

Simplified Model of Dry Matter Partitioning in Relation to Grain Yield Stability in Rice

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Abstract

A new partitioning model was developed for evaluating the dynamics of physiologically degradable materials among rice plant organs. Enzymatic analysis was applied by dividing materials into the following two categories: physiologically degradable, which is regulated by the grain filling rate (dW_{cp}/dt) and grain yield stability (cellular contents, CC), and no degradable structural material comprising the plant cell wall, which cannot be recycled. The CC in dry matter in stover (leaf blade+leaf sheath+culm) and panicle samples were determined using a mixture of α -amylase and protease. The field experiments were performed using two commercial varieties of *japonica* for two years from a paddy field in Japan. The percentage of physiologically degradable matter in dry matter in stover ($W_{cs}\%$) decreased gradually after transplanting time and decreased quickly after heading, and that of *panicle* ($W_{cp}\%$) increased drastically after heading. The dry weight of CC in stover (W_{cs}) increased gradually up to the heading stage and decreased after heading. In contrast, the dry weight biomass of CC in panicle (W_{cp}) increased after heading and drastically decreased 10 d after heading. The derivations of W_{cs} and W_{cp} were calculated for indicating the apparent removal rate from stover to panicle (dW_{cs}/dt), and the grain filling rate was indicated by the term of the fractions of enzymatic analysis. The upper peak of dW_{cs}/dt and the lower peak of dW_{cs}/dt were observed approximately 20 d before heading and 15 d after heading, respectively. The change in dW_{cs}/dt after heading coincided with the change in dW_{cp}/dt . There was a significant negative relationship between dW_{cs}/dt and dW_{cp}/dt , and the regression coefficient (slope) and intercept were estimated at -1.47 and 8.46, respectively. Results suggested that dW_{cs}/dt was a more important and dominant factor for determining dW_{cp}/dt than photosynthesis-governed crop growth rate after heading.

Key words : Crop model, Dry matter, Grain filling, Partitioning, Rice, Yielding

1. Introduction

Grain yield stability of rice (*Oryza sativa* L.) is determined by the balance between the number of spikelets per unit ground area and the grain filling rate. The grain filling rate is affected by the crop growth rate and the removal rate of physiologically degradable matter after the flowering stage (Tsukaguchi et al., 1996; Weng *et al.*, 1982). The amount of physiologically degradable matter that is stored in

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stover before flowering (stock) and the apparent removal rate from stover to panicle (flow) affect the actual amount of removed materials per unit ground area. The apparent removal rate from stover to panicle is determined primarily by the source activity, which is regulated by the degradation and accumulation rates of degradable matter in stover, and by the sink activity of the panicle, which is regulated by the growth potential of grains during the early ripening period (Kobata *et al.*, 2000). Therefore, the dynamics of physiologically degradable matter are important for profiling the partitioning of assimilates in relation to yield stability in rice.

From the viewpoint of plant physiology, plant dry matter can be divided into the following three categories: storage materials, which may be used for growth; biologically active degradable structural material; and no recyclable, no degradable structural material (Thornley, 1977). The physiologically degradable matter includes the storage material and the biologically active degradable structural material.

The simplified process model (Horie *et al.*, 1992) that can express the developmental performances in relation to physiological and meteorological factors was constructed in rice. Sub-process models with the grain filling and partitioning of physiologically degradable matter related to meteorological factors are required to develop a simplified process model for evaluating rice yield stability and productivity under uncertain environmental conditions.

In this report, we focused on the dynamics of physiologically degradable matter to develop a useful process model for evaluating the yield stability in rice. We proposed a new partitioning model that applies enzymatic analysis to divide the matter into the following two categories: physiologically degradable matter in relation to grain filling and grain-yield stability, and no recyclable, no degradable structural material comprising the plant body and canopy.

