Article, Bull. Shinshu Univ. AFC No.13 p.1-p.11, March 2015

Accumulation Efficiency of Degradable Matter during the Early Grain-Filling Period in Rice

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Abstract

The dry weight of cellular contents in the whole rice plant (dWc/dt) is partitioned from the crop growth rate (dW/dt), and the resulting rate represents the accumulation efficiency of degradable matter (dWc/dW). The grain yielding ability and stability are significantly affected by the dry matter partitioning to cell wall during grain filling stage. Comparative studies for dWc/dW during the early grain-filling period were conducted using diverse genotypes of rice varieties in eight experimental fields in Japan, China, and Thailand for 2 yr to develop a simplified process model with submodels for partitioning. Nine rice varieties-2 *japonica*, 3 *indica*, *indica*×*japonica*, *indica*×*javanica*, *javanica*, and NERICA-were used. dWc/dW was measured by enzymatic analysis. The relationship between dW/dt and the accumulation rate of cellular contents per unit ground area (dWc/dt) was described using a linear regression equation, and the proportionality factor k (slope), which represents accumulation efficiency, was estimated using data from each variety. The k values varied from 0.570 for the traditional indica cv. Ch86 (CH) to 0.765 for the WAB450 line (WA), which is a NERICA variety. High values of dWc/dW were observed in the modern varieties developed by remote crossing [Takanari (TA) and WA]. The average k value from the results of multi-site experiments was 0.681. TA and WA showed high accumulation efficiency by high sink activity under various dW/dts that fluctuated according to environmental conditions at the cultivation sites. Conversely, CH, classified as a “grassy rice” phenotype, formed a cell wall during the early grain-filling period.

Key words : Grain filling, Model, Partitioning, Rice, Translocation.

Introduction

From a physiological viewpoint, dry plant matter can be divided into three categories : storage materials, which may be used for growth ; degradable structural materials, which are biologically active ; and non-degradable structural materials, which cannot be recycled (Thornley, 1977). The physiological degradable matter includes the storage and degradable structural materials that are biologically active.

A simplified process model (Horie *et al*., 1992) expressing developmental performances in relation to physiological and meteorological factors, was constructed for rice (*Oryza sativa* L.). To develop this model for evaluating rice-yield stability and productivity under uncertain environmental conditions in the future, the physiological viewpoint of plant dry matter proposed by Thornley (1977) was useful in constructing the sub-process models with grain filling and partitioning of physiological degradable matter related to meteorological factors.

The sub-process model, with the dynamics for allocating physiologically degradable matter, was

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Received December 3, 2014
Accepted February 2, 2015

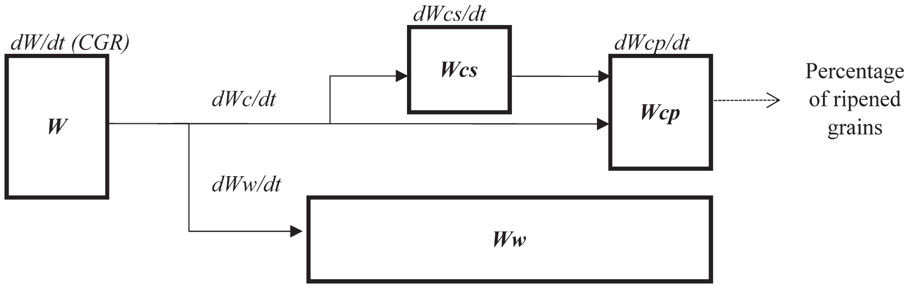


Fig. 1. Growth model for analyzing partitioning during the grain-filling stage in rice.

