Comparison of the robustness of methods for estimating leaf development for crop growth models

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Abstract

In most crop growth models used for estimating yields, much information, including environmental data and the cultivars planted, must be obtained in advance. Such models are difficult to use when this information is lacking. The aim of the present research was to evaluate the ability of methods to estimate leaf biomass with limited information. We used crop biomass data for maize, rice, and soybean that were gathered continuously at locations throughout Japan between 1951 and 1980 and compared several models that used different methods for estimating the biomass of each plant tissue of a crop species. The results showed that allometry-type models, which predict the biomass of a plant tissue using the relative relationship between the tissue biomass and another crop parameter such as total biomass, were more robust than partitioning-type models, which predict the increase in biomass of each tissue per unit time from the daily partitioning of photosynthate. In cases when it is difficult to acquire detailed crop information, such as for global-scale predictions, the use of an allometry-type model allows more robust estimates to be obtained.

Key words: Allometry, Crop growth model, Maize, Partitioning, Regional-scale model, Rice, Soybean

1. Introduction

Mounting evidence that increasing greenhouse gas concentrations are changing the global climate (IPCC, 2013). Crop productivity is highly susceptible to climate change (IPCC, 2014). With a growing global population and progressive climate change, the need to develop methods to evaluate the effect of climate change on future crop production is increasingly important. While there are several models that simulate global crop yields (e.g., Rosenzweig et al., 2014; Müller et al., 2017), the uncertainties of the estimations of the models are still large (Porwollik et al., 2017).

Most crop growth models estimate crop growth processes at the scale of an agricultural field (e.g., Asseng et al., 2013; Li et al., 2015). Many of these models require for their calculations not only environmental data, such as soil characteristics, daily maximum and minimum temperatures, solar radiation, and rainfall, but also cropping system data such as planting density, planting day, and cultivar. Using these input data, the models then calculate the photosynthesis rate and allocate the photosynthate to the leaves, stems, panicles, and roots (e.g., Bouman et al., 2001; Stöckle et al., 2003).

For simulations of crop growth at a small scale, such information can often be acquired. However, for simulations at a large scale, it may not be possible to obtain all of the required information. Moreover, for global-scale crop yield prediction, the unit area for calculation is on the order of 10 to 100 km². As a result, many different crop cultivars may be grown in a unit area, making estimation of global crop yields particularly difficult. Thus, a model that can provide robust estimates is needed when the cultivar is uncertain or unknown. In other words, models with parameter sets that are applied for many crop cultivars are preferable for large-scale estimation.

The aim of this study was to identify a robust method for estimating plant tissue biomass for crop cultivars. Plant growth models can be roughly classified into two types: allometry-type and partitioning-type. Allometry-type models predict the biomass of a plant tissue from the relative relationship between the biomass of that tissue and another crop parameter such as total biomass of the plant. These models are often used in forestry. For example, the TREE-BGC model uses the relative relationship between diameter at breast height or tree height and biomass (Korol et al., 1995). In contrast, partitioning-type models predict the increase in biomass per unit time of each tissue from the daily partitioning of photosynthate. For example, the well-known crop model ORYZA2000 uses assimilate partitioning to predict the daily increase in leaf biomass of rice (Bouman et al., 2001). Most crop growth models in use are partitioning-type models. Although photosynthate partitioning to different plant tissues varies greatly depending on growth stage and crop cultivar, partitioning-type models can produce robust estimates for each tissue if the cultivar and its parameters are well specified. However, when the cultivar is unknown, which type of model is more robust for the estimation of the biomass of each crop tissue?

To compare the robustness of the two types of models, we conducted a cross-validation experiment for maize, rice, and soybean. We first estimated the parameters of each model type using observed biomass data of one to five cultivars of each crop. Then we simulated crop biomass of the other cultivars that were not used for the parameter estimation and evaluated...
the estimation accuracy of each model type. A model type with high accuracy in this experiment is interpreted as being robust, because it simulates biomass relatively accurately even for those cultivars that are not used in parameter calibration. In other words, such a model can be adopted for large-scale estimation in which most crop cultivars are uncertain.