2. Materials and Methods

2.1. Materials and experimental methods

Two commercial varieties of *japonica* rice (cv. Koshihikari (KO) and cv. Mochihikari (MO)) were used (Table 1). The field experiments were carried out in experimental fields (altitude, 720 m; latitude, 35°51') in the paddy field at AFC of Shinshu University, Minamiminowa, Nagano Prefecture, Japan. The pH (H_2O), cation exchange capacity (CEC), and electrical conductivity (EC) in the soil of the experimental field were 6.6, 22.5 meq, and 0.1 mS cm^{-1} , respectively. Seeds were sown in nursery beds in the first week of April at the location, and the seedlings at the three-leaf stage were transplanted to the main paddy fields in the last week of May 1998 and 1999 in rows 0.30 m apart, with 0.15-m spacing between plants. The plots were arranged in a randomized block design with three replications. The planting density was 22.2 hills m^{-2} for each variety. The amount of potassium oxide (K_2O) and phosphorus pentoxide (P_2O_5) applications were 12 g m^{-2} and 28 g m^{-2} , respectively. Nitrogen (N) chemical fertilizer was applied as follows: 8 g m^{-2} as basal dressing and, for each variety, 2 g m^{-2} as a top dressing 20 d before the full heading date (defined as the date at which 90% of tillers bear ear heads). The two varieties were grown in a field plot 30 × 10 m under nearly optimal management of water, weeds, diseases, and pests.

2.2. Meteorological data

Daily air temperature and solar radiation (photosynthetic active radiation: PAR) were measured during the growth periods. PAR sensors (Prede, PCL-01, KADEC-UP data logger) were placed at the water surface of the flooded paddy field and at the upper surface of the leaf canopy. Accumulated PAR was calculated using the data observed by two sensors for each variety.

2.3. Samples and pretreatment

The rice plant samples for chemical analysis were collected at every 10 d during the growth periods. The samples were dried at 80°C in an air drying oven. After the full heading stage, the rice plant body was divided into the following two parts : panicle and stover (leaf blade + leaf sheath + culm). The samples were ground using a Wiley mill and centrifugal high-speed mill (Fritsch P-16) and passed through a 0.5-mm sieve.

2.4. Chemical analysis

The amount of non-structural carbohydrate (NSC) can be rapidly obtained using the α -amylase degradation procedure (Yamamoto *et al.*, 1980). The degradable structural matter can be analyzed using the detergent or protease degradation method developed for animal science (Abe, 1988). In this study, a one-step degradation method using a protease and α -amylase mixture (Koga and Abe, 1994) was used for simplicity and convenience. The percentage of Cellular Contents (CC) with storage materials in dry matter weight that can potentially be degraded, recycled, and removed to other organs was obtained using the simple method that follows.

The CC of the dry matter in stover and panicle samples were degraded using a mixed solution of *Bacillus subtilis* α -amylase (α -amylase no. 015-03731, Wako Junyaku, Japan) and *Streptomyces griseus* protease (Actynase E[®], Kaken Kagaku, Japan). The rice samples were gelatinized using water on a hot plate before enzymatic degradation and incubated with the enzyme solution for 16 h at 40°C. The concentration of enzymes in the buffer solution was 400 ppm α -amylase and 2500 ppm protease (Actynase E[®]). The enzymes were dissolved in pH 5.8 acetic buffer solution containing 40 ppm calcium acetate [Ca (CH₃COO)₂ 3H₂O]. The pH of the acetate buffer was adjusted using CH₃COOH (0.42 g L⁻¹) and CH₃COONa (7.85 g L⁻¹). After incubation, the samples were washed into a filter funnel with hot distilled water, ethanol, and acetone, and dried in an air-drying oven for 2 h at 135°C, and the percentage of moisture in each sample was determined.

The percentages of CC in stover ($W_{cs}\%$) and panicle ($W_{cp}\%$) were expressed on a dry matter basis. The percentage of cell wall (CW), nitrogen (N), ether extract (EE), and crude ash (CA) were determined using standard methods of chemical analysis, and expressed as dry matter. The equations for NSCs and chemical traits were obtained using experimental measurements of 50 samples in each stage ($R^2=0.85, 0.87, 0.85, 0.89$ and 0.82). The $W_{cs}\%$, $W_{cp}\%$, and CW in dry matter were also estimated using near infrared reflectance spectroscopy as well as N in developing a convenient analysis method.

2.5. Assumption and formulation of the model

The basic scheme assumed is shown in Fig. 1 and described as follows.