$W = Wc + Ww$	W : total dry weight in whole plant (biomass) Wc : dry weight of cellular contents in whole plant (non-structural materials) Ww : dry weight of cell wall in whole plant (structural materials)
$Wc = Wcp + Wcs$	Wcp : dry weight of cellular contents in panicle Wcs : dry weight of cellular contents in stover (Stover includes leaf sheath, leaf blade, culm, and panicle before flowering)
$dW/dt = dWc/dt + dWw/dt$	dW/dt : crop growth rate, CGR dWc/dt : accumulation rate of cellular contents in whole plant dWw/dt : accumulation rate of cell wall in whole plant
$dWc/dW = k$	dWc/dW : Accumulation efficiency of degradable matter k : the proportionality factor
$dWc/dt = dWcp/dt + dWcs/dt$	$dWcp/dt$: grain-filling rate $dWcs/dt$: apparent removal rate from stover to panicle (The rate is affected by accumulation, degradation, and translocation of cellular contents)

useful in evaluating the rice genotypes having higher grain-yield stability under unfavorable meteorological conditions in tropical areas, to develop the simplified process model for rice (Horie *et al*., 1992 ; Yin *et al*., 1997a, 1997b). In future studies, the relationships between yielding ability, grain-filling rate, apparent removal rate, and environmental conditions needs to be analyzed by such models and the parameters for removal rate also determined in relation to thermal conditions in the paddy field.

Kobata *et al*. (2000) also showed that grain growth rates during the grain-filling period are fairly stable under various radiant conditions, suggesting the importance of the growth potential of grains for production. Under different environmental conditions in Asian countries, by using the Asian Rice Network (ARICE-Net), the apparent removal rate of degradable matter from stover to panicle was passively affected by thermal conditions ; the dominant factor was the maximum daily air temperature, and the maximum recorded temperatures were approximately 26°C, as described by nonlinear functions for each variety (Yang *et al*., 2005a, 2005b). Further, Matsushima *et al*. (1957) reported the rate of carbon assimilation and noted that the carbohydrate concentration in different organs of rice plants was affected by the activities of carbohydrate-degrading synthetic enzymes in stover.

Previous study (Inoue *et al*., 2000) assessed the relationship between apparent removal and grain-filling rates. Results of analyses using the partitioning model suggest a significant relationship between the grain-filling rate ($dWcp/dt$) and the apparent removal rate from stover to panicle ($dWcs/dt$) during the early ripening period, and a compensatory relationship between growth rates ($dWcp/dWcs$) can be derived as follows :

$$dWcp/dWcs \fallingdotseq -1.47$$

The equation expresses the compensatory relationship between stover and panicle under sufficient

Table 1. Materials and nitrogen fertilization.

Variety name	Code	Origin	Type	Remarks	Nitrogen application (g m^{-2})		
					Basal	Top**	Total
Takanari	TA	Japan	*indica (I)*× *japonica (Jp)*	High-yielding variety with large panicle under intensive management	4	8.4	12.4
IR72	IR	IRRI	*I*	High-yielding variety with multi-tilllering under intensive management	4	9.2	13.2
Shan gui chao	SK	China	*I*	High-yielding variety with large panicle under intensive management	4	8.6	12.6
CH86	CH	China	*I*	Traditional variety with yellow leaf color	1	4.3	5.3
IR65564-44-2-2*	NP	IRRI	*I*× *javanica (Jv)*	Improved variety with new plant type of IRRI	4	9.4	13.4
Nipponbare	NI	Japan	*Jp*	Improved variety with small panicle and multi-tilllering type	4	8.0	12.0
Takenari	TE	Japan	*Jp*	Old variety with multi-tilllering type	4	8.8	12.8
Banten	BA	Indonesia	*Jv*	Traditional variety with large panicle	1	4.9	5.9
WAB450-1-B-P-38-HB*	WA	WARDA	*glaberrima*× *sativa*	NERICA	4	8.6	12.6

*Strain name.

**Amount of the total nitrogen as top dressing was expressed as the average of all experimental sites. $(NH_4)_2SO_4$ or urea was applied at 20-d intervals after the planting date to the 10th day after the full heading date.

demand of photosynthates (dry weight of cellular contents in the whole plant: non-structural materials, Wc) (Fig. 1); however, a sufficient supply to meet the demands of Wc cannot always be ensured, because dW/dt usually varies under fluctuating meteorological conditions in Asian countries.