2. Materials and Methods

2.1 Data

We used crop biomass data provided by the Ministry of Agriculture, Forestry and Fisheries of Japan (AFFRCS, 1987), which were obtained by continuous field measurements at agricultural experimental stations and research institutes from 1978 to 1982 for various crop types and cultivars. Crops were sampled approximately once every 3 weeks for about 4 months each year (Table 1). Dry weights of leaf blades, dead leaf blades, roots, and total weight were collected over a period of 3 to 5 years for four to six cultivars of each of three crop species (maize, Zea mays; rice, Oryza sativa; soybean, Glycine max). The target of our analysis is crop biomass, which is strongly related to crop yield (e.g., Ying et al., 1998; Tittonell et al., 2005; Zhang et al., 2009; Arora et al., 2011; Huang et al., 2016). Thus, improving a model’s ability to estimate crop biomass contributes to the estimation of crop yields.

Daily temperature data (maximum and minimum) were obtained from the MeteoCrop DB model-linked crop meteorological database (Kuwagata et al., 2011), which contains temperature data from the Automated Meteorological Data Acquisition System (AMeDAS) of the Japan Meteorological Agency. Data collected at the AMeDAS observatories closest to the actual cultivation locations were used (Table 2, see also Table S1, S2 and S3 for detailed information about the sites).

2.2 Summary of the evaluation method

We compared partitioning-type and allometry-type models to determine which provides more robust estimates of plant tissue biomass. We set up a partitioning-type model to estimate the biomass increase of the target tissue from the biomass increase of the whole plant and the amount of increase that is allocated to the target tissue (see section 2.3). We set up allometry-type models to estimate the ratio of leaf biomass to total plant biomass (see section 2.3). We then used the observation data described in section 2.1 to compare the robustness of leaf biomass estimation between the two types of models.

To evaluate the robustness of each model type, we conducted a cross-validation. First, we selected m cultivars from among

| Crop | Time interval | Sites | Cultivars | Average observation period (days) | Average observation interval (days) | Sample size (n) |
|------|---------------|-------|-----------|---------------------------------|----------------------------------|---------------|
| Maize | 1978–1982     | Sapporo, Shiojiri, Miyakonojo | Hokkuyu, P3715, Takanewase, P3360, Ko10 | 126.8 | 21.13 | 280 |
| Rice  | 1978–1980     | Konosu, Chikugo, Morioka | Toyonishiki, Kochihibiki, Toyotama, Akihikari | 114.2 | 19.96 | 121 |
| Soybean | 1978–1982    | Sapporo, Kariwano, Shiojiri, Kumamoto | Enrei, Okasirome, Wasesiroge, Nakasennari, Kitamusume, Akiyoshi | 118.1 | 19.94 | 310 |

| Crop | Lat., long. | Closest AMeDAS site | Lat., long. |
|------|-------------|---------------------|-------------|
| Kounosu | 139.31, 36.02 | Hatoyama | 139.34, 35.98 |
| Chikugo | 130.3, 33.12 | Omuta | 130.47, 33.01 |
| Morioka | 141.1, 39.41 | Shiwa | 141.13, 39.55 |
| Sapporo | 141.25, 43 | Sapporo | 141.33, 43.06 |
| Kariwano | 140.22, 39.32 | Yashima | 140.14, 39.24 |
| Shiojiri | 137.57, 36.07 | Kiso-fukushima | 137.69, 35.84 |
| Kumamoto | 130.45, 32.53 | Matsushima | 130.45, 32.52 |
| Miyakonojo | 131.05, 34.31 | Shibushi | 131.1, 31.48 |

\( N_c \) cultivars \((N_c = 5 \text{ for maize}, N_c = 4 \text{ for rice}, \text{ and } N_c = 6 \text{ for soybean})\) for each crop as training data. Using the data of \( m \) cultivars, we estimated the values of parameters in the function used by the partitioning-type model to calculate the ratio of the leaf biomass increase to the total biomass increase \((\text{partitioning rate: } PR)\) at each developmental stage (Model 1, see below). Similarly, we estimated the parameter values of the functions used by the allometry-type models to calculate the ratio of leaf biomass to total biomass \((\text{leaf weight ratio: } LWR)\) at each developmental stage (Models 2–5, see below). Then, using the estimated parameter values, we predicted the leaf biomass at each developmental stage for the other cultivars (those not used for the parameter estimation) of each crop. Finally, we evaluated the robustness of each model by comparing the predicted leaf biomass values with the observed values (test data). This procedure was repeated \( n \) times, where \( n \) is the possible number of combinations of the cultivars.

