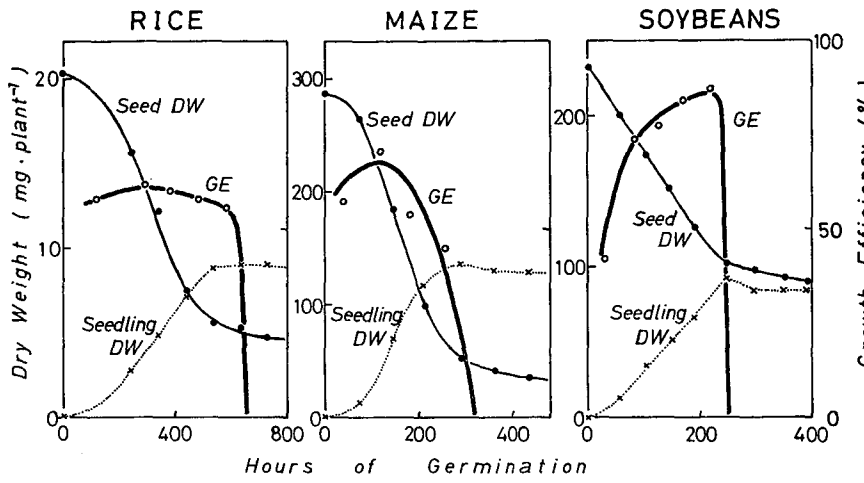

Fig. 2. Dry weigh (*DW*) of seeds and seedlings, and growth efficiency (*GE*) at successive growth stages of rice, maize, and soybeans germinating in the dark at 25°C.

of the seeds when the decrease of seed weight discontinued, respectively. This value was higher in maize (89 percent) and lower in soybeans (62 percent).

The *GE* was slightly lower at the initial stage of germination, became higher during early stages when the growth of seedlings was active, and then decreased abruptly when the stored substances in the seeds were exhausted. The *GE* during the actively growing period was 60~65 percent in rice, 65~70 percent in maize, and 75~85 percent in soybeans.

Effect of Temperature on Growth Efficiency

Rice seeds were germinated in the dark at 15, 20, 25, 30, and 35±1°C. In a separate experiment maize seeds (Wisconsin Hybrid Corn No. 95) were germinated in the dark at 10, 15, 20, 25, 30, 35, and 40±1°C. Samplings were made at successive stages of germination, the dry weights of seeds and seedlings were measured, and the *GE* values were worked out[98].

In rice the higher the temperature, the higher the growth rate of seedlings (Fig. 3, top). The maximum dry weight of seedlings attained during germination was almost the same between 25 and 35°C. The maximum weight was smaller and the final weight of seeds was larger at 15 and 20°C than that at higher temperatures (Table 4). The utilization percentage of stored substances in the seeds was higher at higher temperatures within the range from 15 to 25°C, and was kept constant above 25°C.

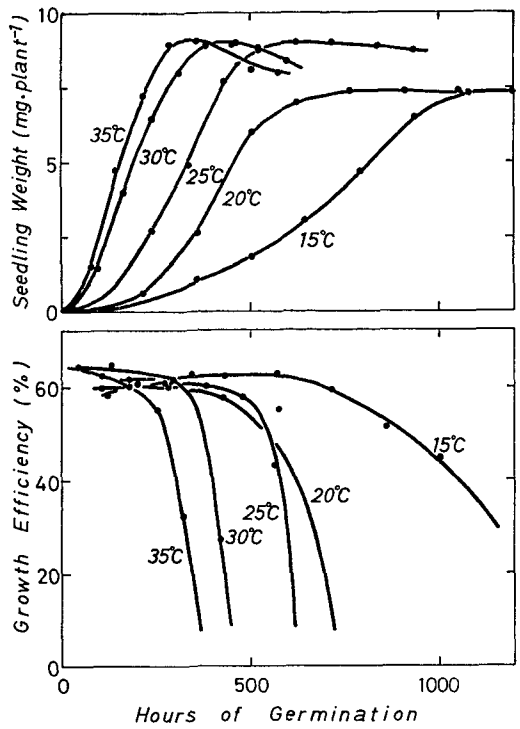

Fig. 3. Dry weight (top) and the growth efficiency (bottom) at successive growth stages of rice seedlings germinating in the dark at various temperatures.

TABLE 4. Maximum dry weight (*DW*) of seedlings, final dry weight of seeds, and the utilization percentage of stored substances of rice and maize germinated in the dark at various temperatures.

Crop	Rice			Maize		
Temperature (°C)	Maximum Seedling *DW* (mg·plant^{-1})	Final Seed *DW** (mg·plant^{-1})	Utilization percentage** (%)	Maximum Seedling *DW* (mg·plant^{-1})	Final Seed *DW** (mg·plant^{-1})	Utilization percentage** (%)
15	6.78	9.09	56	131	48.0	83
20	7.59	5.84	72	130	39.6	86
25	9.11	4.66	77	138	32.8	89
30	9.11	4.71	77	133	32.4	89
35	9.28	4.72	77	128	34.4	88
40				82	44.8	84

* Dry weight of seeds when the decrease of seed weight discontinued.
** Utilization percentage=(A−B)/A×100,
A: the initial weight of seeds. B: the final weight of seeds.

TABLE 5. Dry weight (*DW*) of seeds and seedlings, and the growth efficiency (*GE*) of rice and maize germinated in the dark at various temperatures.

Crop	Rice*				Maize**			
Temperature (°C)	Seed *DW*	Loss of seed *DW*	Seedling *DW*	*GE*	Seed *DW*	Loss of seed *DW*	Seedling *DW*	*GE*
	(mg·plant^{-1})			(%)	(mg·plant^{-1})			(%)
15	19.71	0.79	0.45	57	269	21	12	55
20	18.81	1.69	1.05	62	222	66	43	65
25	15.59	4.91	2.96	60	179	109	74	67
30	9.57	10.93	6.78	62	128	160	103	64
35	6.41	14.09	8.64	61	90	198	121	61
40					155	133	60	45

* 250 hours of germination, ** 150 hours of germination.

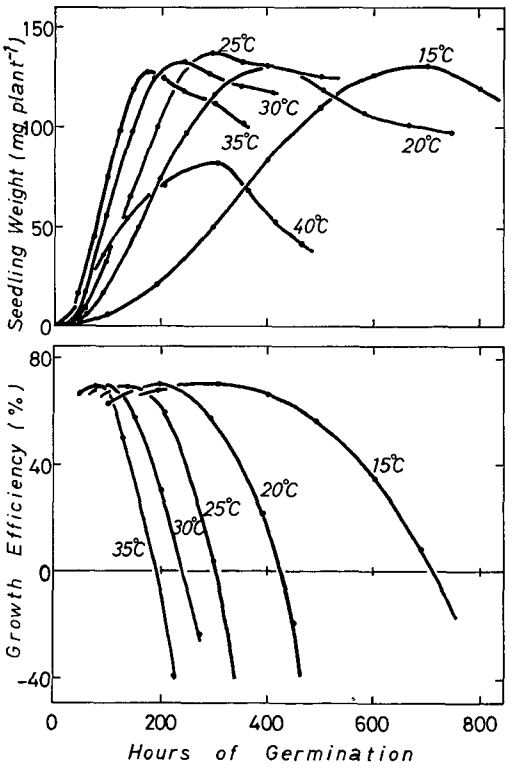

Fig. 4. Dry weight (top) and the growth efficiency (bottom) at successive growth stages of maize seedlings germinating in the dark at various temperatures.

The *GE* during the period of active germination was maintained at 60~65 percent regardless of the temperature (Fig. 3, bottom). The *GE* began to decrease earlier at higher than at lower temperatures. The dry weights of seeds and seedlings, and the *GE* at different temperatures at 250 hours of germination are shown in Table 5. In this case the *GE* was calculated with the dry weights of the seeds and the seedlings at 0 and 250 hours of germination. The increase of seedling weight and the decrease of seed weight were larger at higher than at lower temperatures, but the *GE* was kept almost constant at 60~62 percent between 20 and 35°C, and was slightly lower at 15°C.

In maize the rate of germination was extremely slow at 10°C (4 and 20 mg•seedling^{-1} at 600 and 1200 hours, respectively), and the higher the temperature, the higher was the growth rate of seedlings within the range from 15 to 35°C (Fig. 4, top). The rate at 40°C was comparable to that at 35°C during early stages, but was far lower at late stages. The dry weight of seedlings decreased after reaching a maximum, and this decrease was more prominent at higher temperatures. There was no significant difference in the maximum dry weight of seedlings between 15 and 35°C, and was apparently smaller at 40°C (Table 4). The utilization percentage of stored substances in the seeds was higher between 25 and 35°C (88~89 percent), and was lower at 15 or 40°C (83~84 percent).

The *GE* was kept at 65~70 percent regardless of the temperature from 15 to 35°C for a certain period, and the lower the temperature, the longer the period (Fig. 4, bottom). The *GE* started to decrease after this period, and the decrease was more rapid at higher temperatures. At 150 hours of germination the dry weight of seeds was smaller, and that of seedlings was larger at higher temperatures except at 40°C (Table 5). The *GE* was nearly constant (61~67 percent) between 20 and 35°C, lower at 15°C, and very low at 40°C.

Growth of Each Organ and Growth Efficiency in Maize

Maize seeds (Wisconsin Hybrid Corn No. 95) were germinated at 24±1°C. Samples were taken at successive growth stages, separated into the seeds, root, coleoptile, mesocotyl, and each leaf, and the dry weight of each organ was determined[98].

The total dry weight of seedlings attained a maximum at about 300 hours of germination, and then decreased gradually (Fig. 5). The roots, the 1st mesocotyl, and the coleoptile started to grow first, and then the 1st leaf. When the coleoptile and the 1st mesocotyl reached their maximum

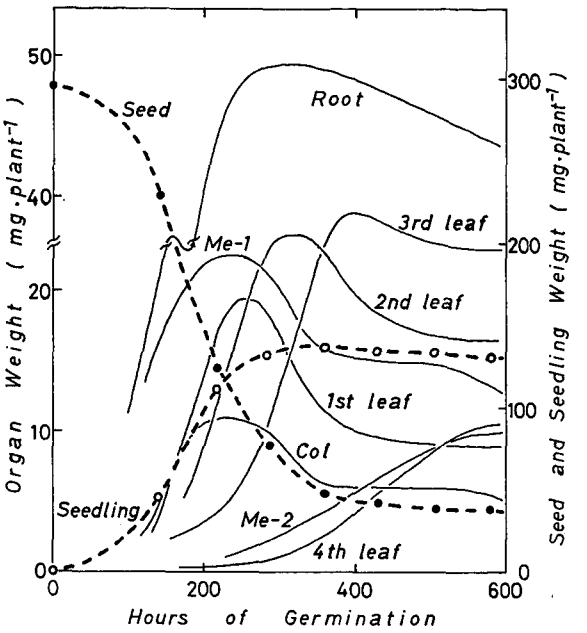

Fig. 5. Dry weight of various organs of maize at successive growth stages germinating in the dark at 24°C (Col: coleoptile, Me: mesocotyl).

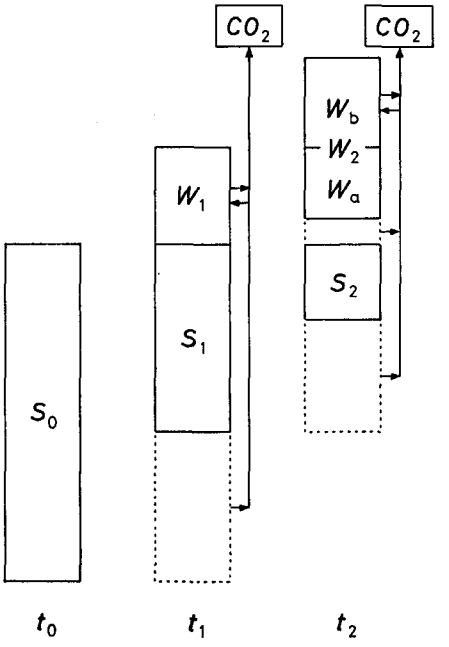

Fig. 6. Diagram of the changes of dry weight of the seed and the seedling during germination in the dark.

S_0, S_1, and S_2: Seed weight at t_0, t_1, and t_2, respectively.

W_1, W_2: Seedling weight at t_1 and t_2, respectively.

t_0: Before germination.

t_1: When all organs are gaining weight.

t_2: When some organs are losing weight.

weights, the 2nd leaf was growing actively and the 3rd leaf started to grow. Then, the dry weight of the 3rd leaf increased rapidly, while that of the coleoptile and the mesocotyl, etc. began to decrease. At the next stage of germination the dry weight of the 2nd leaf started to decrease, and the 4th leaf and the 2nd mesocotyl began to gain weight.

This situation suggests that when the stored substances in the seed are exhausted, the increase of dry weight of new organs is supported by the decrease of dry weight of older organs as illustrated in Fig. 6. From this figure the growth efficiency (GE_d) during the period between t_1 and t_2, when substances in the older organs $[(S_1-S_2)+(W_1-W_a)]$ are utilized for the growth of new organs (W_b), can be calculated by the following formula:

$$GE_d = W_b/\left[(S_1-S_2)+(W_1-W_a)\right] \qquad (3)$$

The GE_d was practically the same with the GE for about 200 hours, and then maintained at about 50 percent for 600 hours although the GE decreased rapidly (Fig. 7).

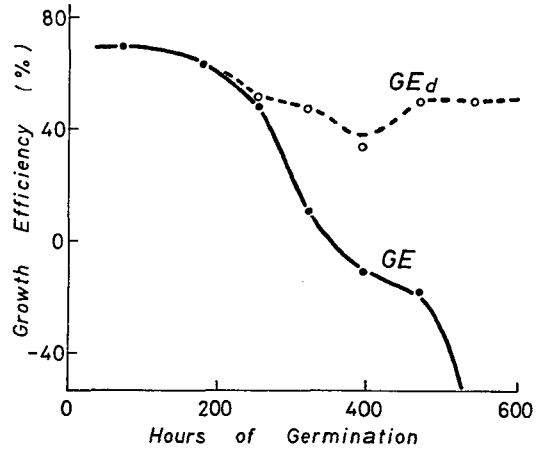

Fig. 7. Growth efficiency of maize seedlings germinating in the dark at 24°C (GE: growth efficiency based on the total dry weight of seedlings and seeds; GE_d: growth efficiency based on the differences between gaining and losing weight among organs).

Discussion

The GE of seedlings germinating in the dark was kept constant at 60~65 percent in rice, 65~70 percent in maize, and 75~85 percent in soybeans at the actively growing stage of germination in the dark (Fig. 2). This means that the dry matter production is accompanied by respiration, and

a certain *GE* is maintained with a given chemical composition of substances for the growth. Thus, the *GE* of rice or maize, whose seeds are rich in starch, is lower than that of soybeans, whose seeds are rich in lipids and proteins. In the case of seeds rich in starch, 60~70 percent of stored substances are converted to constituents of the seedlings by the energy liberated by consuming the other 30~40 percent in respiration. Whereas, in the case of seeds rich in lipids, a larger amount of seedlings is produced by consuming less in respiration on an dry weight basis, since stored substances utilized for growth are richer in energy.