The demand of Wc for grain filling will be met by sufficient dW/dt. From the viewpoint that dW/dt partitions to dWc/dt, the accumulation rate will essentially be an important trait in a dry matter production basis in rice grain yielding and stability. For this reason, the accumulation efficiency of degradable matter (dWc/dW), referring to partitioning between the whole plant and one of the plant's parts in rice on a dry matter basis, plays an important role after heading under favorable or unfavorable conditions for solar radiation, irrigation, and fertilization.

Here, we performed comparative studies for dWc/dW during the early grain-filling period using diverse genotypes of rice varieties (*japonica*, *indica*, *javanica*, *indica*×*japonica*, *indica*×*javanica*, *glaberrima*×*indica*) in several fields of Asian countries to develop a simplified partitioning model.

Materials and Methods

1 Materials and experimental methods

The nine commercial varieties used in the field experiments of ARICE-Net included those from *japonica*, *indica*, *indica*×*japonica*, *indica*×*javanica*, *javanica*, and NERICA (Table 1). The multi-field experiments were performed in the same manner at the experimental paddy fields of three Asian countries (Table 2). Rice seeds were sown in nursery beds at optimal seedling time according to the location, and

Table 2. Experimental sites and years.

Site	Latitude	Altitude (m)	Country	Year
Kitakami, Iwate	39°21′	180	Japan	2001, 2002
Ina, Nagano	35°51′	720	Japan	2001, 2002
Kyoto	35°01′	60	Japan	2001, 2002
Mastue, Shimane	35°30′	40	Japan	2001, 2002
Nanjing	32°06′	20	China	2001, 2002
Taoyuan, Ynnan	26°13′	1200	China	2002
Ubon	15°20′	130	Thailand	2001, 2002
Chiang Mai	18°47′	340	Thailand	2001, 2002

the seedlings at the 3-leaf stage were transplanted into the main paddy fields in rows 0.30 m apart with 0.15 m between plants. The plots were arranged in a randomized block design with three replications in each year. The planting density was 22.2 hills per m^2 for each variety. Nine rice varieties were grown in a field plot 20×10 m under almost optimal management of water, weeds, diseases, and pests, and an optimal application rate of potassium oxide and phosphorous pentoxide. Nitrogen chemical fertilizer was applied with almost optimal management on each site, as shown in Table 1. The full heading date was defined as the date at which 90% of tillers bear ear heads.

2 Meteorological data

Daily air temperature and solar radiation (photosynthetic active radiation: PAR) were measured during the growth periods. PAR sensors were placed on the upper surface of the rice leaf canopy.

3 Samples and pretreatment

The rice samples for chemical analyses were picked at the full heading date (FH) and at two weeks after FH (2WAFH), and the rice body was separated into panicles and stovers. The samples were dried at 80°C in an air-drying oven. The rice plant body was divided into two parts: panicle and stover (leaf blade+leaf sheath+culm) at FH and 2WAFH. The samples collected from each experimental site were brought to Shinshu University, where they were ground using a Wiley mill and a centrifugal high-speed mill (Fritche P-16), and then passed through a 0.5-mm sieve to ensure sample uniformity and control of chemical analyses.

4 Chemical analyses

The amount of non-structural carbohydrates (NSC) can be rapidly obtained using the α-amylase degradation procedure (Yamamoto *et al*., 1980). The degradable structural matter can be analyzed using either the detergent or the protease degradation method developed for experiments in animal science (Abe, 1988). In this study, one-step degradation using a mixture of protease and α-amylase in solution (Koga and Abe, 1994) was applied as a simplified and convenient method to measure the amount of NSC. The percentage of cellular contents with storage materials based on dry matter weight that can potentially be degraded, recycled, and moved to other organs was obtained using the convenient method described below.