2.3 Models

\( PR \) and \( LWR \) are mathematically defined as follows:

\[
PR_t = \frac{\Delta \text{Leaf}_{t} + \Delta \text{Leaf}_{t+1}}{\Delta \text{Total}_{t+1}} \tag{1}
\]

\[
LWR_t = \frac{\text{Leaf}_{t}}{\text{Total}_{t}} \tag{2}
\]

where \( \text{Leaf}_t, \text{Total}_t, \) and \( \Delta \text{Leaf} \) represent leaf, total plant, and dead leaf biomass \((\text{g m}^{-2})\) at time \( t \). \( \Delta \) indicates the difference between times \( t \) and \( t - 1 \). Therefore, \( \Delta \text{Leaf} = \text{Leaf}_t - \text{Leaf}_{t-1} \). \( \Delta \text{Total} = \text{Total}_t - \text{Total}_{t-1} \), \( \Delta \text{Leaf} \) for leaf biomass estimation between the two types of models.

Although in many actual crop growth models the everyday increase of the whole plant biomass \((\text{ΔTotal})\) is calculated according to sub-models relevant to elements such as photosynthesis rate and respiration rate, we used observation
data for \( \Delta \text{Total}_i, \text{Total}_i, \) and \( \Delta \text{DLeaf}_i \) for simplicity: we assumed that we know the true values of each at each developmental stage. Therefore, \( \text{Leaf}_i \) is estimated as:

\[
\text{Leaf}_i = \text{Leaf}_{i,1} + \hat{\text{PR}}_{i,1} \cdot \Delta \text{Total}_i - \Delta \text{DLeaf}_i
\]

for partitioning-type

\[
\text{Leaf}_i = \text{LWR}_i \cdot \text{Total}_i
\]

for allometry-type

where \( \text{Leaf}_i \) indicates the estimated leaf biomass at time \( t \), and \( \hat{\text{PR}}_{i,1} \) and \( \text{LWR}_i \) indicate the estimated \( \text{PR} \) and \( \text{LWR} \) values, which are estimated from the observed data other than of cultivar \( i \) at time \( t \) with the statistical models introduced below.

As the model relating \( \text{PR} \), to the degree of crop development, we used a local regression (LOESS) model with \( \hat{\text{PR}}_i \) as the dependent variable and the degree of development as the independent variable (Model 1, see below). As an index of the degree of crop development, we used the fraction of growing degree-days (\( f\text{GDD} \)); that is, the ratio of growing degree-days (\( \text{GDD} \)) at the observation time \( t \) to the total growing degree-days that is needed to reach maturity. To represent the relationship between \( \text{LWR} \) and the degree of crop development, we used two regression models, a LOESS model (Models 2 and 4, see below) and a non-linear, parametric regression model based on a logistic function (Models 3 and 5). Further, for each \( \text{LWR} \) regression model, we used two indexes for degree of crop development: \( f\text{GDD} \) and days after crop emergence (\( \text{DAE} \)), which is the number of elapsed days after the date of germination.

Thus, we set up a total of five models, one partitioning-type model (Model 1) and four allometry-type models (Models 2–5), as follows:

\[
\text{Model 1: } \hat{\text{PR}}_{i,1} = \alpha_{i,1} + g_i(f\text{GDD}_{i,1}) + \epsilon,
\]

\[
\text{Model 2: } \hat{\text{LWR}}_{i,1} = \alpha_{i,2} + g_i(f\text{GDD}_{i,1}) + \epsilon,
\]

\[
\text{Model 3: } \hat{\text{LWR}}_{i,1} = \frac{\beta_i}{1 + \exp \left( \gamma_i f\text{GDD}_{i,1} + \delta_i \right)} + \epsilon,
\]

\[
\text{Model 4: } \hat{\text{LWR}}_{i,1} = \alpha_{i,4} + g_i(\text{DAE}_{i,1}) + \epsilon,
\]

\[
\text{Model 5: } \hat{\text{LWR}}_{i,1} = \frac{\beta_i}{1 + \exp \left( \gamma_i \text{DAE}_{i,1} + \delta_i \right)} + \epsilon,
\]

where \( \alpha, \beta, \gamma, \) and \( \delta \) are parameters, \( \epsilon \) represents an error term, \( f\text{GDD} \) indicates the fraction of growing degree-days, and \( \text{DAE} \) indicates days after crop emergence. Subscript \( i \) represents crop cultivar and \( t \) represents time. Therefore, \( f\text{GDD}_{i,1} \) indicates the fraction of growing degree-days of cultivar \( i \) at time \( t \). Function \( g \) indicates a smooth function, estimated using the ‘loess’ function of \( \text{R} \) software with default settings (span = 0.75, degree = 2), which fit a polynomial surface determined by a numerical predictor using local fitting (R Core Team, 2016).