The partitioning model of rice before fertilization at flowering time has two dependent variables as follows : 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 follows :

$$W = W_c + W_w,$$

Where, W_c is the dry weight of the CC in whole plants, pertaining to the storage materials and degradable components of structural materials, and W_w is the dry weight of the cell wall in whole plants, pertaining to the no degradable component of structural materials. The fraction of W_c includes NSCs as a traditional category used by crop scientists.

The partitioning model of rice at flowering time has three dependent variables as follows : W_w ; the CC in stover (W_{cs}) containing storage materials and degradable components of structural materials, including leaf blade, leaf sheath, and culm ; and the CC in the panicle (W_{cp}), containing the accumulated and degradable components of dry weight in the panicle (Fig. 2).

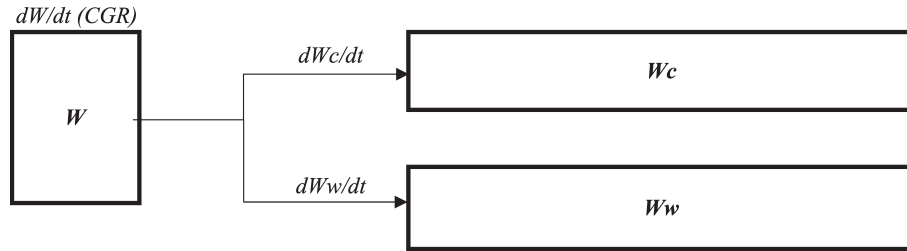


Fig. 1. A model for analyzing partitioning before the grain filling stage in rice.

$$W = Wc + Ww$$

W : total dry weight in whole plant (biomass)

Wc : dry weight of cellular contents in whole plant (nonstructural materials)

Ww : dry weight of cell wall in whole plant (structural materials)

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

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

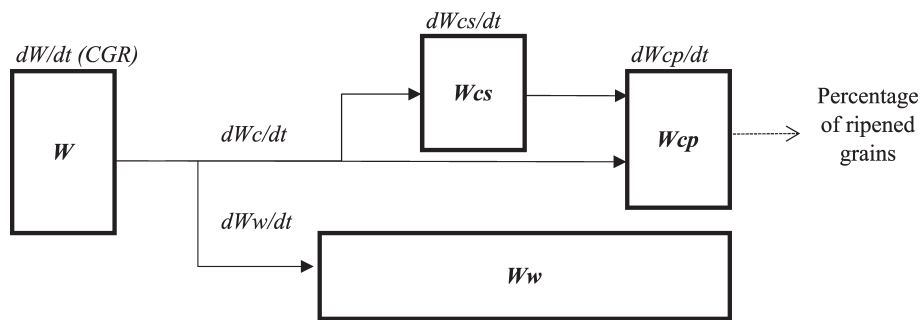


Fig. 2. A model for analyzing partitioning during the grain filling stage in rice.

$$Wc = Wcp + Wcs$$

Wcp : Dry weight of cellular contents in the panicle

Wcs : Dry weight of cellular contents in stover

(Stover includes leaf sheath, lead blade, culm, and panicle before flowering)

$$dWc/dt = dWcp/dt + dWcs/dt$$

$dWcp/dt$: grain filling rate

$dWcs/dt$: apparent removing rate from stover to panicle

(The rate is affected by accumulation, degradation, and translocation of cellular contents)

crop growth rate (CGR)

After fertilization in rice, the major sink is the panicles and the major sources are photosynthesis during the grain filling period and translocation of degradable matter from stover to panicle ; therefore, the following two variables are introduced for the analysis for partitioning :

$$Wc = Wcp + Wcs,$$

Where, Wcp is the dry weight of CC in the panicle and Wcs is the dry weight of CC in the stover. The values of Wcp and Wcs are determined by enzymatic analysis with protease and α -amylase, and also can be easily estimated by near infrared reflectance spectroscopy.

Crop growth rate (CGR) can be expressed by

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

$$dW/dt = dWcp/dt + dWcs/dt + dWw/dt.$$

In this new model, $dWcp/dt$ refers to the grain filling rate measured by the degradation using the protease and α -amylase mixture, and $dWcs/dt$ refers to the apparent accumulation rate, which comprises the stored materials and degradable structural materials in stover. After changing from the vegetative

growth stage to the reproductive growth stage, the removal rate from stover to reproductive organs, during which the CC in stover degrades, should be more than the accumulation rate from photosynthesis and accumulation of plant nutrients on a dry matter basis. The apparent rate should decrease under conditions in a normal cultivation site and can be termed the *apparent removal rate*. The major sink of degraded matter is the spikelets after fertilization.