The cellular contents in the dry matter of stover or panicle samples were degraded using a mixed solution of α-amylase (α-amylase no. 015-03731, Wako Pure Chemical Industries, Ltd, Osaka, Japan), which was obtained from *Bacillus subtilis*, and protease (Actinase ER, Kaken Pharmaceutical Co. Ltd., Osaka, Japan), which was obtained from *Streptomyces griseus*. Water and a hot plate were used to gelatinize the rice samples before enzymatic degradation, after which the samples were incubated with the enzyme solution for 16 hr at 40°C. The concentration of enzymes in the buffer solution was 400 ppm α-amylase and 2500 ppm Actinase E. The enzymes were dissolved in an acetic buffer solution (pH 5.8) containing 40 ppm calcium acetate [$Ca(CH3COO)_2 \cdot 3H_2O$]. The pH of the acetate buffer was adjusted by CH_3COOH (0.42 $g \cdot L^{-1}$) and CH_3COONa (7.85 $g \cdot L^{-1}$). After incubation, the samples were washed onto a

Statistical model

Relationship between crop growth rate (CGR) (dW/dt) and accumulation rate of cellular contents per unit ground area (dWc/dt) can be described by a linear regression as follows,

$dWc/dt = j + k\ dW/dt$

where j (intercept) and k (slope) can be estimated by the least square method.

If $j = 0$, then

$dWc/dW = k$

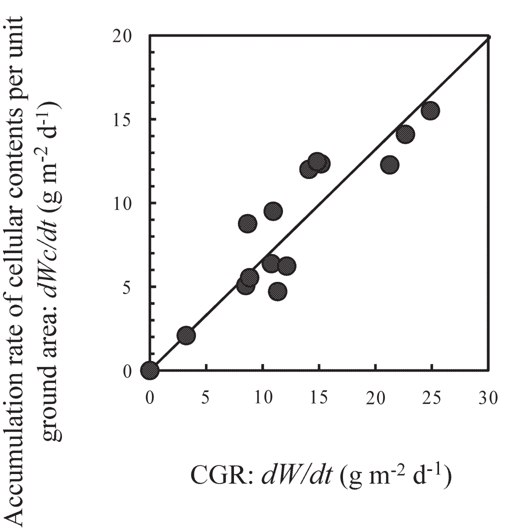
where k is a proportionality factor, and represents the accumulation efficiency of degradable matter in whole plants.

In the case of Nipponbare (NI) on figure, the parameters were obtained statistically as follows:

$dWc/dt = 0.141 + 0.657\ dW/dt$

($r = 0.968$, $P < 0.001$, $n = 13$)

$k = 0.657$



Example of relationship between CGR and accumulation rate of cellular contents per unit ground area in NI.

Fig. 2. Statistical determination of the accumulation efficiency of degradable matter during the early grain-filling stage in rice.

filter funnel with hot distilled water, ethanol, and acetone, and dried in an air-drying oven for 2 hr at 135°C to reduce the moisture. The percentage of moisture in the samples was determined after air drying for 2 hr at 135°C. The chemical analysis was carried out at Inoue Laboratory in the Faculty of Agriculture, Shinshu University.

5 Assumption and formulae for the model

The assumed schematic for the model is shown in Fig. 1 and is described below. The partitioning model of rice before fertilization at flowering has two dependent variables: the non-degradable component of structural dry weight and the degradable component of dry weight. From these basic variables, the dry weight of whole plants (W) is expressed as:

$$W = Wc + Ww,$$

where, Ww is the dry weight of the cell wall in whole plants and represents the non-degradable component of structural materials. Wc is the dry weight of the cellular contents in whole plants and represents the storage materials and degradable components of structural materials. A fraction of Wc includes NSC as a traditional category used by crop scientists.

dW/dt can be expressed as:

$$dW/dt = dWc/dt + dWw/dt.$$

From the partitioning model, dWc/dW in whole plants is easily measured by degrading the plant with a mixture of protease and amylase in solution. After a transition from the vegetative to the reproductive stage, the major sink of degraded matter is the spikelets after fertilization, and the major sources are net photosynthesis and the stored degradable materials in stover. dWc/dW plays a role in stabilizing grain filling and yielding, and the degradation rate of stored materials will usually compensate for the photosynthetic rate.