It was reported that the maximum dry weight of the sprout from a potato tuber germinating in the dark was positively correlated with the initial tuber size, but the ratio of dry weight of the sprout to that of the tuber was almost constant[24]. A similar trend was also observed among rice strains with different seed sizes[87,91]. This evidence indicates that the *GE* is independent of the difference of the amount of stored substances.

With an increase in temperature, the growth rate of seedlings increased and the *GE* was kept constant except for cases with extreme temperatures, such as below 15°C or above 35°C (Figs. 3 and 4). The temperature coefficient (Q_{10}) of the respiratory rate is reported to be about two for various plant tissues[35,76]. The Q_{10} for the growth rate of maize seedlings was calculated from the data shown in Fig. 4. Although the value tended to decrease with the age of seedlings, it was 1.8~2.4 at the most actively growing stage (Table 6).

TABLE 6. Temperature coefficient (Q_{10}) for the growth of maize seedlings germinating in the dark at various temperatures.

Hours of germination	Temperature interval (°C)			
	15~20	20~25	25~30	30~35
50		2.64	2.61	4.39
100		3.49	2.96	1.77*
150		2.90	1.95*	1.38
200		2.09*	1.45	
250		1.73		
300	5.56	1.41		
350	3.78			
400	2.44*			
450	1.70			

* The value obtained at the most actively growing stage.

These facts suggest that the efficiency of respiration for growth remains constant within a wide range of temperatures, although an increase in temperature accelerates growth and respiration. If the amount of substances for growth is constant, the maximum amount of seedlings produced is constant regardless of temperature. However, at extreme temperatures, either lower or higher, the *GE* becomes lower probably because of physiological disturbances.

The *GE* decreased abruptly when the stored substances in the seed were exhausted, and the weight of old organs started to decrease; and it became a negative value at later stages (Figs. 2, 3, and 4). A plant consists of various organs, and these organs are in different physiological stages at a given stage: Some new organs are growing vigorously, while other older organs are decreasing in weight (Fig. 5). During later stages of germination, an increase of dry weight of new organs is supported by the constituents in older organs, since the supply of stored substances in the seeds is limited. This may be the cause of the low *GE* value at the late stages of germination. However, the GE_d, which is calculated by the net gain of dry weight of growing organs and the net loss of the dry weight of old organs is kept at about 50 percent for a longer period (Fig. 7).

The difference between the *GE* and the GE_d is significant: The *GE* is 60~85 percent depending upon the chemical composition of seeds, while the GE_d is about 50 percent. This discrepancy may possibly be attributable to the difference of chemical composition between the stored substances in the seed and the plant constituents. When the re-translocation of materials occurs among organs, the GE_d is 10~20 percent lower than the *GE* which is obtained under the condition of direct utilization of stored substances (in the case of seeds rich in carbohydrate).

In the case of maize and soybeans the *GE* was lower at the very early stages of germination (Figs. 2 and 4). This phenomenon is more prominent in soybeans whose seeds are rich in lipids. The following causes may be responsible for these lower *GE* values: (i) The production of heat[14,69], (ii) conversion of lipids to sugars in the seed which is often observed at the initial stage of germination[85], and (iii) an experimental error, because the scutellem is included in the seed (endosperm) and it occupies a significant portion of the weight of the whole kernel (11 percent of ungerminated seed of maize[107]).

IV. GROWTH EFFICIENCY OF PLANTS GROWING IN THE LIGHT

Respiration and Growth Efficiency of the Rice Plant, with Special Reference to Each Organ

Seedlings (27-days old) were transplanted to 14-liter pots containing a culture solution on May 31, 1973. The plants flowered on August 14 (75 days after transplanting) and matured on October 2 (124 days). The concentration of nitrogen in the culture solution was 20 ppmN at earlier stages and increased stepwise to 40 ppmN during flowering. The concentration of other nutrient elements was also changed proportionally to that of nitrogen to maintain the ratio of the composition of the standard culture solution (Table 1). After the milky stage only tap water was supplied.

The respiratory rate and the dry weight of various organs were measured weekly from transplanting to maturity. To measure the respiratory rate of various organs of the shoot, the respiration of the entire shoot was measured first; then the leaf blades and the panicles (only after flowering) were removed successively; and the respiratory rate of the remaining portion of

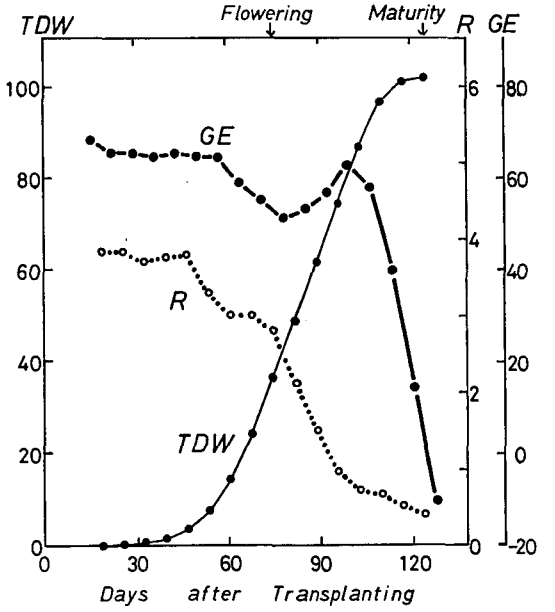

Fig. 8. Total dry weight (*TDW*, g·plant^{-1}), respiratory rate per unit dry weight (*R*, mgCO_2·g^{-1}·hr^{-1}), and the growth efficiency (*GE*, %) of a whole plant at successive growth stages of rice plants grown in a culture solution (1973).

the shoot was measured at each stage of the removal of organs; the respiratory rates of each organ were worked out by the difference of successive measurements[117].

The *GE* of each organ was calculated with the rate of dry matter production and the respiratory rate of each organ by the formula (2). Due to this procedure, the *GE* of a given organ has limited meaning because there is translocation of substances from or into the organ. Thus, it is better to call it the *apparent growth efficiency.*

The increase in the total dry weight of plants was slow for 40 days after transplanting, more rapid until the milky stage, and then slowed down till maturity (Fig. 8). The growth rate and the respiratory rate of the plants were low for 40 days after transplanting, and then increased significantly towards flowering (Fig. 9). The growth rate was kept high for another 30 days, and then decreased abruptly. The respiratory rate decreased after flowering, but the rate of this decrease was much lower than that of the growth rate. The gross photosynthetic rate (P'_g, the sum of growth rate and respiratory rate) was maximum at about flowering, decreased slowly during the early ripening stages, and then rapidly decreased toward maturity.

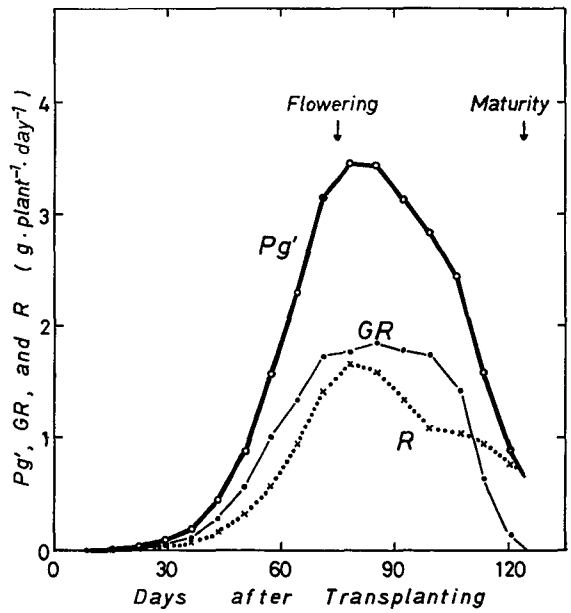

Fig. 9. Gross photosyhnthetic rate (P'_g), growth rate (GR), and respiratory rate (R) at successive growth stages of rice plants grown in a culture solution (1973).

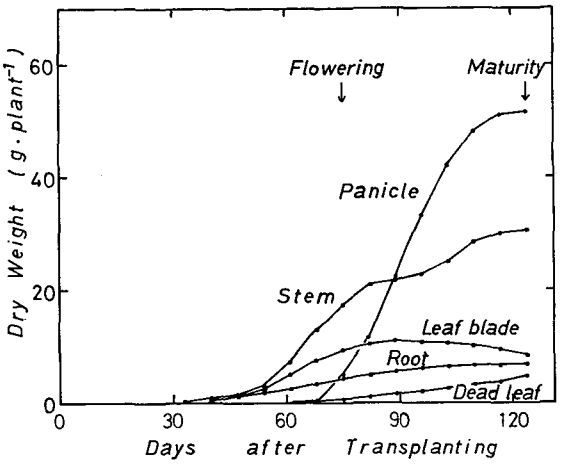

Fig. 10. Dry weights of various organs at successive growth stages of rice plants grown in a culture solution (1973).

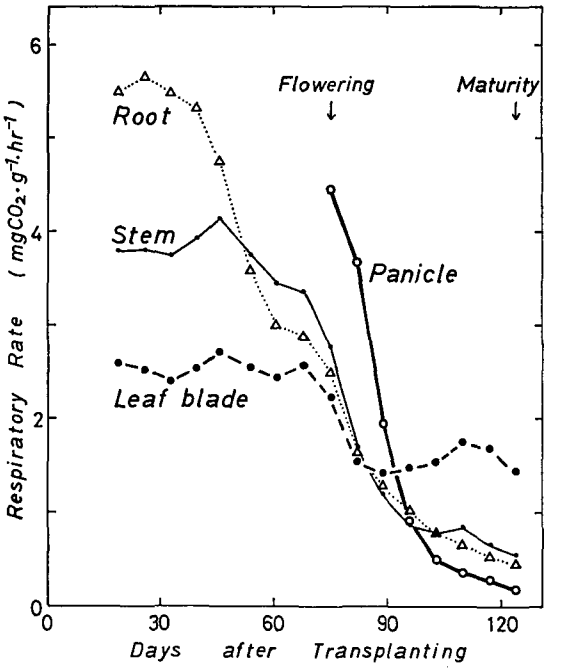

Fig. 11. Respiratory rate per unit dry weight of various organs at successive growth stages of rice plants grown in a culture solution (1973).

The respiratory rate per unit dry weight of a whole plant was about 3.8 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ for 50 days after transplanting, about 3 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ before flowering, and then decreased successively with growth (Fig. 8). The *GE* of the whole plant was maintained at about 65 percent throughout the vegetative growth stage, dropped slightly prior and after flowering, increased again to about 60 percent at the milky stage, and then declined rapidly.

Dry weights of the leaf blades, the stem (leaf sheath and culm), and the roots began to increase rapidly about 40 days after transplanting (Fig. 10). The dry weight of the leaf blades reached a maximum at a few days after flowering, and then decreased gradually. The increase of dry weight of the stem stopped tentatively at flowering and became larger again during the late ripening stage*. The dry weight of the roots was small for about 40 days after transplanting, and then increased gradually until the middle of ripening stage. The dry weight of the panicles started to increase rapidly soon after flowering, and increased actively till maturity. The dry weight of the dead leaves (leaf blades and sheath) continued to increase until maturity.

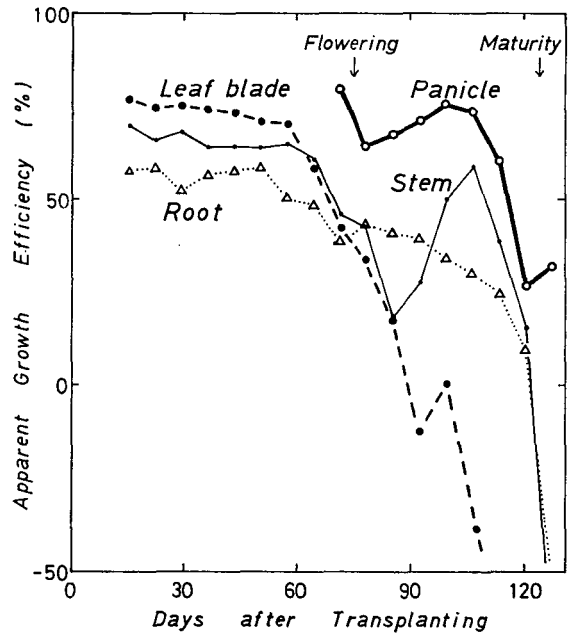

Fig. 12. Apparent growth efficiency of various organs at successive growth stages of rice plants grown in a culture solution (1973).

* Growth of the stem at later stages is not a normal phenomenon and it occurred because of late tillering.

The respiratory rate per unit dry weight of each organ was high at early stages of growth, and decreased progressively with growth (Fig. 11). During early vegetative growth stages the respiratory rate was about 5.5, 4.0, and 2.5 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$, for the roots, the stem, and the leaf blades, respectively. Those of the stem and the leaf blades were kept almost constant until flowering, while that of the roots decreased rapidly. The respiratory rates of these organs decreased after flowering, became 1.5 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ about 10 days after flowering, and thereafter continued to decrease in the roots and the stem, but increased tentatively in the leaf blades at the milky stage. The respiratory rate of the panicles was high, 4.4 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$, at flowering, decreased progressively with ripening, and was nearly zero at maturity.

The apparent *GE* during vegetative growth stages was 70~75 percent in the leaf blades, 64~67 percent in the stem, and 55~60 percent in the roots (Fig. 12). After flowering, it decreased in the leaf blades and the roots,

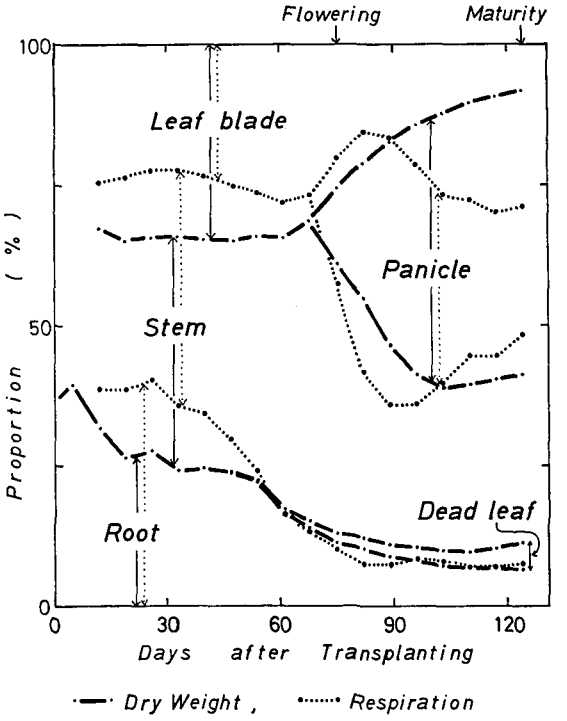

Fig. 13. Proportions of various organs to the whole plant in dry weight and respiration at successive growth stages of rice plants grown in a culture solution (1973).

and increased for certain periods in the stem. The apparent *GE* of the panicles was 65~75 percent throughout ripening and decreased rapidly from about 10 days before maturity.