Models 1, 2, and 3 use \( f\text{GDD} \) to estimate \( \text{PR} \) or \( \text{LWR} \). By comparing the results between Models 1 and 2, we can examine whether a partitioning-type or allometry-type model can make more robust predictions. Comparisons of Models 2 and 3 and of Models 4 and 5 show whether nonparametric or logistic regression is better suited for making predictions. By comparing Models 2 and 4 and Models 3 and 5, we can evaluate the difference between the \( f\text{GDD} \) and \( \text{DAE} \) indexes.

\( \text{GDD} \) and \( f\text{GDD} \) are mathematically defined as:

\[
\text{GDD}_{i,t} = \text{GDD}_{i,t-1} + (T_i - T_0),
\]

\[
f\text{GDD}_{i,t} = \frac{\text{GDD}_{i,t}}{\text{TGDD}_{i,t}}.
\]

where \( T_i \) represents the average temperature (\( ^\circ \text{C} \)) at time \( t \), \( T_0 \) is the threshold (8°C in this study, according to Yin and van Laar, 2005), \( \text{GDD}_{i,t} \) indicates the growing degree-days, and \( \text{TGDD}_{i,t} \) indicates the total growing degree-days. Subscript \( i \) represents crop cultivar and \( t \) represents time.

Because we had exact information about the maturity date, we set \( \text{TGDD}_{i,t} \) after making certain assumptions. First, we estimated the relationship between observed \( \text{LWR} \) and \( \text{GDD} \) with a linear regression model for each cultivar. Then, we estimated the value of \( \text{GDD} \) at which the \( \text{LWR} = 0 \) from the linear regression model. We assumed that this \( \text{GDD} \) value = \( \text{TGDD} \). In this assumption, we define maturity as the day when the biomass of living leaf \( = 0 \). The \( \text{TGDD} \) of each cultivar is described in Table S4.

### 2.4 Model comparison

The verification procedure for maize is illustrated in Figure 1a as an example. First, we calculated \( \text{PR} \) values by using the observed data for \( m = 2 \) cultivars selected from among the 5 maize cultivars (Fig. 1a: ○). Then, we estimated a smooth function using a LOESS model using the “loess” function in \( \text{R} \) (R Core Team, 2016). Next, we estimated the leaf biomass using the estimated LOESS model with the observed biomass data (\( \Delta \text{Total}_i \) and \( \Delta \text{DLeaf}_i \)) for the 3 cultivars that were not used for the estimation of the parameters of Model 1 (Fig. 1c). The accuracy of the model was then estimated by comparing the predicted leaf biomass values (▲) with the observed values (○). We used the same procedure to evaluate Model 2 (Fig. 1b, d).

The method used to estimate the model parameters differed slightly between the models using nonparametric and parametric regression. In the models using parametric regression (3 and 5), the parameter values were estimated for each cultivar used as training data. Then the average value of each parameter (\( \hat{\beta}, \gamma, \) or \( \delta \)) was used to estimate \( \hat{\text{LWR}}_{i,1} \). In the models using nonparametric regression (1, 2, and 4), we averaged the \( \hat{\text{PR}}_{i,1} \) or \( \hat{\text{LWR}}_{i,1} \) values predicted by the LOESS models for each cultivar, and used those averaged values in the prediction model, as shown in equations (11) and (12).

### 2.5 Index of evaluation

To assess the validity of each model, we used the root mean square error (RMSE), which we calculated by comparing the predicted leaf biomass values with the observed values. Then we averaged the RMSE values. We considered that a model with a low average RMSE can make more robust predictions of leaf biomass.