6 Calculation of growth parameters and statistical method

dWc/dW can be measured by enzymatic analysis. The relationship between dW/dt and the accumulation rate of cellular contents per unit ground area were described using a linear regression equation, as shown in Fig. 2, and the parameters were estimated statistically by using the least square method. In the

Table 3. Yield and yield components.

Code		Yield components			Grain yield (brown rice, g m^{-2})
		Number of spikelets (No. m^{-2})	Percentage of ripened grains (%)	Individual grain weight (mg)	
TA		38064	66.0	22.8	573
IR		38241	57.4	21.9	481
SK		46472	70.9	17.0	560
CH		22906	72.6	22.4	373
NP		29114	54.0	24.1	379
NI		28344	69.2	23.4	459
TE		34383	63.1	22.1	479
BA		20142	59.4	23.2	278
WA		22956	61.7	24.1	341
ANOVA	Genotype (G)	***	*	***	***
	Environmrnt (E)	***	***	**	***
	Year	***	*	n.s.	***
	G×E	n.s.	*	***	*

*, **, and *** are significance at $P < 0.05$, 0.01, and 0.001, respectively.

Table 4. ANOVA for crop growth rate (CGR) (dW/dt) from full heading (FH) date to 2 weeks after full heading date (2WAFH).

Factor	S. S.	d. f.	M. S.	Fo	F	P (0.99)
Total	7734.2	125				
Genotypes (G)	506.9	8	63.4	1.40	0.212216	2.81
Environments (E)	2221.9	6	370.3	8.21	1.42E-06	3.10
G×E	2163.1	48	45.1	1.00	0.496819	1.87
Error	2842.3	63	45.1			

linear equation, k (slope), which is a proportionality factor, represents the accumulation efficiency expressed under various environmental conditions in Asian countries. In this report, k in each rice variety was estimated by data from seven experimental sites over 2 yr, as shown in Table 2.

Results

The averages of the yield and yield components in the experiments are shown in Table 3. The levels of grain yields, number of spikelets, percentage of ripened grains, and individual grain weight varied among genotype, sites, and years. The interaction between genotypes and the environmental conditions at the cultivation sites (G×E) was detected statistically as levels of grain yield, percentage of ripened grains, and individual grain weight. The environmental conditions were determined by weather, soil, water and other cultivation technology.

The analysis of variance (ANOVA) revealed significant differences in dW/dt from FH date to 2WAFH among the cultivation sites (Table 4). In contrast, the accumulation rate of cellular contents per unit ground area from FH date to 2WAFH (dWc/dt) differed among genotypes (G) and environmental conditions at the cultivation sites (E) (Table 5). A G×E interaction was not detected from the results of ANOVA.

The accumulation efficiency in each variety was estimated statistically by linear regression analysis, as shown in Fig. 3 and Table 6. The proportionality factor k (slope), representing the accumulation efficiency of physiologically degradable matter in whole plants, varied from 0.570 in Ch86 (CH) to 0.765 in

Table 5. ANOVA for accumulation rate of cellular contents per unit ground area (dWc/dt) from full heading date (FH) to 2 weeks after heading (2WAFH).

Factor	S. S.	d. f.	M. S.	Fo	F	P (0.99)
Total	3581.1	125				
Genotypes (G)	475.8	8	59.5	3.84	0.000983	2.81
Environments (E)	976.1	6	162.7	10.51	4.72E-08	3.10
G×E	1153.8	48	24.0	1.55	0.051	1.87
Error	975.4	63	15.5			

Table 6. The varietal difference of accumulation efficiency k.

Code	Type	k	r	P	n
TA	*I×Jp*	0.750	0.909	**	13
IR	*I*	0.693	0.815	*	13
SK	*I*	0.759	0.937	***	14
CH	*I*	0.570	0.886	**	14
NP	*I×Jv*	0.623	0.889	***	14
NI	*Jp*	0.657	0.968	***	13
TE	*Jp*	0.607	0.860	**	14
BA	*Jv*	0.705	0.942	***	13
WA	*glaberrima×sativa*	0.765	0.894	**	13
Average			0.681		

*, **, and *** mean significance at $P<0.05$, 0.01, and 0.001, respectively.