2.6. Calculation of growth parameters and statistical methods

The removal rate of CC from stover to panicle ($dWcs/dt$) and the grain filling rate ($dWcp/dt$) as measured by enzymatic analysis were expressed in terms of dry weight per unit ground area per day. The averages of two varieties, 2 years, and three replications were calculated and are plotted in Fig. 3 and 4. The approximate curve fitted the data expressing the changes in $Wcs\%$, $Wcp\%$, Wcs , Wcp , $dWcs/dt$, and $dWcp/dt$.

3. Results

The averages of the yield and yield components in the experiments are shown in Table 1. No lodging or damage by insects, diseases, or weeds was observed during the growth periods. The level of yield, number of spikelets, and percentage of ripened grains slightly exceeded the yield level in an average year. The data of PAR were observed to be approximately 10, 9, 8, and 8 MJ day⁻¹ m⁻² in June, July, August, and September, respectively. The accepted PAR for the rice canopy was observed from 3 to 10 MJ day⁻¹ m⁻² during the experimental growth periods. Mean air temperature fluctuated between 18°C and 25°C during the experimental growth periods.

The NSCs and CC on a dry matter basis are presented in Table 2. The fraction of CC analyzed enzymatically includes the parts of EE, crude protein, and CA in whole plants. The relationships between NSC and CC can theoretically be used to set up the simple equations for stover or panicle in each stage.

The $Wcs\%$ and $Wcp\%$ were plotted using the average of the two varieties, 2 years, and three replications and the approximated curve was fitted for each part (Fig. 3a). $Wcs\%$ as physiologically degradable matter changed gradually after transplanting time and decreased quickly after heading, whereas $Wcp\%$ increased dramatically.

The dry weight of CC per unit ground area can be calculated by the percentage of CC and dry matter per unit ground area. The dry weights of CC as the stock of the potential removable matter that can be degraded by internal enzymes is also shown in Fig. 3b. Wcs increased gradually up to the heading stage and decreased after heading. In contrast, Wcp increased after heading. In particular, Wcp increased dramatically 10 d after heading.

The derivations of Wcs and Wcp were calculated to indicate the apparent removal rate from stover to panicle ($dWcs/dt$) and the grain filling rate ($dWcp/dt$), using the term of the fractions of enzymatic analysis. The values of $dWcs/dt$ and $dWcp/dt$ are shown in Fig. 3c. The upper peak of $dWcs/dt$ was observed approximately 20 d before the heading. The lower peak of $dWcs/dt$ was detected approximately 15 d after the heading. The change in $dWcs/dt$ after heading coincided with the change in $dWcp/dt$.

The correlation between $dWcs/dt$ and $dWcp/dt$ is shown in Fig. 4 and uses the synchronous response between $dWcs/dt$ and $dWcp/dt$ suggested in Fig. 3c. There was no difference between the two varieties for the regression equations that expressed the relationships between $dWcs/dt$ and $dWcp/dt$; therefore, one linear regression formula was developed using all the data from the two varieties (Fig. 4). The regression coefficient (slope) and intercept were estimated to be -1.47 and 8.46, respectively.

4. Discussion

4.1. The evaluation of model and methods of chemical analysis

Table 1. Materials and Experimental Data.

| Variety name | Amylose content in brown rice (%) | Dry matter yield (g m ⁻²) | Yield components | | | Grain yield (brown rice, g m ⁻²) |
|------------------|-----------------------------------|---------------------------------------|--------------------------------------------|----------------------------------|------------------------------|----------------------------------------------|
| | | | Number of spikelets (No. m ⁻²) | Percentage of ripened grains (%) | Individual grain weight (mg) | |
| Koshihikari (KO) | 14-16 | 1354 | 36207 | 86.9 | 22.0 | 692 |
| Mochihikari (MO) | 0 | 1607 | 44128 | 91.9 | 20.8 | 844 |

Yield and yield components were obtained from the average of 2 years and from three blocks.