The proportion of dry weight of the leaf blades, the stem, and the roots to that of total plant weight was about 35, 40, and 25 percent, respectively, during vegetative growth stages (Fig. 13). During ripening stages, the proportion of the stem increased and that of the roots decreased. After flowering the proportion of the panicles increased markedly and became about 50 percent at maturity.

The proportion of respiration of the leaf blades, the stem, and the roots to the total plant respiration was about 25, 35~45, and 40~30 percent, respectively, during vegetative growth stages; later that of the stem increased and that of the roots decreased until flowering. After flowering the proportion of respiration of the leaf blades decreased tentatively, became larger again at the active ripening stage, and was about 30 percent at maturity. The proportion of respiration of the stem decreased for about 20 days after flowering, then increased after the middle stage of ripening, and was about 40 percent at maturity. During ripening the proportion of respiration of the roots was 10 percent or lower. The proportion of respiration of the panicles was about 50 percent at about 10 days after flowering and decreased appreciably with growth.

Respiration and Growth Efficiency of the Maize Plant

The following four experiments were conducted to collect data during early, middle, and late growth stages, and on the ear[100,113].

Experiment 1: Wisconsin Hybrid Corn No. 95 was planted in vermiculite contained in small pots on May 16, 1968 and was grown for 34 days in a glass-house.

Experiment 2: D403×D405 was planted in 4-liter pots containing the soil on May 15, 1968 and was grown for 73 days in a glass-house.

Experiment 3: Fukko No. 8 was sown in the field on May 11, 1968 under the standard culture conditions, silked on August 9 (90 days after sowing), and was harvested on October 2 (145 days).

Experiment 4: Fukko No. 8 was sown in the field on May 10, 1969 under the standard culture conditions. The plant silked (50%) on August 11 and was harvested on September 27. At about 10-day intervals from silking to harvest, the uppermost ear was taken from 10 plants, the base of the shank was dipped in water, and respiratory rate of the ears was measured.

Data of the total dry weight, the respiratory rate, and the *GE* of the maize plant at successive stages of growth in Expts 1, 2, and 3 are summarized in Table 7.

During juvenile growth stages (Expt. 1), the dry weight of seeds decreased and that of seedlings increased with growth. The total dry weight of the seed and seedling decreased at early stages of germination, and then increased markedly. The respiratory rate per unit dry weight of the seedlings was

TABLE 7. Total dry weight, respiratory rate per unit dry weight, and the growth efficiency (*GE*) at successive growth stages of maize plants (1968).

Days after sowing	Leaf age	Total dry weight ($g \cdot plant^{-1}$)	Respiratory rate ($mgCO_2 \cdot g^{-1} \cdot hr^{-1}$)	*GE* (%)
	Juvenile growth stage (Expt. 1 in small pot)			
8	—	0.032	—	
13	—	0.095	3.78	66
17	2.7	0.157	5.62	62
21	3.4	0.276	3.91	65
25	4.0	0.505	2.96	73
30	5.2	0.834	5.78	59
34	5.8	1.281	4.07	57
	Vegetative growth stage (Expt. 2 in soil-pot)			
17	3.0	0.118	6.31	
24	4.5	0.450	9.12	61
31	7.3	2.37	9.02	62
38	9.0	9.41	6.29	61
45	11.2	21.5	3.72	59
52	14.0	48.9	4.40	64
59	15.5	76.5	3.66	49
66	17.0	106.9	2.08	51
73	—	134.9	2.05	50
	Reproductive growth stage (Expt. 3 in the field)			
69	11.0	19.9	3.55	
77	13.5	40.8	3.00	63
86	14.0	84.6	2.16	68
96	16.5	133.4	1.16	63
108	—	178.1	0.87	59
116	—	203	0.78	56
126	—	230	0.71	51
137	—	244	0.66	30

3~6 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$. The *GE* was 66~62 percent at early stages of germination, raised to 73 percent at about 23 days after sowing, and declined to 57 percent at the end of the experiment.

During vegetative growth stages (Expt. 2), the total dry weight of the plant increased slowly at the early growth stage, and then more rapidly. The dry weight of the roots ceased to increase at later growth stages, and then decreased slightly from 66 days after sowing. The respiratory rate per unit dry weight was low at early growth stages, reached a maximum about 30 days after sowing, and then decreased successively with growth. The *GE* was about 60 percent for 50 days after sowing, and then decreased to about 50 percent at later growth stages.

During reproductive growth stages (Expt. 3), the total dry weight of the plant increased successively with growth until harvest. The respiratory rate per unit dry weight was high before silking, and then decreased during ripening. The *GE* was about 63 percent 70 days after sowing, attained a maximum (68 percent) at about 80 days after sowing, and then decreased gradually to 30 percent at the late growth stage.

Expts 1 and 2 were performed with pots to make the measurement of respiration of small plants more accurate. Environmental conditions, however, differed between the pot and the field experiments: The mean temperature was 4°C higher in the former than in the latter, and plants in the pots suffered from malnutrition by the end of experiments due to limited amount of the growth media. Moreover, the varieties used were different among these three experiments. Nevertheless, as demonstrated in Table 7, the total dry weight, the respiratory rate per unit dry weight, and the *GE* were similar between Expt. 1 and Expt. 2 at the 3rd leaf stage, and also between Expt. 2 and Expt. 3 at the 11th leaf stage. Based on this fairly good agreement, the data from sowing to the 3rd leaf stage of Expt. 1, those from the 3rd leaf stage to the 11th leaf stage of Expt. 2, and those from the 11th leaf stage of Expt. 3 were combined by adjusting the days after sowing to that of the field experiment on the basis of the leaf age (Fig. 14).

The growth rate and the respiratory rate increased progressively with growth, reached maximum values at silking (5.1 and 2.1 $g \cdot plant^{-1} \cdot day^{-1}$, respectively), and then the growth rate decreased markedly during ripening, and was nearly zero at maturity, while the respiratory rate was kept at its maximum value for about 30 days, and then decreased slightly. The gross photosynthetic rate (P'_g) increased rapidly with growth until silking, then decreased during ripening. The *GE* was kept at 60~65 percent until silking,

decreased gradually for a certain period, and then more rapidly to 20 percent at maturity.

The increase of dry weight of the ear (Expt. 4) started soon after silking

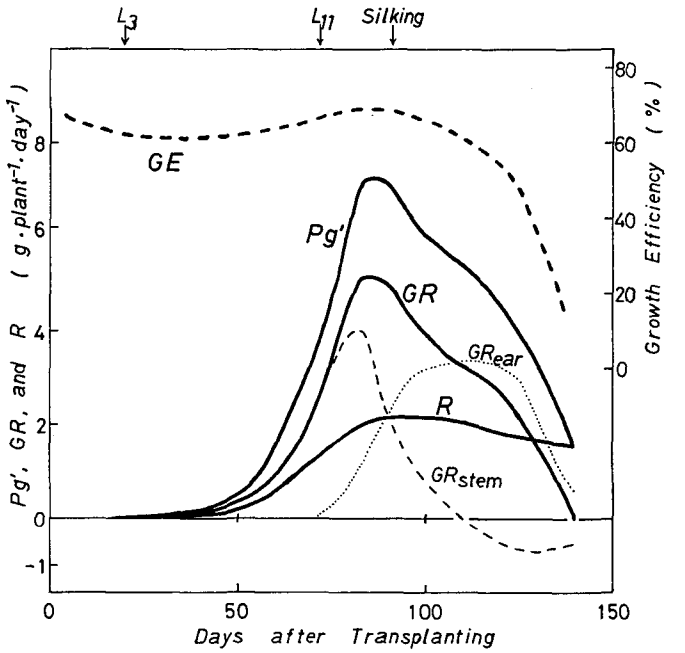

Fig. 14. Gross photosynthetic rate (P_g'), growth rate (GR), respiratory rate (R), and growth efficiency (GE) at successive growth stages of maize plants (combined, See: Text.).

L_3 and L_{11} are the 3rd and 11th leaf stage, respectively.

TABLE 8. Dry weight, respiratory rate per unit dry weight, and the growth efficiency (GE) of the ear at successive ripening stages of maize plants grown in the field (1969).

Days after silking	Dry weight ($g \cdot plant^{-1}$)	Respiratory rate ($mgCO_2 \cdot g^{-1} \cdot hr^{-1}$)	GE (%)
−3	2.07	—	
3	8.29	2.38	76
15	27.0	2.03	70
25	69.4	1.55	67
37	96.9	0.90	69
47	147	0.46	

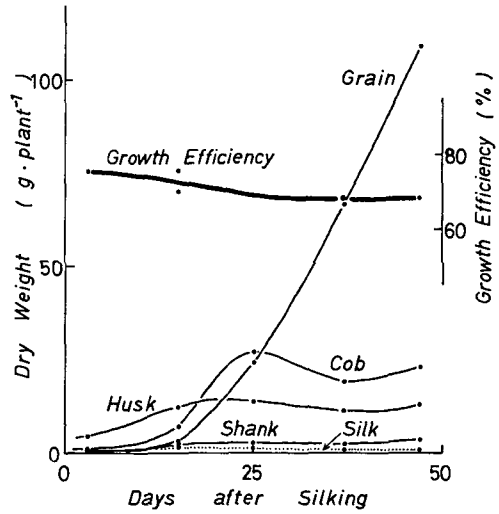

Fig. 15. Dry weight of various organs and the growth efficiency of the ear at successive growth stages of maize plants grown in the field (1969).

and continued actively until maturity (Table 8). The increase of grain weight was the major portion of an increase of the ear weight during ripening, especially after 20 days from silking (Fig. 15). The respiratory rate per unit dry weight of the ear decreased successively from about 2.4 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ soon after silking to about 0.5 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ at maturity (Table 8). The *GE* was maintained almost constant at about 70 percent throughout ripening, although it tended to decrease slowly with growth.

Respiration and Growth Efficincy of the Soybean Plant

The following four experiments[114] were carried out as in the case of maize plant described above.

Experiment 1: Seeds were planted in vermiculite contained in small pots on June 17, 1969, and plants were grown in a glass-house for 22 days with the standard culture solution (60 ppmN).

Experiment 2: Seeds were planted in 4-liter pots containing the soil on May 24, 1969 and the plants were grown for 72 days in a net-house. Seedings emerged on June 10 (17 days after sowing) and flowering occurred from July 18 (55 days) for about two weeks.

Experiment 3: Seeds were sown in the field on May 18, 1969 under the standard culture conditions. Flowering started on July 28 (71 days after sowing) and lasted for about two weeks, and harvesting was done on October 9 (143 days).

Experiment 4: Seeds were sown in the field on May 15, 1973 under the standard culture conditions. Fifty percent flowering was on July 25 (71 days after sowing), and harvesting was on October 8 (146 days). The dry weight of the pods (hulls and seeds) was measured weekly. In a separate experiment, seeds were planted in 14-liter pots containing soil on May 19, 1973, and grown in a glass-house. The respiratory rate of the pods was measured every three to five days from 19 days after the start of flowering to maturity. For the measurement of the respiratory rate, an intact raceme consisting of two to six pods was enclosed in a $3\times5\times5$ cm^3 plastic chamber. At each measurement three to six racemes at various positions on the plants were chosen, so that pods with various growth stages were included.

TABLE 9. Total dry weight, respiratory rate per unit dry weight, and the growth efficiency (*GE*) at successive growth stages of soybean plants (1969).

Days after sowing	Leaf age*	Total dry weight ($g\cdot plant^{-1}$)	Respiratory rate ($mgCO_2\cdot g^{-1}\cdot hr^{-1}$)	*GE* (%)
Juvenile growth stage (Expt. 1 in small pot)				
6	E	0.050	4.29	
10	P	0.133	7.49	73
14	0.2	0.293	6.69	61
18	1.3	0.497	6.40	56
22	2.0	0.885	8.06	55
Vegetative growth stage (Expt. 2 in soil-pot)				
30	P	0.207	5.01	
37	1.3	0.682	7.40	57
44	3.2	1.938	3.96	60
51	4.8	4.12	3.83	61
58	7.0	8.06	3.08	59
65	9.0	11.2	2.94	57
72	11.1	16.8	1.62	61
Reproductive growth stage (Expt. 3 in the field)				
67	8.7	5.26	4.79	
77	10.9	13.9	3.60	61
87	11.4	21.6	2.98	43
99	11.5	32.4	2.68	42
109	12.0	41.2	2.12	38
128	12.1	52.8	1.02	34

E: Emergence.
P: Developing primary leaves.
* Number of developed trifoliated leaves on the main stem.

Results of the total dry weight, the respiratory rate, and the *GE* of the soybean plant at successive stages of growth in Expts 1, 2 and 3 are tabulated in Table 9.

During juvenile growth stages (Expt. 1), the dry weight of cotyledons decreased and that of seedlings increased with growth. The dry weight of seedlings was about 0.9 g·plant^{-1} when the 2nd trifoliate leaf developed. The respiratory rate per unit dry weight was low at the initial stage of germination, increased to 7.5 mgCO_2·g^{-1}·hr^{-1} at the primary leaf stage, decreased successively with growth, and raised again at the end of the experiment. The *GE* was high, 73 percent, soon after the start of germination, decreased progressively with growth, and was 55 percent at the 2nd leaf stage.

During vegetative growth stages (Expt. 2), the growth rate was low at early growth stages, and then became higher at late growth stages. Almost all stored substances in the seed were exhausted when the total dry weight attained about 1 g·plant^{-1}. The total dry weight of the plant was about 6 g·plant^{-1} at the start of flowering and 17 g·plant^{-1} at 72 days after sowing. The respiratory rate per unit dry weight was lower at the early growth stage, high, 7.4 mgCO_2·g^{-1}·hr^{-1} at the 1st leaf stage, and then decreased continuously with growth. The *GE* was kept almost constant at

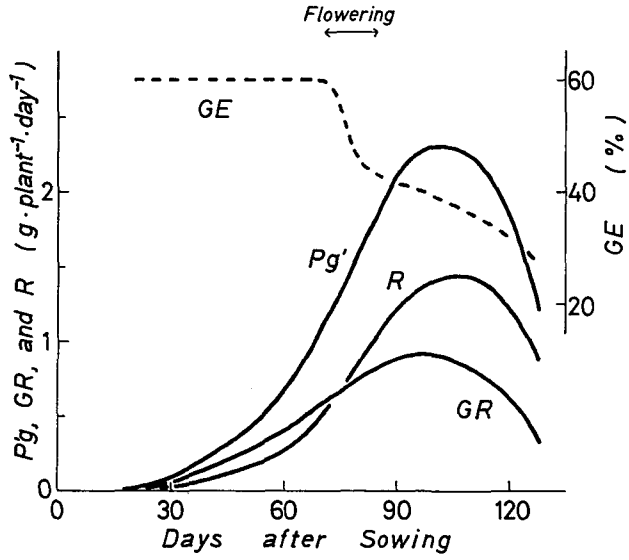

Fig. 16. Gross photosynthetic rate (P'_g), growth rate (*GR*), respiratory rate (*R*), and the growth efficiency (*GE*) at successive growth stages of soybean plants (combined, See: Text).

about 60 percent during vegetative growth stages.