We also evaluated the statistical significance of the results. The main null hypotheses are (q1) there is no difference in the robustness between the allometry-type and partitioning-type models; (q2) there is no difference in the robustness between a nonparametric and a regression model (logistic model); and (q3) there is no difference in robustness between the models using
To test \( \varphi_1 \), we compared the results of Model 1 with those of Model 2 by using the Brunner–Munzel test using the “lawstat” package in R (R Core Team, 2016). Because there were 11 comparisons relevant to testing hypothesis 1 (see Fig. 2), we corrected the \( P \)-values using Bonferroni’s correction. To test \( \varphi_2 \), we compared Models 2 and 3 and Models 4 and 5. The \( P \)-values of the 22 multiple comparisons were corrected by Bonferroni’s correction. To test \( \varphi_3 \), we compared Models 2 and 4 and Models 3 and 5. The \( P \)-values of the 22 multiple comparisons were also corrected by Bonferroni’s correction.

3. Results

Figure 2 shows the RMSEs for each model and each crop according to the number of extracted cultivars (see also Table 3). For all crop species and all numbers of extracted cultivars, the RMSEs of Model 1 tended to be higher than those of Model 2. Because there were significant differences between Models 1 and 2 in some comparisons, we reject the null hypothesis that there is no difference in robustness between allometry-type and partitioning-type models.

For all crop species and all numbers of extracted cultivars, the RMSEs of Models 2 and 4 tended to be lower than those of Models 3 and 5, respectively (Fig. 2). There were significant differences between Models 2 and 3 and between Models 4 and 5 in some comparisons, so we reject the null hypothesis that there is no difference in robustness between nonparametric and logistic regression models.

In general, the RMSEs of Models 2 and 3 tended to be lower than those of Models 4 and 5 in some comparisons, we reject the null hypothesis that there is no difference in the robustness between nonparametric and logistic regression models.

Fig. 1. An example of model setup (top panels) and the prediction of leaf biomass (bottom panels). In this example, two cultivars (○ in a and b) were selected among five cultivars. Then nonparametric regressions (— in a and b) were conducted for the relationship between (a) the fraction of growing degree-days (\( f_{GDD} \)) and partitioning rate (\( PR \)) or (b) \( f_{GDD} \) and leaf weight ratio (\( LWR \)). Then leaf biomass (g m\(^{-2}\)) of the other cultivars (○ in c and d) that were not used for model estimation were predicted using (c) \( PR \)- or (d) \( LWR \)-estimated nonparametric regression. ▲ Predicted values of leaf biomass. (a, c) Model 1; (b, d) Model 2.
the models using $fGDD$ or $DAE$.

### 4. Discussion

We aimed to identify robust methods for estimating leaf biomass when information required for many crop growth models, particularly crop cultivar, is lacking. Comparison of the RMSEs of different models showed that allometry-type estimation was more robust than partitioning-type estimation.

Two factors may account for smaller RMSEs of models using $LWR$ (allometry-type) rather than $PR$ (partitioning-type): (1) accumulation of differences between observed and predicted values (that is, discrepancy accumulation), and (2) no consideration in the models of re-translocation of nutrients in leaf turnover.

Concerning the first factor, in the partitioning-type model, the leaf biomass was obtained by using the estimated $PR$ to calculate...
how much photosynthate is allocated to the leaves at a certain time point, then adding the result to the previously calculated leaf biomass. Accordingly, past estimated values that do not match the observed value carry through to the next time point and the discrepancies accumulate. In contrast, because \( LWR \) is calculated by estimating the fraction of the total plant biomass that is accounted for by the leaf biomass and then using it to calculate the latter from the former, \( LWR \) is determined at each time point independently of past data. Accordingly, the range of the deviation will likely be limited even if there is a gap between the estimated and observed leaf biomass values. For example, the relationship between the discrepancies and the index for the degree of plant development (Fig. 3) suggests that the difference between the estimated and observed values is larger in Model 1 than in Model 2.

With regard to the second factor, in the estimation of \( PR \), we did not consider the effect of the translocation of nutrients in leaf turnover. The model estimating the increase of leaf biomass during crop growth considered only the partitioning of photosynthate (the increase of total biomass). However, photosynthate is translocated from leaves to other tissues (Hozumi and Kurachi, 1991). When leaves age or light availability is low, some of the leaf nitrogen is re-translocated to new organs (Hikosaka et al., 2005; Hirose and Oikawa, 2012). Therefore, it is possible that the \( PR \) method that we used did not successfully reproduce the leaf biomass because leaf turnover was not considered. The differences between observed and predicted values were probably increased in our results because Model 1 did not take account of the translocation of nutrients in leaf turnover.