Table 2. Relationship between non-structural carbohydrates (NSC) and cellular contents determined by enzymatic analysis.

| Part | Stage | Equation | Ether extract (%) in CC | Crude ash (%) in CC |
|---------|------------------------------------|---------------------------------|-------------------------|---------------------|
| Stover | Full heading (FH) | $NSC = CC - 5.1 \cdot N - 7.4$ | 3.1 | 5.1 |
| Stover | 2 weeks after full heading (2WAFH) | $NSC = CC - 5.1 \cdot N - 6.7$ | 2.5 | 5 |
| Stover | Maturing (M) | $NSC = CC - 5.1 \cdot N - 5.5$ | 2.2 | 4.1 |
| Panicle | 2WAFH | $NSC = CC - 5.1 \cdot N - 8.8$ | 6 | 3.6 |
| Panicle | M | $NSC = CC - 5.1 \cdot N - 10.2$ | 9 | 2 |

DM : dry matter.

DM = CC + CW.

CC : percentage of cellular contents in DM determined by enzymatic analysis.

CW : percentage of cell wall contents in DM determined by enzymatic analysis.

$NSC = CC - CP_{cc} - EE_{cc} - CA_{cc}$.

CP_{cc} : crude protein (CP) in CC. $CP_{cc} = 0.82 \cdot CP - 0.8$.

CP : crude protein in DM. $CP = 6.25 \cdot N$.

N : Kjeldahl nitrogen (%) in DM.

EE_{cc} : ether extract (EE) in CC. $EE_{cc} = EE$.

EE ; ether extract in DM.

CA_{cc} : crude ash (CA) in CC. $CA_{cc} = 0.37 \cdot CA$.

CA : crude ash in DM.

A model for the photo thermal responses of flowering in rice can be used to forecast rice development (Yin *et al.*, 1997a, 1997b). The partitioning rate of photosynthetic materials to various rice organs was investigated in building the crop growth model because it is also an important factor in crop canopy development and in governing crop growth rate (Horie, 1972). The concept of a traditional growth model for partitioning on a dry matter basis was formed using morphological differences of dry matter partitioning to different organs (leaf, stem, and reproductive organs), and many crop models have adopted the empirical formulae dependent on the developmental stage. Recently, Morita *et al.* (2004) pointed out that source activity in the panicle and in stover were independently affected by thermal conditions in each organ. In addition, the close relationship between mean air temperature and the apparent removal rate from stover to panicle, and the maximum daily air temperature for removal rate, were determined from field experiments using multiple locations and genotypes (Yang *et al.*, 2005). The key element in developing a successful sub model of dry matter partitioning as affected by photo thermal conditions appears to be the methods of chemical analysis employed. The removable fractions in the CC, including NSC, N, CA, and EE, could easily be obtained using the approximate chemical analysis applied in this study, and the change in concentration, amounts per unit ground area, and deviation of physiologically active and degradable matter could also be calculated on a dry matter basis.

For rice yield, the removal rate from stover to panicle is an important factor that was affected by the