During reproductive growth stages (Expt. 3), the total dry weight of the plant increased successively throughout the growth. The growth rate was high during early pod-filling stages, and then decreased at later growth stages. The increase of the total dry weight during ripening was large mostly due to the increase in seed weight, while that of the leaves and the stem (including petiole) was much smaller. The dry weight of the pods began to increase significantly from about 15 days after the start of flowering, and occupied 57 percent of the total dry weight at harvest. During late ripening stages the dry weight of the leaves and the stem decreased: A part of their decrease was attributable to defoliation of senescent leaves. The respiratory rate per unit dry weight was higher before flowering, 3~4 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ at flowering, decreased with growth, and was about 1 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ at maturity. The *GE* was about 60 percent before flowering, dropped to about 43 percent during ripening, and was about 30 percent at maturity.

The data of growth rate, respiratory rate, and the *GE* from sowing to the 1st trifoliate leaf stage are taken from Expt. 1, those from the 1st

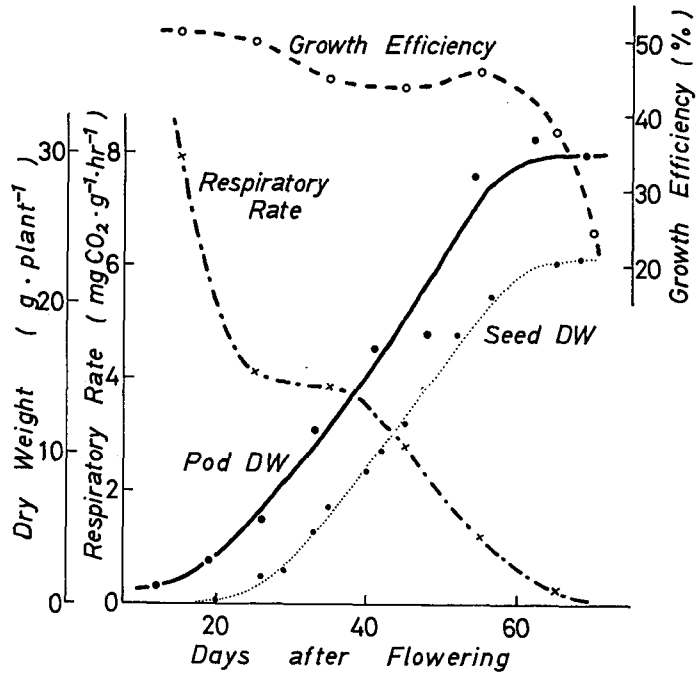

Fig. 17. Dry weight (*DW*), respiratory rate per unit dry weight, and growth efficiency of the pod (hull and seed) at successive ripening stages of soybean plants (1973).

leaf stage to flowering are from Expt. 2, and those from flowering to maturity are from Expt. 3, and they are arranged on a basis of the leaf age and the days after sowing in the field experiment (Fig. 16).

The growth rate and the respiratory rate increased progressively with growth until the early reproductive growth stage, in which the former was larger than the latter during vegetative growth stages, but thereafter the latter exceeded the former. Both rates decreased during ripening, and the decrease of the respiratory rate was smaller than that of the gross photosynthetic rate (P'_g). The GE was kept almost constant at about 60 percent from shortly after sowing to flowering, decreased abruptly during flowering, and then gradually during ripening.

The dry weight of the pods of the plant grown in the field (Expt. 4) began to increase remarkably at about 10 days after flowering and continued to increase until the end of growth (Fig. 17). The increase in seed weight became rapid about 15 days after the start of active growth of the pods, and the dry weight of the seeds occupied 77 percent of the pod weight at maturity.

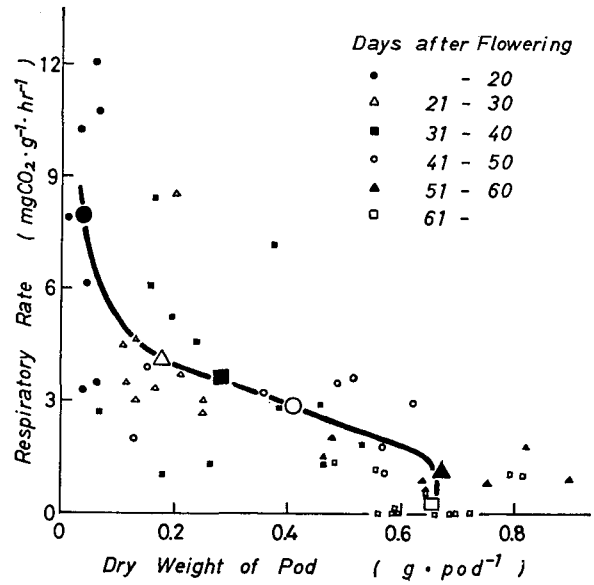

Fig. 18. Relationship between dry weight and respiratory rate per unit dry weight of the pod at successive ripening stages of soybean plants grown in soil-pots (1973).
(Small symbols: values of each measurement,
Large symbols: mean values for each 10-day period).

The respiratory rate per unit weight of the pods was high at the early ripening stage, and decreased with age, although there was a large fluctuation among samples, especially at early growth stages (Fig. 18). The mean values of respiratory rate and dry weight of the pods in the pot experiment were calculated at 10-day intervals during ripening (solid line in Fig. 18), and the change of respiratory rate of the pods in the field experiment (Fig. 17) was estimated on the basis of the dry weight through the relationship between the dry weight and the respiratory rate obtained in the pot experiments.

The respiratory rate per unit dry weight of the pods was high at early ripening stages (about 8 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$, 15 days after the start of flowering), decreased rapidly with ripening, and was nearly zero at maturity. The *GE* of the pods was about 50 percent from flowering to about 25 days after flowering, 44~46 percent when the seed development was active, and then decreased until maturity.

Discussion

The growth of young plants which are germinating in the natural light is dependent upon the stored substances in the seeds during the early period, and becomes gradually self-supporting through its own capability of photosynthesis and mineral absorption[13,113].

The percentage of dependence of plant growth on stored substances is examined with the results of Expt. 1 of the maize plant in Table 7. The *GE* of maize seedlings germinating in the dark was maintained at 65~70 percent (Fig. 4). An increase in seedling weight (b) which is derived from the stored substances can be estimated with the decrease of the seed weight (a) by assuming that the *GE* of the seedling dependent on the stored substances is 70 percent. The balance between the actual dry matter production (c) of the plant in the light and the value of (b) can be considered as the amount produced from current photosynthates (Table 10). Hence, the b/c ratio indicates the percentage of dependence of the growth of plants germinating in the light on the stored substances in the seed. The percentage is 100 percent at the very early stage of germination, becomes smaller with growth, and is nearly zero at the 3rd leaf stage (21 days after sowing).

The percentage of dependence on the stored substances of soybean seedlings germinating in the light is also estimated by assuming that the *GE* of the seedling depending on the stored substances is 75 percent at the initial stage of germination and thereafter 85 percent (Fig. 2). The result (Table 10) is analogous to that of maize seedling.

The nutritional status of the seedling during germination shifts from heterotrophic to autotrophic, while the *GE* changes little during the transi-

TABLE 10. Dependence of the growth of juvenile plants on stored substances in the seed at successive growth stages of maize and soybeans grown in the light.

Days after sowing	Decrease of seed weight (mg·plant^{-1}) a	Gain dependent on stored substances (mg·plant^{-1}) b	Plant weight increase (mg·plant^{-1}) c	Dependence on stored substances (%) b/c
		Maize		
0- 8	48	34	34	100
8-13	86	60	61	98
13-17	51	36	62	58
17-21	27	19	119	16
21-25	12	8.4	229	3.7
25-30	2.0	1.4	329	0.4
		Soybeans		
0- 6	65	49	50	99
6-10	78	67	83	80
10-14	39	33	160	20
14-18	9.3	7.9	204	3.9
18-22	8.3	7.1	389	1.8

b: Estimated from the value of (a) and the growth efficiency (*GE*) in the dark (70% in maize, and from 75 to 85% in soybeans depending on the growth stage as shown in Fig. 2, $b=a\times GE$).

c: Actural increase of dry weight of the plant in the light (Expt. 1 in Tables 7 and 9).

tional period (Tables 7 and 9). Thus, it can be concluded that the energy efficiency is almost the same whether the growth of plants is dependent on the stored substances in the seeds or directly on current photosynthates, if the major constituents of the seeds is carbohydrates.

During the vegetative growth stage, the *GE* of a whole plant is kept almost constant at 60~65 percent and there is no significant difference among crop species tested; rice, maize, and soybeans (Tables 7 and 9, and Fig. 8).

Respiratory rate per unit dry weight of the whole plant of rice, maize, and soybeans was 4~9 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ during early vegetative growth stages, decreased gradually with growth, 2~4 $mgCO_2^{-1} \cdot hr^{-1}$ at flowering and 0.5~1.0 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ at near maturity, although the respiratory rate of soybeans was slightly higher than that of rice or maize throughout the growth.

The respiratory rate per unit dry weight of the rice plant was lowest in the leaf blade among various organs during vegetative growth stages, while the respiratory rate of the leaf blade was maintained relatively high

during ripening (Fig. 11). A higher rate of respiration of the leaf blade during ripening may be associated with active photosynthesis to produce grain, since a high respiratory rate of the leaf is often positively correlated with a high photosynthetic rate[60,88,93,108].

Root respiration occupies a considerable fraction (30~38 percent) of the total respiration of a plant during vegetative growth stages due to a large proportion of the root weight to the total plant weight and to the higher respiratory rate per unit dry weight than the rate of the shoots (Table 11, and Figs. 11 and 13). Similar results were obtained with the roots of maize plants grown in the culture solution[117] and also of woody plant[41]. Thus, root respiration is important for the quantitative evaluation of respiration of the whole plant at early growth stages. However, at later growth stages, the respiratory rate per unit dry weight of the roots decreases more rapidly and becomes smaller than that of the shoots, and also the proportion of root weight decreases. The fraction of root respiration decreases and is about seven percent at maturity.

Since there is translocation of photosynthetic products or stored substances from one organ to another, and also from old to new ones within organs[90], there are various difficulties in interpreting the correct value of the *GE* of each organ. In spite of such restrictions, the apparent *GE* of the leaf, the stem, and the root was about 75, 65, and 55 percent, respectively, during the active vegetative growth stages of the rice plant (Fig. 12). The apparent *GE* of the roots of the maize plant was also about 10 percent lower than that of the shoots[117]. By measuring the photosynthesis and

TABLE 11. Respiration of the root and the whole plant, and the root to the whole plant ratios in dry weight and respiration at successive growth stages of rice plants grown in a culture solution.

Days after transplanting	Respiration ($mgCH_2O \cdot plant^{1-} \cdot day^{-1}$)		Root/whole plant ratio (%)	
	Root a	Whole plant b	Dry weight	Respiration a/b
19	3.2	8.4	27	38
33	16	44	24	36
47	67	223	24	30
61	120	721	17	17
75	167	1660	11	10
89	116	1500	9	8
103	81	1010	7	8
117	59	860	7	7

respiration of stratified heights of a maize population[99,100], it was reported that the ratio of dry matter production to gross photosynthesis (P_g) (the apparent *GE*) was 70~89 percent at the upper stratum where active leaves were located, and this value was higher 5~20 percent than the *GE* of the population.

Comparison of the apparent *GE* of each organ offers suggestions about the significance of respiration of each organ in relation to the growth of a whole plant. For example, the lower *GE* of the roots is probably due to an energy requirement for absorption and assimilation of mineral nutrients in addition to that for their own growth.

Respiratory rate per unit dry weight of reproductive organs of rice, maize, and soybean plants is high, 2.5~8 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ at early ripening stages (Table 8, and Figs. 11 and 17), which is about twice of that of the whole plant at the same stage (Tables 7 and 9, and Fig. 8). However, it decreases with ripening, is similar to the rate of a whole plant at the middle stage of ripening, and is much smaller than the rate of a whole plant at maturity.

The photosynthetic activity of reproductive organs of field crops is assumed to be quite low[18]. TSUNO *et al.*[109] reported that the panicle of the rice plant could be considered as a non-photosynthetic organ, since its photosynthetic rate was very low even under high light intensity. Net photosynthesis of the ear of the maize plant is negative during middle stage of ripening.[101] It is also reported that the apparent photosynthetic rate of the pod of soybeans is positive only under a high light intensity during early ripening, and its contribution to the dry matter production of reporoductive organs is insignificant[65,77]. From these reports it can be concluded that the photosynthesis of reproductive organs is small, and the majority of substances used for growth is photosynthates of leaves.

The respiratory rate per unit dry weight of the pods of the soybean plant is generally high during early ripening stages but the variation among individual pods is large when the pod is small (Fig. 18). The pods, which are extremely low in respiratory rate at early growth stages, may be those which abort later or fail to mature completely.

The proportions of respiration as well as the dry weight of the reproductive organ to those of the whole plant are small at early ripening and increase with ripening (Fig. 19). The proportion of respiration is kept larger than that of dry weight until about the middle stage of ripening. The proportion of respiration is 50~60 percent for about 20 days during actively ripening stages, and then it decreases markedly. The proportion of respiration of the leaf and the stem continues to increase in spite of a decrease in the proportion of dry weight.

Although the *GE* of a whole plant is kept fairly constant during actively growing stages, it begins to decrease with growth and becomes quite low at the late maturing stage (Figs. 8, 14, and 16). These trends were also reported by other investigators[40,65,86].

The decrease of the *GE* during late growth stages is obviously caused by an increased proportion of respiration which is not coupled with growth. Since the proportion of respiration of the reproductive organs decreases (Fig. 19) and that of the stem increases at this stage (Fig. 13), a major portion of the respiration which is not coupled with growth seems to be derived from the stem.