Comparison of regression methods among the models used to estimate \( LWR \) showed that nonparametric regression (LOESS model) tended to provide lower RMSEs than logistic regression. Nonparametric regression reproduces observations better because \( LWR \) changes in a more complicated fashion in relation to crop development than can be captured by a logistic curve. Of course, it is possible that there are other parametric functions that better represent the relationship between \( LWR \) and the degree of crop development (\( fGDD \) or \( DAE \)). We used a logistic function as the parametric function in this study because the dependent variable of this function ranges from 0 to 1. However, there are only two parameters in the logistic model, which restricts the flexibility of the shape of the function. For constructing models that have low computational load, parametric models may be preferable to nonparametric models. Therefore, identifying functions that fit the shape of \( LWR \) is an important task for future work.

Comparison of explanatory variables among the models used to estimate \( LWR \) showed that models using \( fGDD \) achieved...
better results than those using $DAE$. This result implies that using the heat unit approach is better than using the chronological approach for estimating the change in the allometry of crop biomass. The concept of using heat units to evaluate the degree of plant development has long been used in phenological studies (Wang, 1960), and our results confirm that the concept is also useful for estimating the allometry coefficient.

Thus, partitioning-type crop growth models have more model-based limitations because they are influenced by past discrepancies and don’t take translocation into account. Also, because RMSEs were smaller when $LWR$ was estimated, we consider allometry-type crop growth models to be more robust. In addition, except in the case of rice, RMSEs of the model using $fGDD$ with nonparametric regression were clearly smaller than those of the other models. This suggests that the use of $fGDD$ with nonparametric regression is robust for maize and soybean. Interestingly, the average differences in RMSEs between partitioning-type and allometry-type models appear to be particularly large in maize and rice (Table 3). Both maize and rice are grasses and have the same leaf structure: node, sheath, and blade. On the other hand, the leaf structure of soybean is very different. Thus, the robustness of the allometry-type models may differ among taxonomic groups. Further research is needed to reveal the relationship between taxonomic groups and the characteristics of biomass development (partitioning-type or allometry-type).

Finally, we note that some problems remain. The first concerns the absence of settings for estimating stages of crop development. Some crop growth models divide development into several stages. In ORYZA2000, the partitioning value differs according to the developmental stage (Bouman et al., 2001). In the Simulation Model for Rice–Weather relations as well, the radiation absorption rate varies depending on the developmental stage (Horie et al., 1995). However, we did consider changes in partitioning (considering only $fGDD$ or $DAE$). Accounting for development in more detail by the model might change the modeling result.

The second problem is that factors affecting crop development were not taken into account. For example, our models do not include day length, although its influence on crop growth is well known and many crop growth models consider it. However, adding more detail to the model would increase the number of parameters and, thus, the number of parameters needing to be determined for each cultivar. Therefore, if the cultivar is unknown, such elaboration might decrease the robustness of the model.

The third problem is that the experimental setting of this study includes not only the effect of cultivar, but also that of environmental factors at each site. In the observation data, the set of crop cultivars differs slightly across sites. Therefore, we can only conclude that the robustness of allocation-type models is greater than that of partitioning-type models when the cultivar is unknown and/or the environmental conditions differ from that used for the parameter calibration of the model.

Another problem is that no clear definition of a dead leaf is given in the reference data (AFFRCS, 1987). Our results suggest that allocation-type models are robust for estimating the biomass of living leaf. Therefore, if the definition of the living leaf (or dead leaf) is changed, in principle, the robustness of each model may change. Such unclear definitions are a disadvantage of using secondary data. However, a dead leaf is generally understood to be a leaf that does not have the abilities of photosynthesis and respiration, so this issue may have little effect on our conclusion.

It is evident that the use of conventional crop models is superior when clear detailed information is available. However, for large-scale (including global-scale) simulations, obtaining detailed information such as crop cultivar is difficult. We examined which type of model is more robust for the estimation of leaf biomass when the crop cultivar being simulated is unknown but the average parameter values of the model are known. Our findings indicate that in this situation the estimation of leaf biomass by an allometry-type model is more robust than estimation by a partitioning-type model.

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