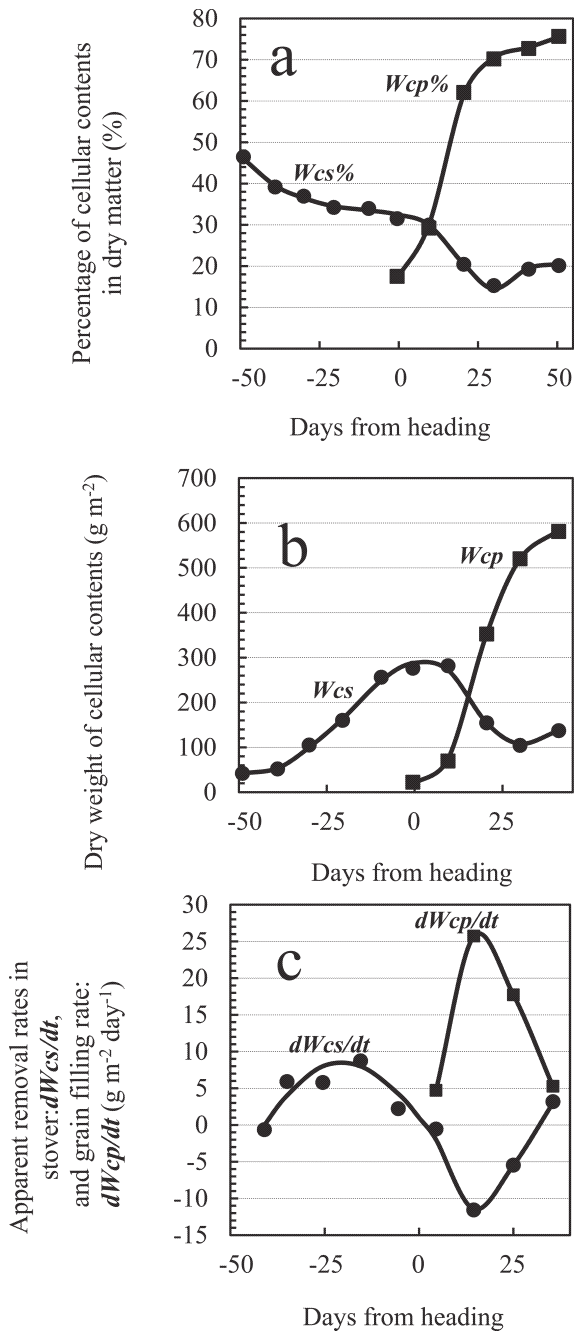
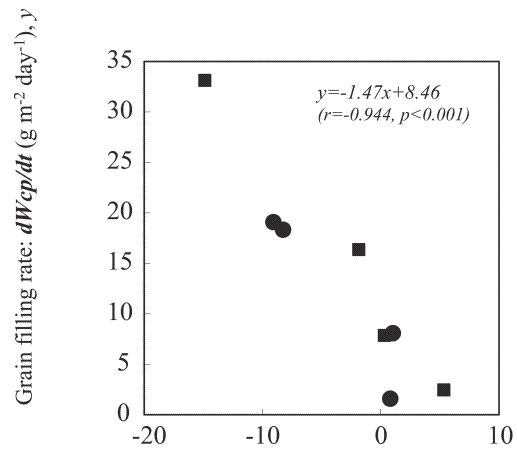


Fig. 3. Dynamics of cellular contents.
(2-year average of cv. KO and MO)

no degradable matter. The CC fraction obtained by external degrading enzymes refers to the matter that is potentially degradable by internal enzymes in the plant body. The changes in $Wcs\%$, $Wcp\%$, Wcs , Wcp , $dWcp/dt$, and $dWcs/dt$ during the growth period were well described by the model and by using the analytical method. The concept, model, and methods for chemical analysis will provide useful tools for forecasting yields and evaluating the genotypes with higher yielding stability under uncertain climatic conditions in the future.

4.2. Potential sink capacity of stover

The degradable components of structural materials and stored carbohydrates accumulated in the vacuole or chloroplast cannot be ignored because the rice grains contain proteins, fats, minerals, and



Apparent removing rate in stover: $dWcs/dt$ ($g\ m^{-2}\ day^{-1}$), x

Fig. 4. Influence of apparent removal rate on grain filling rate on the basis of degradable matter.

● KO ■ MO

sucrose content and the enzyme activities involved in sucrose metabolism in the leaf blade and sheath of rice before heading (Majorowski and Ohsugi, 1996). In the case of floating rice, the distribution of sucrose and the activities of sucrose-metabolizing enzymes in sink organs play important roles in growth under submergence conditions (Hirano *et al.*, 1996). These reports suggested that both a physiological model and a morphological partitioning model are required for evaluating rice yield stability, a calculation which involves removing accumulated and stored matter as well as a morphological partitioning model.

In this report, we focused on the dynamics of physiologically degradable matter. We presented a new partitioning model and applied enzymatic analysis to divide matter into two categories as follows: physiologically degradable matter and

materials that generally accounts for approximately 10%-20% of the total dry weight. From the vegetative growth stage to heading, the leaf blade and leaf sheath of $Wcs\%$ appeared to have higher potential capacity as a sink than that of $Wcp\%$ at heading. In the mountainous areas in the southeastern and northern parts of Asia, higher $Wcs\%$ was often observed under conditions of pollen sterility due to chilling injury after cool weather conditions. The organs comprising stover have a higher sink capacity for compensation of rice yield. After heading, the concentration of degradable matter removable from stover to panicle was markedly reduced from 32% to 15%. The difference in concentration was a potentially favorable indicator of their sink capacity in storing physiologically degradable matter and degradable components of structural materials.