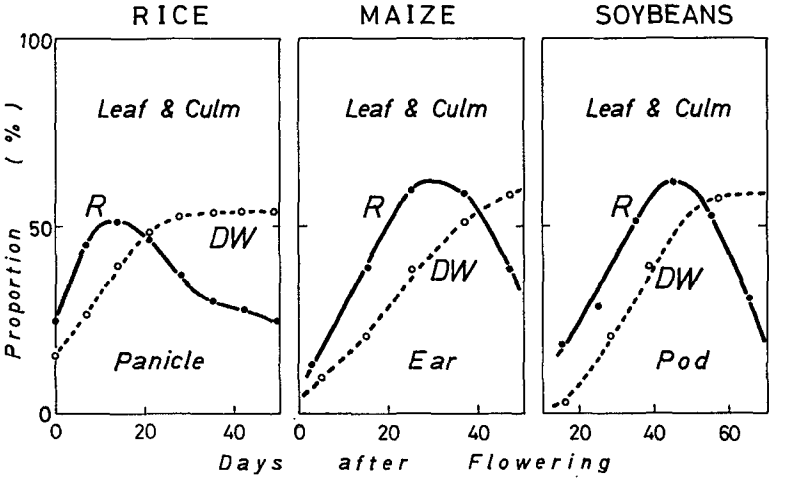

Fig. 19. Changes of the proportions of the reproductive organ or the vegetative organ to the whole plant in dry weight (*DW*) and respiration (*R*) at successive ripening stages of rice, maize, and soybeans. Values are estimated on the basis of Fig. 13 for rice (without root), Tables 7 and 8 for maize, and Table 9 and Fig. 17 for soybeans.

TABLE 12. Dry matter production, respiration, and the growth efficiency (*GE*) of the whole plant during a growth cycle of rice, maize, and soybeans.

Crop	Culture condition	Dry matter production	Respiration*	*GE*
		($g \cdot plant^{-1}$)		(%)
Rice	Solution	101.7	83.8	55
Maize	Field	242.9	143.1	62
Soybeans	Field	52.8	69.6	43

* Expressed as CH_2O.

TABLE 13. Dry matter production, respiration, and the growth efficiency (*GE*) of reproductive organs of rice, maize, and soybeans during ripening*.

Crop	Organ	Dry matter production	Respiration	*GE*
		($g \cdot plant^{-1}$)		(%)
Rice	Panicle	51.5	22.5	69.6
Maize	Ear	145.4	53.0	72.4
Soybeans	Pod	26.9	32.2	45.5

* Rice : From 0 to 50 days after flowering.
Maize : From 3 to 47 days after silking.
Soybeans : From 20 to 70 days after the start of flowering.

In comparison to rice and maize plants, in the soybean plant the decrease of *GE* at later growth stages begins earlier starting from the initial ripening stage (Fig. 16). This may be due to the fact that substances accumulating in the seeds of soybeans require more energy than that of other crops. The *GE* during a whole growth cycle is 55~60 percent in rice and maize plants, and is 43 percent in the soybean plant (Table 12). This difference between soybeans and other plants is due to the difference in the *GE* of reproductive organs during ripening. The *GE* of reproductive organs throughout ripening is similar to that during actively ripening stages; about 70 percent in rice and maize, and 45 percent in soybeans (Table 13).

V. GROWTH EFFICIENCY AS AFFECTED BY ENVIRONMENTAL CONDITIONS

Respiration and Growth Efficiency as Affected by Light

Seeds of a maize single cross, D403×D405, were sown on May 28, 1969 in 14-liter pots containing soil in a net-house. Seedlings emerged on June 10, and four plants per pot were established. Starting from July 2 (6.2 leaf stage and 1.8 $g \cdot plant^{-1}$ in the total dry weight), graded shading treatments, *i.e.*, 100 (control), 70, 56, 22, and 6 percent of the light condition in a net-house, were given for 17 days by using combinations of a white screen (light transmission ratio, LTR: 70%) and/or a black screen (LTR: 56%). The light condition in the net-house was 55 percent of the natural light condition in the outdoors which was 537 $gcal \cdot cm^{-2} \cdot day^{-1}$ during the shading treatment. Mean temperature was 20.0°C.

The dry weight and the respiratory rate of a whole plant were measured at the beginning and at the end of the treatment. The *GE* was calculated

from the growth rate ($g \cdot plant^{-1} \cdot day^{-1}$) and the respiratory rate ($gCH_2O \cdot plant^{-1} \cdot day^{-1}$) during the 17-day treatment. Contents of total nitrogen (T-N), carbohydrate (T-Ch, sugars plus starch), and their fractions in the shoot were determined at the end of treatments[116].

The number of leaves on the main stem at the end of experiment was 12.1, 11.2, 11.1, 9.3, and 7.5 at the 100, 70, 56, 22, and 6 percent treatments, respectively. The growth rate decreased almost proportionally with the decrease of light intensity (Fig. 20). At the 6 percent treatment, there was a decrease of the dry weight during the experiment although the leaf age advanced. The rates of respiration and gross photosynthesis (P'_g) decreased with the decrease of light intensity. The decrease was more significant in gross photosynthesis than in respiration. The *GE* was kept at 65~60 percent between the 100 and the 50 percent treatments, and decreased markedly with a further decrease of light intensity.

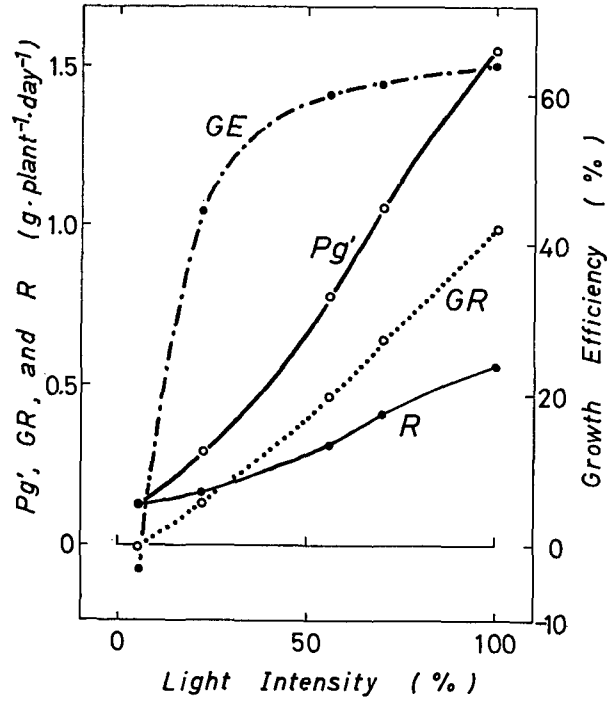

Fig. 20. Gross photosynthetic rate (P'_g), growth rate (GR), and respiratory rate (R) of maize plants grown at graded light conditions (1969). 100% in light intensity represents the natural conditions in the net-house (295 $gcal \cdot cm^{-2} \cdot day^{-1}$).

Contents of T-N, soluble nitrogen (Sol-N), and the Sol-N/T-N ratio in the shoot at the end of treatment increased with the decrease of light intensity (Fig. 21). The content of T-Ch and the T-Ch/T-N ratio decreased with the decrease of light intensity. Contents of sugars and starch decreased with the decrease of light intensity, but the content of starch increased slightly with the extremely heavy shading. Contents of NH_4-N, amide-N, amino-N, and NO_3-N increased with the decrease of light intensity (Table 14). Change of the content of soluble-protein-N (Sol-prot-N) was small throughout all treatments.

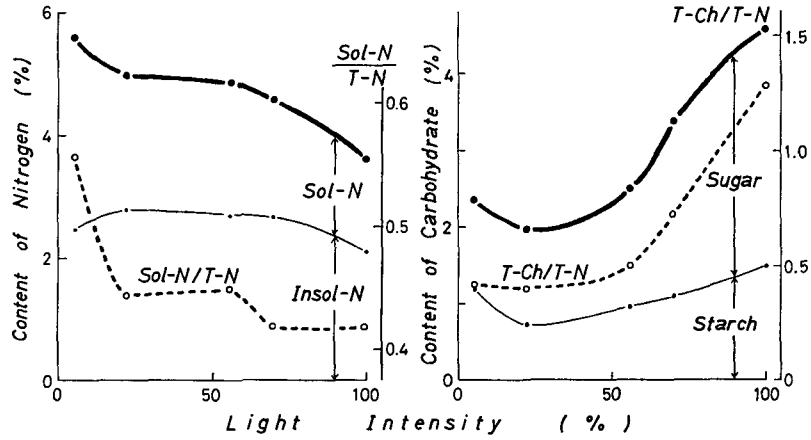

Fig. 21. Contents of soluble nitrogen (Sol-N), insoluble nitrogen (Insol-N), sugar, and starch, and soluble-N to total-N ratio (Sol-N/T-N) and total carbohydrate to total-N ratio (T-Ch/T-N) in the shoot of maize plants grown at graded light conditions (1969).

TABLE 14. Various fractions of soluble nitrogen in the shoots of maize plants grown at graded light conditions.

Light intensity (%)*	Sol-prot-N	NH_4-N	amide-N	amino-N	NO_3-N
	(N% on dry matter basis)				
100	0.36	0.024	0.09	0.088	0.51
70	0.31	0.030	0.15	0.133	0.80
56	0.32	0.034	0.18	0.137	1.16
22	0.31	0.038	0.31	0.135	1.30
6	0.46	0.107	0.79	0.315	1.38

* 100% represents the natural light conditions in the net-house (295 gcal·cm^{-2}·day^{-1}).

To elucidate the nature of respiration of the plants by measuring the changes of respiration and the growth of organs in the dark, a separate experiment was carried out. Maize plants, which were grown with the same condition as in the previous experiment, were transferred to a dark room kept at 23±0.5°C on July 18, when the plants were at the apical inflorescence initiation stage, 18.6 g·plant^{-1} in total dry weight, and 124 cm in height. The respiratory rate of a whole plant, the length of apical inflorescence, the number of leaves, and the dry weight were measured at 0, 1, 3, 5, 8, 11, and 14 days after the start of dark treatment.

The number of leaves on the main stem continued to increase for three days in the dark, and the inflorescence continued to elongate for six days, and then these were discontinued (Fig. 22). Although only one leaf at the bottom of culm was dead at the start of treatment, three leaves were dead at the 3rd day, five leaves at the 5th day, and seven leaves at the 8th day, and the whole plant was almost dead at the 14th day of the dark treatment. Respiratory rate per unit dry weight was about 4 mgCO_2·g^{-1}·hr^{-1} at the start of the dark treatment, decreased markedly during a one-day treatment, continued to decrease for a further five-day period, and then gradually continued decreasing until the end of experiment.

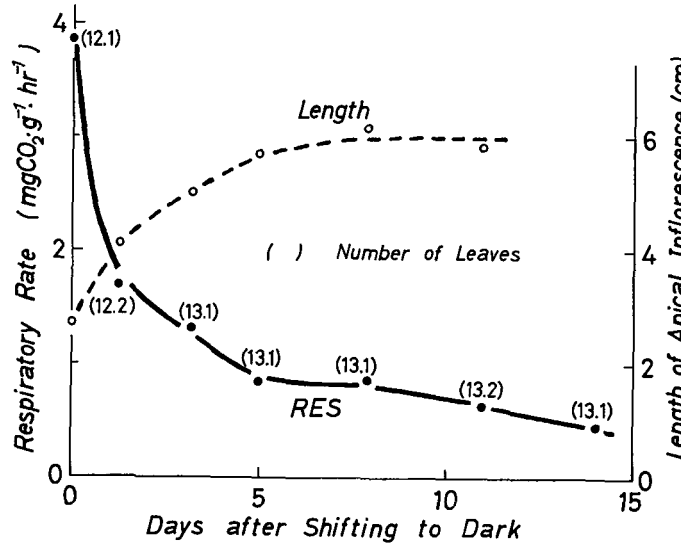

Fig. 22. Changes of respiratory rate per unit dry weight of the shoots, and length of apical inflorescence of maize plants after shifting the plant to the dark.

Respiration and Growth Efficiency as Affected by Nitrogen

Four 19-day-old seedlings of maize (D403×D405, 3.3 leaf stage) were transplanted in 14-liter pots on May 29, 1969, and grown in a glass-house with culture solutions, having graded levels of nitrogen, *i. e.*, 0, 10, 60, 150 and 600 ppmN. The respiratory rate and the dry weight of a whole plant were measured 20 days after transplanting. On this day, additional two treatments were established; *i. e.*, the plants grown with 0 ppmN were shifted to 150 ppmN (0→150 ppmN), and those grown with 150 ppmN were to 0 ppmN (150→0 ppmN). Thus, there were seven treatments. The plants were grown for another 23 days, and then the respiratory rate and the dry weight were measured again. The *GE* was calculated from the growth rate and the respiratory rate during the 23-day treatment. Contents of T-N, T-Ch, and their fractions in the shoot were determined at the end of treatments (43 days after transplanting)[116].

At 20 days after transplanting, the number of leaves per plant ranged from 6.2 at 0 ppmN to 7.2 at 150 ppmN (Table 15). At the end of experiment, the difference in the leaf number was much larger, about three leaves, ranged from 10.9 (0 ppmN) to 14.2 (150 ppmN) leaves per plant. There was a larger difference of the total dry weight among treatments; the largest was 19.6 $g \cdot plant^{-1}$ at 150 ppmN and the smallest was 6.5 $g \cdot plant^{-1}$ at 0 ppmN. The respiratory rate per unit dry weight 43 days after transplanting was 2.1 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ at 0 ppmN, increased with the increase of nitrogen level,

TABLE 15. Number of leaves on the main stem, total dry weight (*TDW*, $g \cdot plant^{-1}$), and respiratory rate per unit dry weight (*R*, $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$) of the whole plant of maize plants grown at graded nitrogen levels.

Nitrogen level (N ppm)	20 days after transplanting			43 days after transplanting		
	Leaf No.	*TDW*	*R*	Leaf No.	*TDW*	*R*
0	6.2	0.53	5.09	10.9	6.5	2.12
10	7.0	0.86	8.09	12.9	11.0	2.47
60	6.9	0.69	8.66	13.5	15.1	2.90
150	7.2	0.94	8.11	14.2	19.6	3.94
600	6.9	0.75	7.55	14.0	17.2	4.16
0→150	—	—	—	12.6	12.6	4.52
150→0	—	—	—	12.1	10.4	1.96

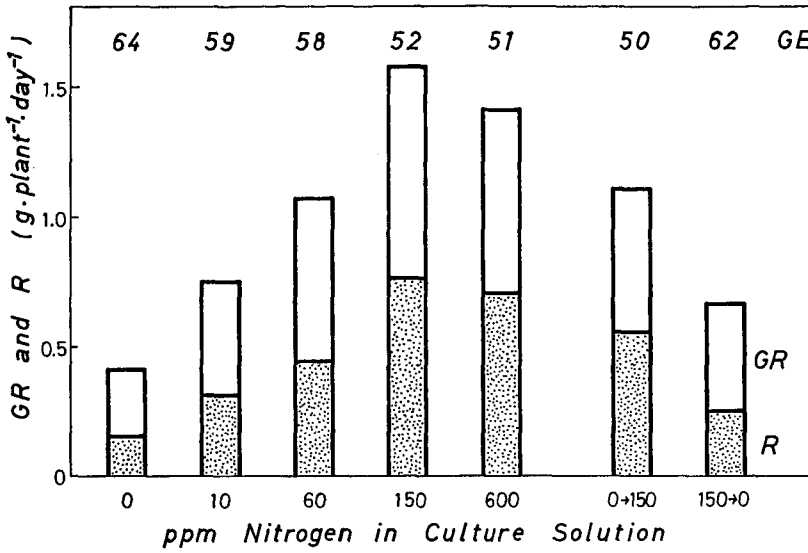

Fig. 23. Growth rate (*GR*), respiratory rate (*R*), and the growth efficiency (*GE*) of maize plants grown at graded nitrogen levels in culture solutions (1969).