WAB450 (WA). High accumulation efficiency was observed in the modern varieties developed by remote crossing (TA and WA). From the results of the multi-site experiments, the average of k was observed as 0.681. These results indicated that on average, under various dW/dts in relation to the environmental conditions of the cultivation sites, 68.1% of dry matter production during the early grain-filling period was allocated to physiologically degradable matter and only 31.9% was allocated to the cell wall.

Discussion

1 A law of partitioning on a dry matter basis

In developing the crop growth model, we investigated the partitioning rate of photosynthates to various organs, because this rate is an important factor in constructing the crop canopy and governing dW/dt (Horie, 1972). The concept of a traditional growth model for the partitioning rate on a dry matter basis arose from morphological differences in dry matter partitioning to different organs (leaf, stem, and reproductive organs). Many crop models with dry matter partitioning to different organs have been developed using the empirical formulae as dependent on the developmental stage. In the future, a new functional growth model without empirical formulae is needed to evaluate the genotypes that express superior yielding ability under diverse environmental conditions.

From the multi-location experimental results, we observed significant differences among the cultivation sites for dW/dt and dWc/dt from the FH date to 2WAFH. However, the relationships between dW/dt and dWc/dt were observed in each variety ; the proportionality factor k (slope) estimated statistically by linear regression analysis represented the accumulation efficiency of physiologically degradable matter in whole plants on a dry matter basis. From the results, a law can be formulated for partitioning to non-degradable (cell wall) or degradable matter (cellular contents) during the early grain-filling period in rice cultivated under various conditions in Asian countries, and the partitioning rate can be expressed as dWc/dW.