Wcs was approximately 300 g m^{-2} at the heading stage and decreased to approximately 100 g m^{-2} 30 d after heading. The biomass of the physiologically degradable matter that can potentially be recycled and relocated appeared to attain a third part of the panicle dry matter at harvesting time. Rice yield stability can be realized through higher CGR and the removal of degradable matter after heading under normal weather conditions. Photosynthesis after heading contributes to 60%-90% of the total carbon accumulation in panicles (Mae, 1997). In our results, the ratio of Wcp at harvesting time to the difference between Wcs at heading time and Wcs 30 d after heading was also approximately 60% of the amount of dry matter (Fig. 3b), and the role of photosynthesis after heading was also taken into account. On the other hand, Kobata et al. (2000) reported that a shortage of assimilate supply resulting from shading treatment during the early and middle grain filling periods does not affect grain potential activity as a sink. From the results, the potential sink capacity of stover before heading, actual source activity of stover to panicle after heading, and sink activity and capacity of grain should determine the grain filling rate using the apparent removal rate.

4.3. Relationship between apparent removal and grain filling rates

In the results of analysis using the partitioning model, a significant relationship between $dWcp/dt$ and $dWcs/dt$ during the grain filling period was observed. If the value of the intercept in the regression is ignored, the relative growth rate in allometry ($dWcp/dWcs$) is approximately -1.47.

The equation indicates that the growth rate of degradable dry matter in stover decreased by one unit and the growth rate of degradable dry matter in the panicle increased coincidentally approximately 1.5 times. The contribution of photosynthesis after heading was relatively higher than that of stored dry matter in stover, accounting for approximately 60% of the total amount of dry matter, both in our results and in a previous study (Mae, 1997). In the case of barley modeling with partitioning according to climatic data (Travasso and Magrin, 1998), grain filling period is temperature dependent and dry matter partitioning corresponds to crop phenology. However, from the point of view of the relative growth rate of allometry in rice, the aforementioned equation expressed that the apparent removal rate ($dWcs/dt$) was an important factor in addition to the grain filling period; in addition, the apparent removal rate was a more dominant factor in determining the grain filling rate ($dWcp/dt$) than in determining photosynthesis-governed CGR after heading under favorable conditions of solar radiation, irrigation, and fertilization.

The apparent removal rate could also be affected by sucrose concentration because sucrose flows along the gradient of concentration among plant organs. Matsushima *et al.* (1957) reported the diurnal change of the rate of carbon assimilation and the carbohydrate concentration in different organs of rice plants and there was an obvious gradient of total sugar content from leaf blade, leaf sheath, culm, and grain. The difference in the concentration arose from the activities of carbohydrate synthetic enzymes in grain and the enzymatic activities of degradation in stover. In particular, it is well known that chloroplasts in the leaf sheath of rice store many starch granules. Kobata *et al.* (2000) also showed that grain growth rates during the grain filling period are fairly stable under differing radiant conditions and suggested the

importance of the growth potential of grains. On the other hand, a close relationship between air temperature and the apparent removal rate was found in the field experiments carried out under different environmental conditions in Asian countries, which revealed that the maximum daily air temperature for removal rate was recorded to be approximately 30°C as described by a nonlinear function (Yang *et al.*, 2005). The results suggested that the apparent removal rate was influenced by enzymatic activities related to the rate of degradation in stover and also the synthetic rate in the panicle, as modulated by air temperature under paddy field conditions.

In developing a simplified process model (Horie *et al.*, 1992; Yin *et al.*, 1997a, 1997b), the sub-functional model with dynamics for partitioning of the physiologically degradable matter appears to be useful in evaluating rice genotypes with higher grain yield stability under unfavorable meteorological conditions in tropical areas. In further studies, the relationship among yield potential, grain filling rate, apparent removal rate, and environmental conditions needs to be analyzed using such models, and the parameters for removal rate also determined in relation to thermal conditions in paddy fields.

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