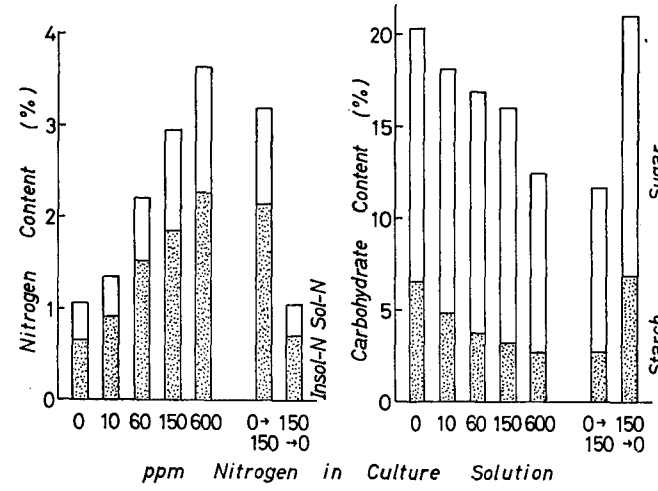

Fig. 24. Contents of soluble nitrogen (Sol-N), insoluble nitrogen (Insol-N), sugar, and starch in the shoots of maize plants grown at graded nitrogen levels in culture solutions (1969).

and was 4.2 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ at 600 ppmN. The rate at 0→150 ppmN was largest, while that at 150→0 ppmN was smallest among treatments.

The growth rate and the respiratory rate increased with the increase of nitrogen level from 0 to 150 ppmN, and decreased slightly at 600 ppmN (Fig. 23). The *GE* decreased progressively with the increase of nitrogen level. In the treatment of 0→150 ppmN or 150→0 ppmN both the growth rate and the respiratory rate ranked between the values obtained at 0 ppmN and those at 150 ppmN. The *GE* at 0→150 ppmN was lowest among all the treatments and that at 150→0 ppmN was slightly lower than that at 0 ppmN.

Contents of T-N, Sol-N, and Insol-N in the shoot increased, and those of sugars and starch decreased with the increase of nitrogen level in the

TABLE 16. Soluble-N to total N ratios (Sol-N/T-N) and total carbohydrate to total-N ratios (T-Ch/T-N) of the shoot of maize plants grown at graded nitrogen levels in culture solutions.

Nitrogen level (N ppm)	Sol-N/T-N (%)	T-Ch/T-N (%)
0	40.2	19.0
10	34.8	13.4
60	33.5	7.7
150	37.5	5.5
600	44.6	3.5
0→150	39.5	3.7
150→0	36.2	20.1

TABLE 17. Various fractions of soluble nitrogen in the shoot of maize plants grown at graded nitrogen levels in culture solutions.

Nitrogen level (N ppm)	Sol-prot-N	NH_4-N	amide-N	amino-N	NO_3-N
	(N% on dry matter basis)				
0	0.17	0.049	0.004	0.030	0.020
10	0.20	0.046	0.014	0.040	0.025
60	0.23	0.047	0.010	0.091	0.051
150	0.29	0.073	0.037	0.114	0.098
600	0.27	0.084	0.173	0.215	0.261
0→150	0.28	0.053	0.160	0.136	0.216
150→0	0.12	0.056	0.014	0.029	0.028

culture solution (Fig. 24). The content of T-Ch at 150→0 ppmN was highest among treatments. The Sol-N/T-N ratio decreased with the increase of nitrogen level, was smallest at 60 ppmN, and increased again with a further increase of nitrogen level (Table 16). The T-Ch/T-N ratio decreased significantly with the increase of nitrogen level. The concentrations of various fractions in Sol-N, especially amide-N, NO_3-N, and amino-N, increased with the increase of nitrogen level (Table 17).

Discussion

The dry matter production decreased almost proportionally with a decrease of the solar energy input (Fig. 20). The *GE* was, however, kept constant at 65~60 percent until about 165 gcal$\cdot$cm$^{-2}\cdot$day^{-1} (56 percent treatment). It is conceivable from these observations that the nature of respiration is unaltered even when the photosynthetic rate is decreased by the limited input of energy, and that respiration is coupled closely with plant growth, although sugar content (Fig. 21) as well as respiratory rate (Fig. 20) decrease with the decrease of photosynthesis. Under such conditions, the conversion rate of inorganic nitrogen absorbed from the roots to proteins is kept high, as demonstrated by the Sol-N/T-N ratio.

Under severe shading conditions, however, the decrease of gross photosynthesis was much larger than that of respiration. Thus, the *GE* decreased at light conditions less than 65 gcal$\cdot$cm$^{-2}\cdot$day^{-1} (22 percent treatment). Under such conditions Insol-N decreased, and NH_4-N, amide-N, amino-N, and Sol-prot-N increased. This fact suggests that the protein synthesis is suppressed, because of the shortage of current photosynthates. NO_3-N content increased with a decrease of light intensity (Table 14). This fact indicates not only a decrease of protein synthesis due to the shortage of photosynthates but also the necessity of light in the reduction of NO_3-N[20,64].

Even if the current supply of photosynthates is discontinued by placing a plant in complete darkness, newly growing organs at the apex continue to grow: The number of leaves increases for about three days and the length of the apical inflorescence elongates for six to seven days in the dark (Fig. 22). These observations suggest that growing organs continue to grow by utilizing various forms of the stored or structural materials in the old organs.

Various attempts to classify the respiration of plants (R) into two components are presented; *i. e.*, growth respiration (R_g) and maintenance respiration (R_m)[48,49]. The R_m is usually considered to be the energy required to maintain the turn over rate of substances and the enzymic activity in living cells.

When an actively growing maize plant was kept in the dark for three days, the growth of new leaf discontinued and the respiratory rate per unit dry weight was 1.3 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ (Fig. 22). From this observation it is assumed that respiration at this rate is required to maintain the plant body. As the respiratory rate when the plant was shifted to the dark was 3.9 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$, the R_m/R ratio is estimated to be 0.33. Similarly, the respiratory rate was 0.85 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ when the elongation of an apical inflorescence discontinued: Then, the R_m/R ratio is 0.22. When the plant was subjected to various light intensities, the dry matter production was nearly zero at 18 $gcal \cdot cm^{-2} \cdot day^{-1}$ (6 percent treatment), where the respiratory rate was 0.13 $mgCH_2O \cdot plant^{-1} \cdot day^{-1}$ (Fig. 20). With this value the R_m/R ratio is 0.23 (=0.13/0.56).

From these discussions, the R_m of actively growing plants is estimated to occupy 22~33 percent of total plant respiration: The variation is fairly large due to conditions, so that further experiments are necessary to confine the R_m/R ratio of plants under various conditions. However, if this R_m/R ratio is employed, out of gross photosynthates in an actively growing plant under ordinary conditions, 8~12 percent is consumed as maintenance respiration, 27~23 percent is utilized as growth respiration, and about 65 percent becomes the newly produced consituent of plants.

The distinction between R_g and R_m mentioned above is operational than biochemical, as pointed out by EVANS[15]. From the viewpoint of biochemical function, the metabolic energy of the plant can also be partitioned into several fractions; the energy for synthetic and catabolic reactions, that for translocation, and that for absorption of minerals, etc. The energy required for these activities is as well supplied with respiration and is mutually associated with R_g and R_m. An analysis of plant respiration through the energetics involves many problems to be solved and is a subject for a future study.

The *GE* decreases when the nitrogen level in culture solution is high; it was 64 percent at 0 ppmN and 52 percent at 150 ppmN (Fig. 23). This phenomenon can be explained by the increase of nitrogen content and the decrease of carbohydrate content in the plant (Fig. 24). The *GE* decreases with an increase of the protein content, because a larger amount of energy is required for the synthesis of proteins than that of carbohydrates.

Under conditions of extremely high nitrogen (600 ppmN), a part of the nitrogen is accumulated as amide-N, but the remainder of the nitrogen exists as NO_3-N in the plant because of the shortage of photosynthates for assimilation (Table 17). Under such conditions the growth rate is smaller and the

GE is lower than that at 150 ppmN (Fig. 23), since the respiratory rate per unit dry weight increases and the metabolism of the plants is disordered with an excess accumulation of nitrogenous compounds.

If a plant which is insufficiently supplied with nitrogen is placed in abundant nitrogen, the *GE* becomes lower, because of the stimulation of respiration by the higher rate of incorporation of rapidly absorbed nitrogen into proteins. In contrast, the *GE* becomes higher when a plant rich in nitrogen is shifted to low nitrogen conditions, because the protein synthesis slows down.

VI. GENERAL DISCUSSION

Growth Efficiency of Plants at the Actively Growing Stage

The *GE* of whole plants of rice, maize, and soybeans was maintained almost constant at 65 percent during the actively growing stages; *i. e.*, from the juvenile growth stage to flowering or to the early ripening stage (Figs. 8, 14, and 16).

Numerous studies on dry matter production, photosynthesis, and respiration of plants growing in the light have been conducted. Although various expressions of the quantitative relationship between photosynthesis and respiration are employed in the literature, reported data are recalculated to the *GE* or the ratio of the net to the gross photosynthetic rate (P_n/P_g ratio) and tabulated in Table 18. The difference between the *GE* and the P_n/P_g ratio can be ignored for all practical purposes, because the difference is relatively small, 2~3 percent, in which the former is higher than the latter on a basis of the same amount of primary photosynthates due to mineral content.

The *GE* values of various crops at the actively growing stage in Table 18 is in the range of 50~70 percent. This range is substantially large even if differences in growing conditions are taken into consideration. Nevertheless, when the substrate for plant growth is assumed to be glucose as a primary product of photosynthesis, the *GE* of a whole plant growing actively under natural conditions is considered to be about 65 percent, according to the results (i) obtained in this study, (ii) which show that the retention percentage of carbon is about 60 percent in the ^{14}C feeding experiment[43], and (iii) that the *GE* of seedlings germinating in the dark is 60~70 percent for seeds rich in carbohydrates (Figs. 3 and 4). However, this value (65 percent) may still lead to an error of about five percent.

The differences of the *GE* values between the C_3 and C_4 plants, between gramineous and leguminous plants, and between seedlings germinating in

TABLE 18. List of growth efficiencies (*GE*, percent) of various annual crops reported in the literature*1.

Crops	*GE*	Growth stage	Growth condition	Literature cited
Rice	53~32*2	Early ripening stage	Field (in tropics)	TANAKA *et al.*[95]
	60	Actively growing stage	"	TANAKA and YAMAGUCHI[96]
	60~0>*3	Reproductive growth stage	"	"
	60*4	Successive growth stage	"	COCK and YOSHIDA[10]
	72~55*5	"	Field (early planting)	SUZUKI and MURATA[86]
	77~60*5	"	" (normal planting)	"
	69~71	Booting to heading stage	Field	TAKEDA *et al.*[89]
Maize	67~78*2,3	10~30 days after emergence	Growth cabinet	HEICHEL[25]
	67	10 days after silking	Field	TANAKA and YAMAGUCHI[99]
Wheat (winter)	52	30~35 days after sowing	Growth cabinet	KING and EVANS[38]
	app. 85	Early growth stage	Field	KOH and KUMURA[40]
	73	Booting to flowering	"	"
	75~0>*3	Late ripening stage	"	"
Soybeans	59~53	Before flowering	Field	OJIMA[65]
	50~30	Seed filling stage	"	"
Garden pea	47	21~36 days after sowing	Growth cabinet	MINCHIN and PATE[56]
Buckwheat	66	0.5~1.5 months after sowing	Field	IWAKI[33]
Sugar beet	71	Throughout growth	Field (low nurtient)	THOMAS and HILL[104]
	67	"	" (high nutrient)	"
	44	"	Field	MONTEITH[58]
Sweet potato	70~80	"	"	TSUNO and FUJISE[108]
Ryegrass	55	1~12 weeks after sowing	Growth cabinet	ROBSON[79]
Green panic	63	6~8 weeks after sowing	Glass-house	HESLEHURST and WILSON[26]
Alfalfa	61~65	1st to 3rd cuttings	Field	THOMAS and HILL[104]
	51~60	4th and 5th cuttings	"	"
	30~32	10~15 days after sowing	Growth cabinet	KING and EVANS[38]
White clover	62~57*3	50~66 days from germination	"	MCCREE and TROUGHTON[50]
Subterranean clover	34~40	45~65 days after sowing	"	KING and EVANS[38]
Siratro	62	6~8 weeks after sowing	Glass-house	HESLEHURST and WILSON[26]
Cotton	54±4*6	Young plant	Phytotron	BAKER *et al.*[1]

*1 Most of the values are expressed as the ratio of net photosynthesis to gross photosynthesis. *2 Variation due to varieties. *3 Decreased with growth. *4 Constant over a wide range of LAI and varieties. *5 An average value of 67 percent, tending to decrease with growth. *6 Constant at 26 and 32°C.

the dark (seeds rich in carbohydrate) and plants growing in the light are small. These facts suggest that photorespiration has little effect, if any, upon the quantitative relationship between dry matter production and respiration (dark respiration), although various controversies on photorespiration in relation to plant growth have occurred[8,9,23,106]. It should also be noted that energy efficiency in animals and microorganisms are analogous to that in plants[7,17,46,51,62,66,68,84]. Thus, it appears that the energy metabolism of animals and plants can be discussed in a common way, if the nature and quantitative significance of respiration in growth is elucidated.

Cause of a Decrease of Growth Efficiency at the Late Growth Stage

The *GE* of plants was kept high (65 percent) until a certain stage of growth, as discussed above, but thereafter decreased significantly; *i. e.*, 20 percent or lower at near maturity (Figs. 8, 14, and 16). Lower values of the *GE* are obviously derived by the inefficiency of respiration in producing dry matter. Hence, a decrease of the *GE* at the late growth stage may result in a lower productivity of plants.

A decrease of the *GE* at the late growth stage is attributable to (i) an increased proportion of respiration which is not coupled with growth and (ii) re-translocation of substances among organs.