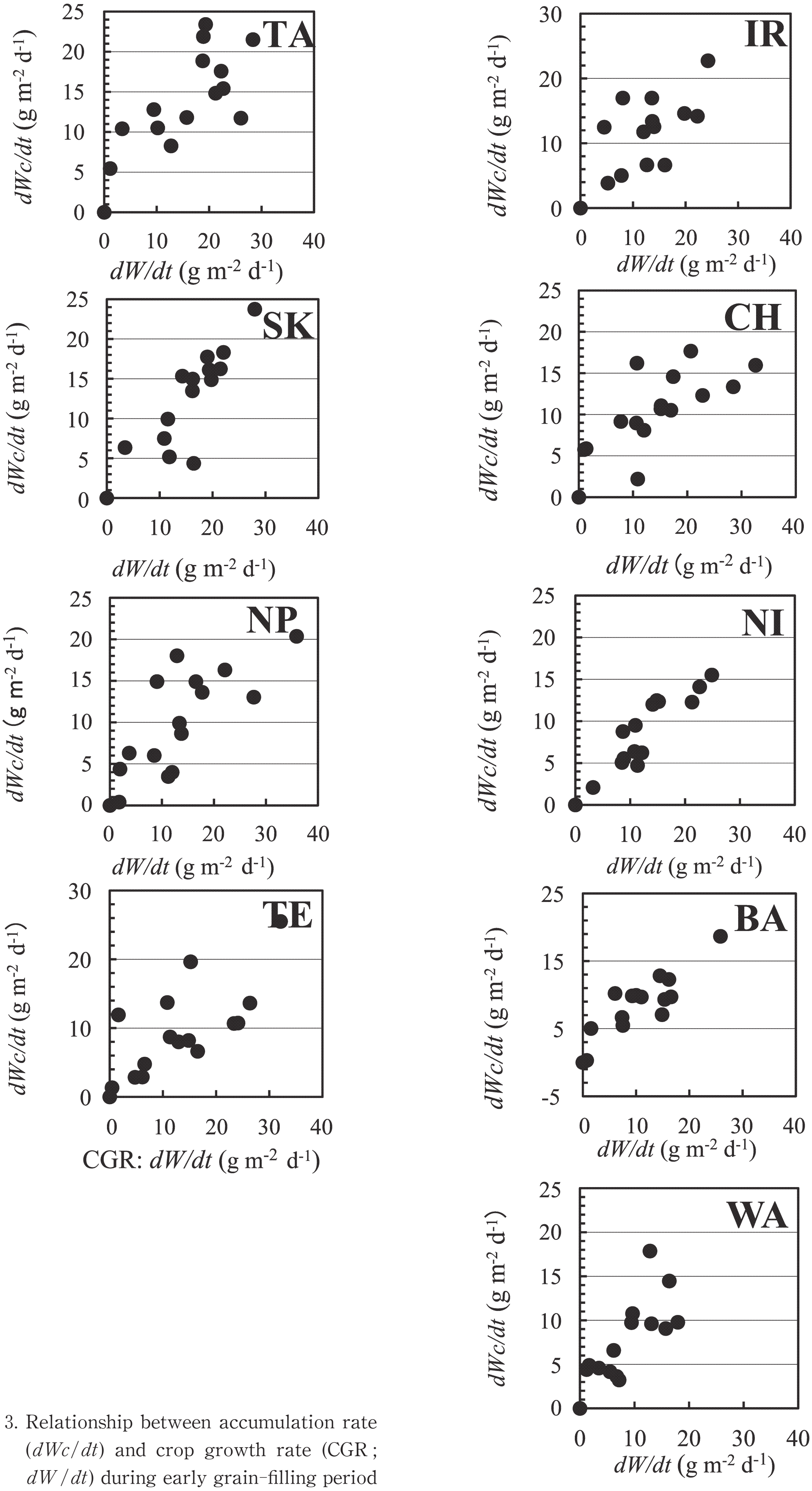


Fig. 3. Relationship between accumulation rate (dWc/dt) and crop growth rate (CGR ; dW/dt) during early grain-filling period in rice.

The close relationship between mean air temperature and $dWcs/dt$, and the maximum daily air temperature for removal rate were found in field experiments using several locations and genotypes (Yang *et al*., 2005a). The results also suggested that the response curves of the apparent removal rate were regulated by genotype because the pattern of the response curve differed among rice varieties.

In addition, Inoue *et al*. (2000) reported that there was a significant relationship between $dWcp/dt$ and $dWcs/dt$ during the ripening period, and $dWcs/dt$ compensated for photosynthesis during the early ripening period. The results and previous reports suggested that the parameters of dWc/dW and $dWcs/dt$ could be estimated as a specific value of a genotype to develop a new crop model for evaluating $dWcp/dt$ and yield stability.

2 Accumulation efficiency based on the rice genotype

From the results of the proportionality factor k that represents the accumulation efficiency of physiologically degradable matter in whole plants, a lower efficiency type was observed. Ch86 (CH), classified as a grassy type of the traditional variety in China, which could produce cell wall during the early grain-filling stage, was evaluated as a lower efficiency type for producing the edible fraction. In contrast, the higher efficiency type was observed in the modern varieties developed by remote crossing (TA and WA). TA was derived from the crossing between *O. sativa* subsp. *indica* and *O. sativa* subsp. *japonica*, and the WA line of NERICA was developed from the crossing between *O. glaberrima* and *O. sativa* subsp. *indica*. The diversity of the proportionality factor among genotypes will be important in the stabile yielding that dry matter appropriately distributes limited resources. It was suggested that the modern breeding system of remote crossing tended to lead to higher accumulation efficiency, on the other hand, decreased the competitive ability against paddy weeds.