When the total plant respiration (R) is partitioned into growth respiration (R_g) and maintenance respiration (R_m), the R_m/R ratio of actively growing plants is estimated to be 22~33 percent, as discussed in Chapter V. By reviewing published data PENNING DE VRIES[72] estimated the rate of maintenance respiration per unit dry weight (r_m) of young plants of various crops to be within a range of 8~25 mg glucose$\cdot g^{-1}$dry weight$\cdot day^{-1}$ with an average value of 15 mg$\cdot g^{-1}\cdot day^{-1}$. The r_m value obtained in Chapter V is 14~21 mg$\cdot g^{-1}\cdot day^{-1}$, which is almost identical to the values reported in the literature.

However, the respiratory rate per unit dry weight of plants was high, 6~8 mg$CO_2\cdot g^{-1}\cdot hr^{-1}$ (98~131 mg$CH_2O\cdot g^{-1}\cdot day^{-1}$) at the early growth stage, but thereafter decreased progressively with growth, and finally became very low, 0.5 mg$CO_2\cdot g^{-1}\cdot hr^{-1}$ (8 mg$CH_2O\cdot g^{-1}\cdot day^{-1}$) or even less at the late growth stage (Tables 7 and 9, and Fig. 8). Hence, the respiratory rate of plants during later growth stages often exceeds the r_m values reported, if the r_m is considered to be constant throughout growth stages. Consequently, it is not likely that the r_m is a simple function of plant dry weight.

On the basis of this evidence, it is reasonable to postulate that the r_m estimated in this way is still a function of the growth of plants, of which *GE* is about 65 percent. If this assumption is accepted, the relatively large variations of the r_m values (*e. g.*, 8~25 mg$\cdot g^{-1}\cdot day^{-1}$) obtained by several

investigators under different conditions can be easily explained by the fact that the respiratory rate of plants fluctuates largely with growth even at the young growth stages.

Thus, the fraction of R_m is considered to be 22~33 percent of total plant respiration as long as the GE is maintained at about 65 percent. Since the GE on the basis of R is expressed as $GE=GR/(GR+R)=GR/(GR+R_g+R_m)$, the growth efficiency on the basis of R_g, $GE_g=GR/(GR+R_g)$, becomes about 70 percent when the GE is 65 percent with the R_m/R ratio of 0.22~0.33.

Assuming that the GE_g is kept at 70 percent throughout growth, fractions of respiration during later growth stages of rice plants grown in a culture solution (Chapter IV) is estimated (Table 19). The R_g/R ratio decreases with growth and is only 7 percent at maturity, while the R_m/R ratio becomes more than 90 percent. In this aspect, a decrease in the GE of plants at the late growth stage is due to an increased fraction of respiration unconnected with growth. Since the proportion of respiration in the stem increases and its dry matter production is low during late ripening (Fig. 19), the fraction of respiration unconnected with growth occurs mostly in the stem.

As pointed out by BEEVERS[5], an increase of R_m at the late growth stage is partly attributable to wasteful respiration in older cells, in which a sizable amount of glucose is consumed through the pentose-phosphate pathway without ATP formation.

TABLE 19. Total, growth, and maintenance respiration during late ripening stages of rice plants grown in a culture solution (1973).

Days after transplanting	Growth rate ($g \cdot plant^{-1} \cdot day^{-1}$)	Respiration* ($gCH_2O \cdot plant^{-1} \cdot day^{-1}$)			$\frac{R_g}{R}$	$\frac{R_m}{R}$
	GR	R	R_g	R_m	(%)	(%)
96–103	1.74	1.09	0.74	0.35	68	32
103–110	1.42	1.03	0.61	0.41	65	40
110–117	0.64	0.95	0.27	0.68	29	71
117–124	0.13	0.77	0.06	0.71	7	93

* $R=R_g+R_m$,
where R : total respiration,
R_g : growth respiration,
R_m : maintenance respiration,
R_g was estimated as $GE_g=GR/(GR+R_g)=0.70$.

At the late growth stage a decrease of dry weight of the leaf and stem occurs along with an increase of dry weight of the reproductive organ (Figs. 10 and 14). This indicates that there is a re-translocation of substances from the shoot to the grain. As discussed earlier (Chapter III) the *GE* of a whole plant decreases when re-translocation of substances occurs among organs, although the GE_d, which is calculated by the net gain of dry weight of growing organs and the net loss of dry weight of old organs, is kept higher. Thus, the decrease of the *GE* at the later growth stage is also due to re-translocation of substances.

A decrease of the *GE* during late growth stages has been observed with rice[86], soybeans[65], and wheat[40]. Marked decrease of the *GE* was reported in tall stature tropical rice varieties[96]: Respiration at the lower strata of the canopy already occupied about 50 percent of plant respiration at flowering, being unconnected with growth because of mutual shading, and this proportion increased largely during ripening. TANAKA, KAWANO, and YAMAGUCHI[95] also reported that during ripening the *GE* was lower and the translocation percentage (the ratio of straw weight decrease to panicle weight increase) was larger in tall than in short-stature rice varieties, although the photosynthetic rate at flowering was similar among varieties. They concluded that an earlier, and larger decrease of the *GE* resulted in the lower yield of tall varieties. Hence the potential productivity of modern varieties in rice, wheat, and sorghum, etc. has been improved by the short-stature plant type.

Difference of Growth Efficiency Due to Difference in Chemical Composition of Substrates and Products

The *GE* of reproductive organs at the actively ripening stage (Figs. 12, 15, and 17) or throughout ripening stages (Table 13) is about 70 percent in rice and maize and about 45 percent in soybeans. This difference is mostly attributable to the difference of chemical composition of reproductive organs; *i. e.*, grains (Table 20).

The inter-specific difference of the *GE* during the production of the grains indicates that the grain weight of about 70 g of rice or maize, and of about 45 g of soybeans, is produced from 100 g of primary photosynthetic products. In other words, the grain yield of 10 ton$\cdot$ha^{-1} of rice or maize is bio-energetically equivalent to that of about 6 ton$\cdot$ha^{-1} of soybeans: These two figures well correspond with the reasonably good yields of respective crops.

Percentages of proteins, lipids, carbohydrates, and ash in the grains are expressed as *P*, *L*, *C*, and *A*, respectively. It is considered that lipids

TABLE 20. Contents of crude proteins (Prot), lipids, carbohydrates (Ch)*, and crude ash (Ash), and the heat of combution (HC) of reproductive organs at the actively ripening stage and grains (or seeds) at maturity of rice, maize, and soybeans.

Crop	Growth stage	Plant part	Contents (%DW)				HC	Sample reference
			Prot	Lipid	Ch	Ash	(cal·g^{-1})	
Rice	Milky stage	Panicle	13.1	2.1	80.6	4.2	4350	1
	Maturity	Grain (hulled)	14.6	2.1	81.0	2.3	4440	2
	ditto	ditto	9.2	2.7	86.2	1.9	4360	3
Maize	Milky stage	Ear	12.7	1.6	82.2	3.5	4420	4
	Maturity	Grain	11.8	5.1	81.7	1.4	4540	5
	ditto	ditto	10.4	5.0	83.0	1.6	4500	6
Soybeans	Filling stage	Pod	33.4	8.2	51.4	7.0	5040	7
	Maturity	Seed	37.2	19.5	37.7	5.6	5490	8
	ditto	ditto	36.3	19.6	38.7	5.4	5520	9

* Carbohydrates were determined as nitrogen-free extract.

Ref.: 1. At 21 days after flowering, solution culture, 1973, cv. Yūkara (Chapter IV).
2. At maturity, ditto.
3. Standard culture in a field of Hokkaido Univ., 1972, cv. Yūkara.
4. At 25 days after silking, solution culture, 1972, line, D 403 × D 405 (YAMAGUHI, *et al.*[117]).
5. Standard culture in a field of Hokkaido Univ., 1973, cv. Wisconsin Hybrid Corn No. 115.
6. Seeds produced at the Breeder's Stock Farm, Takikawa, cv. Fukko No. 8.
7. At 33~41 days after flowering in the field, 1973, cv. Kitamishiro (Chapter IV).
8. At maturity in the field, ditto.
9. Seeds produced at Hokkaido Agr. Exp. Stat., 1972, cv. Kitamishiro.

and carbohydrates in the grains are produced from glucose which is translocated into the grains. The amount of lipids or carbohydrates produced from a unit amount of glucose is defined as the conversion efficiency (*CE*), and the *CE* for lipids and for carbohydrates are denoted as CE_l and CE_c, respectively. It is also assumed that proteins in the grains are produced from glutamate ($C_5H_9O_4N$, 9.52%N) and glucose which are translocated into the grains. Then, the gram weight of glutamate required to produce 100 g of grains, *GN*, can be calculated from the percentage of proteins in the grains (*P*) by knowing the nitrogen percentage of proteins (it is assumed to

be 16%); *i.e.*, $GN=P\times 16/9.52$. If the gram weight of glucose required to produce P with GN is expressed as GL, the efficiency of glucose to produce proteins (E_p) can be expressed as $E_p=P/GL$. Then the amount (gram) of glucose required to produce 100 g of grains with a supply of GN can be calculated as $[P/E_p+L/CE_l+C/CE_c]$.

The amount of respiration to produce 100 g grains, R (g glucose), can be calculated with the $GE(\%)$ as $R=100\,(100-GE)/GE$. Since A and GN are substances which come into the grain from outside, $[(100-A-GN)+R]$ also expresses the gross amount (gram) of glucose required to produce 100 g grains. Hence, the following formula can be obtained:

$$P/E_p+L/CE_l+C/CE_c=(100-A-GN)+R \qquad (4)$$

An example of the calculation of E_p, CE_l, CE_c is drawn below, by assuming that the chemical compositions of rice, maize, and soybeans are shown as samples No. 2, No. 5, and No. 8 in Table 20, respectively, and that the GE of these crops is 70, 70, and 45 percent, respectively:

For rice;

$$GN=(14.6/5.95)\times(100/9.52)=25.8$$

$$R=100\times(100-70)/70=42.9$$

Thus, $(100-A-GN)+R=(100-2.3-25.8)+42.9=114.8$

Similar calculations are made for maize and soybeans.

By assuming that the E_p and CE are identical among three crops, the following three-dimensional linear equations (5) are produced;

$$\left.\begin{aligned} 14.6/E_p+\ 2.1/CE_l+81.0/CE_c&=114.8 \quad \text{(Rice)}\\ 11.8/E_p+\ 5.1/CE_l+81.7/CE_c&=121.6 \quad \text{(Maize)}\\ 37.2/E_p+19.5/CE_l+37.7/CE_c&=148.2 \quad \text{(Soybeans)} \end{aligned}\right\} \qquad (5)$$

By solving these equations (5);

$$E_p=0.92\,,\qquad CE_l=0.33\,,\qquad CE_c=0.87 \qquad (6)$$

These three solutions (6) mean that 0.33 g of lipids or 0.87 g of carbohydrates is produced with 1 g glucose, and 0.92 g of proteins is produced with 1 g glucose and 1.55 ($=0.92\times16/9.52$) g glutamate.

On the basis of various measurements (including replications), the allowance for the GE and the best fit value of the CE or E_p were estimated by computer simulation (Table 21). Under the condition of a GE of 70 ± 2 percent in rice or maize and 45 ± 2 percent in soybeans, the CE is about 0.84 for carbohydrates and about 0.31 for lipids, and the E_p is 1.02. The

conversion efficiency for proteins from glutamate and glucose is denoted here CE_p. The amount of glutamate required to produce 100 g protein with nitrogen percentage of 16 is $16\times100/9.52=168$ g, and that of glucose is $100/1.02=98$ g. Thus, CE_p is $100/(168+98)=0.38$, which is a little higher than CE_l.

The heat of combustion (kcal·g^{-1}) of proteins, lipids, and carbohydrates is calculated on the cases in Table 18 by the least squares method and is 5.7, 9.25, and 4.2, respectively, which are almost the same as the values in the literature[16,46]. By using these values the CE based on dry matter is re-evaluated to that based on calorie (Table 21). The CE on calorie basis, $CE_{(e)}$, is 0.94 for carbohydrates, 0.77 for lipids, and 0.58 for proteins (as glucose plus glutamate).

TABLE 21. Conversion efficiency of various chemical constituents during the process of grain formation.

Constituent	Conversion efficiency	
	DW basis (CE)	Calorie basis* ($CE_{(e)}$)
Protein	0.38**	0.58
Lipid	0.31	0.77
Carbohydrate	0.84	0.94

* $CE_{(e)l}=CE_l\times HC_l/A$,
$CE_{(e)c}=CE_c\times HC_c/A$,
$CE_{(e)p}=100\times HC_p/(A\times98+B\times168)$,
where HC_l, HC_c, HC_p: Combustion heat of each constituent (5.7, 9.25, and 4.2 kcal·g^{-1} for proteins, lipids, carbohydrates, respectively).
A: Combustion heat of glucose (3.74 kcal·g^{-1}).
B: Combustion heat of glutatamate (3.65 kcal·g^{-1}).

** Estimated from the value of $E_p=1.02$ (See: Text).

TABLE 22. Conversion efficiencies appeared in the literature.

Constituent	'Production value'*		'Work energy'***	
	DW basis	Cal basis**	*DW* basis	Carbon basis
Protein	0.45~0.67	0.67~0.78	0.56	0.68
Lipid	0.36	0.88	0.47	0.68
Carbohydrate	0.86~0.91	0.93~0.96	0.71	1.00

* PENNING DE VRIES[71]. Recently he modified the values to 0.40–0.62, 0.33, and 0.83 for proteins, lipids, and carbohydrates, respectively[73,74].

** *Energy efficiency.*

*** HANSON *et al.*[22]

The *CE* estimated by other investigators is tabulated in Table 22. PENNING DE VRIES[71] defined the *production value* as the amount of plant constituents converted from a unit amount of glucose, and estimated these values theoretically by the most efficient biochemical pathways. Various values for proteins were calculated, considering the source of nitrogen were NO_3^- and NH_4^+ and that of sulfur were H_2S and SO_4^{--}. HANSON *et al.*[22] defined the *work energy* as the amount of energy required for the synthesis of plant constituents from sucrose on a carbon basis. This value is considered to be equivalent to the $CE_{(e)}$ defined in this paper, while the value on the dry weight basis is corrected to match the *CE* with their data.

These values, which are calculated theoretically through knowledge of biochemistry, and the *CE*, which is estimated on the basis of actual measurements, coincide reasonably well for lipids and carbohydrates. However, in the case of proteins, the *CE* value obtained in this paper is lower. This discrepancy suggests that present information concerning the biochemical pathways for protein synthesis are over-estimating the energy efficiency or lack a substantial process of energy release. As LEHNINGER[42] mentioned, details of protein synthesis in living cells are still uncertain even in modern biochemistry.

The efficiency of the transformation of glucose (as a primary product of photosynthesis) to glutamate should be estimated when the over-all efficiency of a plant to produce the grains is evaluated, since the conversion efficiency for proteins has been calculated with a supply of glutamate as a nitrogen source.

In the biosynthetic pathway of glutamate, simplest and most efficient one, it is supposed that glucose is transformed into pyruvate via the EMP pathway, one-half of the pyruvate is converted to oxaloacetate with which the other half of the pyruvate is transformed to citrate and then to α-ketoglutarate through the TCA cycle, and finally NH_3 is incorporated in it:

$$\left.\begin{array}{l} \text{glucose}+O_2\rightarrow\rightarrow\rightarrow 2\ \text{pyruvate}+2H_2O+2NADH_2+2ATP \\ \text{pyruvate}+CO_2+ATP\rightarrow\text{oxaloacetate} \\ \text{pyruvate}+\text{oxaloacetate}+0.5O_2\rightarrow\rightarrow\text{citrate}+CO_2+NADH_2 \\ \text{citrate}\rightarrow\alpha\text{-ketoglutarate}+CO_2+NADH_2 \\ \alpha\text{-ketoglutarate}+NH_3+NADH_2\rightarrow\text{glutamate}+H_2O \end{array}\right\} \quad (7)$$

Thus, the entire sequence of pathways (7) is summarized as follows:

$$\text{glucose}+NH_3+1.5O_2\rightarrow\text{glutamate}+CO_2+3H_2O+3NADH_2+ATP$$

When the energy involved in 1 mole of $NADH_2$ is converted to that in

ATP by cytochrome oxidase, 3 moles of ATP are formed, and thereby the following formula (8) is established:

$$\text{glucose}+NH_3+1.5O_2\rightarrow\text{glutamate}+CO_2+3H_2O+10\text{ATP} \qquad (8)$$

where the transformation efficiency from glucose to glutamate is about 82 (=147.1/180) percent on a basis of gram weight.

However, as shown in the formula (8), 10 moles of ATP are released as the result of biosynthesis of 1 mole of glutamate from 1 mole of glucose. This surplus energy may be utilized in other metabolic pathways. Since 38 moles of ATP per mole of glucose is formed through glycolysis and aerobic oxidation, 10 moles of ATP are equivalent to 47.4 ($=180\times10/38$) g glucose if glucose is supplied as an energy source. Thus, the maximum transformation efficiency from glucose to glutamate becomes about 110 ($=147.1/(180-47.4)$) percent. Whereas, even *in vivo*, the most efficient case, the efficiency is considered to be about 100 percent, because at least 10 percent of glucose may be lost during aerobic respiration or required to absorb NH_4^+ in the root.

If one gram of glutamate is transformed from one gram of glucose with NH_4^+, the value of CE_p obtained under the condition of the supply of glutamate and glucose can be applied to the estimation of protein synthesis with the supply of glucose *per se*.

TABLE 23. Relative yielding ability of various crops estimated from chemical composition* and conversion efficiency** of each composition.

Crop	Chemical content (%)				Yielding ability	
	Prot.	Lipid	Ch.	Ash	g/100 g glucose	Relative*** value
Rice	8.8	2.7	87.0	1.5	73	100
Maize	9.5	5.3	83.7	1.5	70	96
Wheat	12.1	2.3	83.7	1.9	71	97
Barley	11.6	2.2	83.4	2.8	71	98
Soybeans	39.0	19.9	35.4	5.7	45	62
Field bean	24.1	2.6	69.0	4.3	62	86
Potato	9.3	0.5	86.3	3.9	75	103
Sesame	21.2	54.7	18.4	5.7	37	51

* On the basis of dry matter[16];
Prot.: Crude proteins, Ch: Carbohydrates, Ash: Crude ash.

** $CE_p=0.38$, $CE_l=0.31$, $CE_c=0.84$.

*** Yield of rice is the reference standard.

Productivity of various crops, of which grains are different in chemical composition, is estimated with (i) the published data of chemical compositions of products[16] and (ii) the *CE* for each constituent (Table 23), assuming that the entire amounts of primary photosynthates during ripening are utilized for grain production and are equal among crops.

The values in Table 23 demonstrate that the productivity of grain crops (and also potato) is almost similar, that of soybeans is about 60 percent of them, that of field beans is intermediate between these two types of crops, and that of sesame is lowest, about 50 percent of that of grain crops. If a relative yield of some crops in the field is higher than that of other crops, it suggests that the amount of gross photosynthesis (photosynthetic rate and duration) is larger or that there are more substances translocated from the stem to the grain. In contrast, if it is lower, the amount of gross photosynthesis is smaller or current photosynthates are utilized for other than the grain production.

SINCLAIR and DE WIT[83] estimated the productivity of various crop species using the production value of PENNING DE VRIES[73], where the value of 0.40 for proteins was employed assuming nitrate to be the nitrogen source: From 1.0 g of photosynthate, 0.75 g for barley and rice, 0.64~0.67 g for peas, beans, and lentils, 0.50 g for soybeans, and 0.42~0.43 g for rape and sesame are produced. HOWELL[29] compared the grain productivity of soybeans to that of maize, using the *CE* of HANSON *et al.*[22], and concluded that about 45 bushels of soybeans is equivalent to 100 bushels of maize. PATE *et al.*[67] measured the intake and usage of carbon and nitrogen in the developing fruit of white lupin, and reported that the efficiency of conversion of organic imports (sucrose and amino compounds) to food reserves of seeds was 31 percent.

Estimates reported in this paper and those in the literature seem to coincide reasonably well, although the basis of the calculations is diffierent. In a practical cultivation, the sink capacity (size and activity) of harvestable organs as a function of the duration of the ripening period is another important factor limiting the yield[92]. Nevertheless, these estimates are helpful in considering the comparison of potential productivity among crop species and in evaluating the possibility of varietal improvement.

Table 24 is a collection of the *GE* values of the seedlings of various crops germinating in the dark from available data in the literature. The *GE* ranges from 40 to 120 percent. The difference of the *GE* among species at actively germinating stages is mainly attributable to the chemical composition of the seeds: The *GE* is very high in seeds rich in lipids (*e.g.*,

90~120 percent in squash and groundnut), high in those rich in proteins and lipids (*e.g.*, 70~80 percent in soybeans), and low in those rich in carbohydrates (*e.g.*, 50~70 percent in maize, rice, oats, and potato).

TERROINE *et al.*[103] calculated the *energy efficiency* of germinating seedlings, which was defined as $E/(E_1-E_2)$ where E was the heat of combustion of the seedlings, E_1 that of the seeds, and E_2 that of the seed residues at

TABLE 24. The growth efficiency (GE) of seedlings germinating in the dark for various crop species.

Species	Temperature (°C)	GE* (%)	Literature cited
Cucurbita maxima (squash)	25	120	YAMAGUCHI (unpublished)
Apois sp. (groundnut)	20	94	PENNING DE VRIES[70]
	27	93	"
Linum usitatissium (common flax)	—	90	TERROINE *et al.*[103]
Ricinus communis (castor-bean)	25	82	YOKOI[118]
Glycine max (soybeans)	24	73	TANAKA and YAMAGUCHI[97]
Zea mays (maize)	15	68	PENNING DE VRIES[70]
	25	57	"
	24	68	TERROINE *et al.*[103]
	25	60~70**	TANAKA and HAYAKAWA[94]
Phaseolus radiatus (azuki bean)	25	64	YOKOI[118]
Hordium disticum (barley)	22	64	BARNELL[2]
Phaseolus vulgaris (field bean)	18	63	PENNING DE VRIES[70]
	25	68	"
Oryza sativa (rice)	30	50~60**	TAKEDA[87]
	15~30	80~40***	HAYASHI *et al.*[24]
	—	50	TANG *et al.*[102]
	25	47	MIDORIKAWA[54]
	24	62	TANAKA and YAMAGUCHI[97]
Helianthus tuberosus (Jerusalem artichoke)	25	52	MIDORIKAWA[54]
Avena sativa (oats)	24	50	TANAKA and YAMAGUCHI[97]
	24	57~51	MER[53] (HAYASHI *et al.*[24])
Solanum tuberosum (potato)	15~25	40	TANG *et al.*[102]
	15~30	40~60***	BARNELL[2]

*: BARNELL[2]; *utilization coefficient.* MIDORIKAWA[54]; *economic ratio.* TERROINE *et al.*[103]; *material efficiency.*

** and ***: Variation due to the variety and to the growth stage, respectively.

a given stage of germination, and reported that the energy efficiency was about 73 percent for seeds rich in starch (rice and sorghum), about 63 percent for those rich in proteins (peas and lentils), and about 53 percent for those rich in lipids (peanuts and flax).

Variation due to the chemical composition of the seeds is much smaller in the energy efficiency than the *GE*. However, these efficiencies are in reversed trends, suggesting that more energy is required for lipids and/or proteins than carbohydrates, when they are decomposed into simple compounds which are utilizable for the growth of seedlings.

VII. ABSTRACTS

The quantitative significance of respiration in plant growth and crop productivity was studied using the concept of *growth efficiency* (*GE*). *GE* is defined as the ratio of the amount of products to that of substrates: In the case of seedlings germinating in the dark, $GE=(W_{i+1}-W_i)/(S_i-S_{i+1})$, where W_i and W_{i+1} or S_i and S_{i+1} are the dry weights of seedlings or those of seeds at the growth stage of t_i and t_{i+1} after germination; and in the case of plants growing in the light, $GE=GR/(GR+R)$ or $GE=GR/P'_g$, where GR is the growth rate (the rate of dry matter production), R is the amount of substrate utilized by respiration as glucose, and P'_g is the rate of gross photosynthesis (including minerals) during the definite period of growth.

Rice (*Oriza sativa*) and maize (*Zea mays*), whose grains are rich in carbohydrates, and soybeans (*Glycine max*), whose seeds are rich in proteins and lipids, were used as experimental materials.

A summary of results and discussions follows:

1. The *GE* of rice and maize seedlings germinating in the dark was about 65 percent and that of soybeans was about 85 percent during actively growing stages. This fact indicates that the *GE* of seeds rich in lipids and/or proteins is higher that than of seeds rich in carbohydrates.

2. The *GE* of actively germinating seedlings was maintained almost constant within a wide range of germination temperatures (15~35°C), although the growth rate increased remarkably with an increase of temperature. The temperature coefficient (Q_{10}) for the growth of seedlings is estimated to be 1.8~2.4. The results demonstrate that an increase in temperature accelerates the growth rate, but the efficiency of respiration in the growth process is kept constant regardless of temperature. However, *GE* decreases under extreme temperatures, such as below 15°C or above 35°C, suggesting that the efficiency of respiration in growth becomes lower under such conditions.

3. The *GE* of seedlings germinating in the dark started to decrease

abruptly, when the stored substances in the seeds were exhausted. Under such conditions, if the growth efficiency (GE_d) is expressed as the ratio of the gain of dry weight of newly growing organs to the loss of dry weight of old organs, it is ketp at about 50 percent for a longer period.

The difference between GE and GE_d is possibly attributable to the difference of chemical composition between the stored substances in the seeds and the plant constituents, and partly to the additional energy requirement for the re-translocation and re-utilization of constituents of old organs for the growth of new organs.

4. At the initial stage of germination in natural light the growth of seedlings was dependent on stored substances in the seeds, and the growth of plants became dependent eventually on their own photosynthates. However, there was no significant change of GE during this transition. Thus, there is no difference in energy efficiency whether the growth of plants is dependent on stored substances in the seeds (if these are mostly carbohydrates) or on current photosynthates.

5. The respiratory rate per unit dry weight of the whole plant of rice, maize, and soybeans was 4~9 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ during early growth stages, decreased gradually with growth, and was 2~4 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ at flowering. However, the GE of a whole plant of these crops was kept at about 65 percent from the juvenile growth stage to flowering.

These observations demonstrate that there is no characteristic difference in the quantitative relationship among photosynthesis, respiration, and dry matter production during growth between C_4 and C_3 plants, and between grasses and legumes, when they are growing actively.

6. The GE of actively growing plants was maintained constant until the input of solar energy was reduced to about 160 $gcal \cdot cm^{-2} \cdot day^{-1}$, while the growth rate decreased almost linearly with a decrease of light intensity. It is conceivable from these observations that the nature of respiration is unaltered and that respiration is coupled closely with growth, although sugar content as well as respiratory rate decrease with the decrease of photosynthesis. The GE, however, decreased markedly under much weaker light conditions. Under such conditions, protein synthesis is suppressed because of a shortage of current photosynthates.

7. When the actively growing plant was placed in the dark, the growth of actively growing organs (especially an apical growing point) continued to grow by consuming constituents or stored substances in old organs. While respiration is occurring, the growth of an apical growing point ceases under dark treatment or dry matter production becomes zero under graded shading

treatment. If respiration under these conditions is assumed to be a requirement in maintaining the plant body, the fraction of maintenance respiration occupies 22~33 percent of total plant respiration.

Hence, out of gross photosynthates in an actively growing plant under ordinary conditions, 8~12 percent is consumed by respiration for maintenance, 27~23 percent is utilized by respiration to liberate energy for growth, and 65 percent becomes newly produced plant constituents.

8. With an increased nitrogen level in a culture solution, the growth rate and the nitrogen content in plants increased to a certain extent, while the *GE* and the carbohydrate content decreased. From this observation it is concluded that *GE* is higher when the accumulation of carbohydrate is active, while it is lower when the absorption of nitrogen is active and the subsequent synthesis of protein prevails, because a larger amount of energy is required for the synthesis of proteins than that of carbohydrates.

9. During late growth stages the respiratory rate per unit dry weight of the whole plant decreased and became 0.5~1 $mgCO_2 \cdot g^{-1} \cdot hr^{-1}$ at maturity. The *GE* also decreased during late growth stages and finally became very small, 20 percent or less at maturity.

The decrease of the *GE* is most likely due to (i) an increased proportion of respiration which is not coupled with growth, especially in the stem and (ii) the re-translocation of stored substances and/or plant constituents in the stem to the grain.

10. Evaluation of root respiration is important in relation to the growth of a whole plant at the early growth stage, since (i) the respiration of the root occupies 25~30 percent of that of the whole plant, and (ii) the respiratory rate per unit dry weight is highest among organs, probably because of an additional energy requirement for absorption of mineral nutrients, which results in lower *GE* in the roots.

The higher respiratory rate per unit dry wight of the leaves during ripening is possibly related to the higher photosynthetic rate.

11. The *GE* of the reproductive organ of rice or maize (about 70 percent) was higher than that of soybeans (about 45 percent). On this basis the grain yield of 1.0 ton of rice or maize is bio-energetically equivalent to that of about 0.6 ton of soybeans.

The *conversion efficiency* is defined as the amount of chemical constituent produced from a unit amount of glucose and/or amino acids, and is estimated by using the data of the *GE*, the chemical content, and the combustion heat. In the case of ripening grains the conversion efficiency is 0.38, 0.31, and 0.84 on the dry weight basis, and 0.58, 0.77, and 0.94 on

the calorie basis, for proteins, lipids, and carbohydrates, respectively. The potential productivity of various crops, which are different in chemical composition, can be compared in bio-energetical equivalence by using the conversion efficiency obtained.

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