TA recorded a higher sink size according to the data on the number of spikelets per unit ground area, whereas both WA and CH recorded a lower sink size. WA indicated a lower source activity according to the dW/dt, as indicated in Fig. 3. Kobata *et al*. (1986, 1990) clearly showed that the potential grain growth was not realized when the available assimilate failed to meet the assimilate requirement. Moreover, Kobata *et al*. (2000) pointed out that different shading treatments during the early grain-filling period did not affect the potential increase in grain dry matter. The reports indicated that sink activity was relatively important to source activity for grain filling during the early grain-filling period. Our experiments suggested that TA and WA achieved higher accumulation efficiency by realizing higher sink activity under various dW/dts that fluctuated according to environmental conditions at the cultivation sites.

CH is the traditional rice variety characterized by yellow leaves with lower chlorophyll content and lower quantum yield of PSII than other rice varieties. It is suggested that CH depresses the source activity to meet the assimilate requirement ; however, the dW/dt in CH was not lower than that in other varieties. It was indicated that CH produces cell wall materials during the grain-filling stage ; consequently, it has the lowest accumulation efficiency value of all varieties in the multi-site experiments. From the perspective of dry matter partitioning to cellular contents as the fraction of degradable matter or cell wall as the fraction of non-degradable matter that cannot be recycled physiologically in the plant body, CH is classified as belonging to the genotype expressed as the “grassy rice” type that continuously produces vegetative matter during the early grain-filling period.

3 Ecological significance of variation for accumulation efficiency

Inoue and Kato (unpublished data) performed experiments using pots in which the sink size was shortened by cutting the panicles, using two domesticated rice species : African rice *O. glaberrima*, a local strain in the Republic of Senegal, and *O. sativa* cv. Koshihikari from Japan. Koshihikari is the most famous commercial variety in Japan, and is closely related to the Nipponbare used in the ARICE-Net multi-site experiments. Under cutting treatments of panicles, *O. glaberrima* did not produce new panicles and accumulated little degradable matter by assimilation after treatments. *O. glaberrima* did not significantly increase the cell wall content in dry matter, whereas Koshihikari produced new small panicles, cell wall, and degradable matter at the same time. The results of the experiment suggested that *O. glaberrima* had lower morphological and physiological plasticity for panicle formation and accumulation efficiency after heading.

Results of the multi-site experiments among Asian countries indicated that the accumulation efficiency of WA was higher than that in other varieties, and WA showed the "non-grassy" type that produced a relatively small amount of cell wall after heading. The higher accumulation efficiency of WA was suggested to be introduced through NERICA with the genes of the African rice (*O. glaberrima*), which has an innate mechanism for avoiding pending water stress.

Asian and African rice crops are estimated to have evolved from annual wild plants under savanna climatic conditions. Generally, annual plants effectively partition the reproductive organs during the reproductive stage, whereas perennial plants partition the vegetative organs and have a lower accumulation efficiency of degradable matter for accumulating the reproductive organs, and the differences are recognized as the differences in plant life strategy (Gadgil and Solbrig, 1972). In wild rice, variations were found in resource partitioning and adaptive strategies (Sano and Morishima, 1982 ; Morishima *et al*., 1984). Higher accumulation efficiency after rapidly changing from vegetative to reproductive growth phases might be required under the environmental conditions of savannas for immediately ceasing seed production before severe water stress during the dry season.

Acknowledgments

We are grateful to emeritus professor Takeshi Horie at Kyoto University, the coordinator of ARICE-Net, and the research staff of Shinshu University for their support in the field experiments and chemical analyses. The project of ARICE-Net was organized in 2000 by T. Horie, T. Shiraiwa, and H. Matui of Kyoto University, Japan ; W. Cao of Nanjing University, China ; S. Nopporn of Ubon RRC, Thailand ; J. Sakuda of Cheng Mai University, Thailand ; T. Kobata, M. Ohonishi, and K. Kobayashi of Shimane University, Japan ; N. Inoue, M. Hagiwara of Shinshu University, Japan ; H. Nakagawa of Ishikawa Prefecture University, Japan ; H. Kuroda of Iwate University, Japan ; and T. Sasaki and A. Abe of Iwate Agricultural Experiment Station, Japan.

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*In Japanese.

**In Japanese with English Summary.

***In Japanese with English Abstract.