Ontogenetic changes of photosynthetic and dark respiration rates in relation to nitrogen content in individual leaves of field crops

M. OSAKI, T. SHINANO, T. KANEDA, S. YAMADA, and T. NAKAMURA

Graduate School of Agriculture, Hokkaido University, Kita-9, Nishi-9, Kitaku, Sapporo, 060-8589, Japan

Abstract

Ontogenetic changes of rates of photon-saturated photosynthesis (P$_{sat}$) and dark respiration (R$_D$) of individual leaves were examined in relation to nitrogen content (Nc) in rice, winter wheat, maize, soybean, field bean, tomato, potato, and beet. P$_{sat}$ was positively correlated with Nc as follows: P$_{sat}$ = Cf Nc + P$_{sat0}$, where Cf and P$_{sat0}$ are coefficients. The value of Cf was high in maize, medium in rice and soybean, and low in field bean, potato, tomato, and beet, of which difference was not explained by ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO) content. R$_D$ was explained by P$_{sat}$ and/or Nc, however, two models must be applied according to plant species. R$_D$ related linearly with P$_{sat}$ and Nc in maize, field bean, and potato as follows: R$_D$ = a P$_{sat}$ + b, or R$_D$ = a Nc + b', where a, a', b, and b' are coefficients. In other species, the R$_D$/P$_{sat}$ ratio increased exponentially with the decrease of Nc as follows: R$_D$/P$_{sat}$ = a exp(b Nc), where a and b are coefficients. Therefore, R$_D$ in these crops was expressed as follows: ln(R$_D$) = ln(a P$_{sat}$) + b Nc, indicating that R$_D$ in these crops was regulated by both P$_{sat}$ and Nc.

Additional key words: carbon-nitrogen interaction; growth respiration; leaf mass per area; maintenance respiration.

Introduction

Ingestad (1977) reported that the relative growth rate (RGR) showed a close correlation with nitrogen content (Nc) in whole tree seedlings. This concept has been widely applied to develop models for RGR as a function of Nc of whole plants (Hirose 1988, Pons et al. 1994, Wilkström and Ågren 1995), which indicate that the C and N metabolisms are interrelated in plants. The C-N balance was elucidated not only in whole plant, but also at single leaf level. A positive correlation between Nc and the leaf photon-saturated net photosynthetic rate (P$_{sat}$) has often been reported (Gulmon and Chu 1981, Field and Mooney 1986, Hirose and Kitajima 1986, Evans 1989). Moreover, P$_{sat}$ was linearly correlated with Nc for a wide range of C$_3$ species (Field and Mooney 1986). Greenwood et al. (1991), who reported that P$_{sat}$ is limited by Nc, stated that along with leaf senescence and under shade, N is translocated from older leaves to younger ones. This enables such maintenance of active photosynthesis in the younger or less shaded leaves that the relationship between P$_{sat}$ and leaf Nc remains constant. However, the P$_{sat}$-Nc relation varies with growth stages (Murata 1961, Hayami 1982) and species (Evans and Seemann 1989). Thus P$_{sat}$ is regulated not only by Nc, but also by other factors such as ageing, leaf longevity, leaf structure, etc. For example, the surface area of mesophyll cells regulates the diffussion of CO$_2$ (Koike 1988), or the maximum P$_{sat}$ is negatively correlated with leaf longevity (Chabot and Hicks 1982, Koike 1988).

Leaf dark respiration rate (R$_D$) is also an important factor in the regulation of the C balance in leaves. Plant R$_D$ can be divided into growth respiration used for the growth process (e.g., starch, protein, and cell wall synthesis) and maintenance respiration used for the maintenance process (e.g., protein turnover, ion uptake – Penning de Vries 1975). Therefore both growth respiration and maintenance respiration are probably related to N nutrition in the leaves. R$_D$ can be related to Nc of leaf tissue (Connor et al. 1993), but Byrd et al. (1992) showed that R$_D$ is not correlated with Nc. P$_{sat}$ is generally in a positive correlation with R$_D$ (Murata 1961, McCree 1970, Tanaka and Harra 1970, Sato and Kim 1980, André et al. 1982, Azcón-Bieto et al. 1983). Thus the respiratory process is closely related to Nc and P$_{sat}$. According to McCree (1974), R$_D$ of whole plants can be

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Abbreviations: LMA, leaf mass per area; Nc, nitrogen content per dry matter unit; P$_{gp}$, gross photosynthetic rate; P$_{net}$, leaf net photosynthetic rate; R$_D$, leaf dark respiratory rate; RGR, relative growth rate; RuBPCO, ribulose-1,5-bisphosphate carboxylase/oxygenase; RuBPCO-N, content of nitrogen as RuBPCO per dry matter unit.

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Materials and methods

Plants: Rice (*Oryza sativa* L.), winter wheat (*Triticum aestivum* L.), maize (*Zea mays* L.), soybean (*Glycine max* (L.) Merr.), field bean (*Phaseolus vulgaris* L.), potato (*Solana tuberosum* L.), fodder beet (*Beta vulgaris* L. var. *cressa* Alc.), and tomato (*Lycopersicon esculentum* L.) were planted in duplicate with a complete random design in a field belonging to Hokkaido University at Sapporo, Japan (located at the northern part of Japan, 43°03′N, 141°20′E, altitude 17 m, alluvial soil). Crops were cultivated by conventional farmer’s method, of which outline is shown in Table 1.

Measurement of rates of photosynthesis and respiration: To determine leaf position, individual leaves were marked counting from ground level. CO₂ gas exchange rate was measured in individual leaves of one plant by one- or two-week intervals according to crop. *P₅₀* was measured by placing an individual attached leaf in a transparent plastic chamber varying in size and connected to differential-type infrared gas analyser (model LIA-2, Hitachi-Horiba, Tokyo, Japan, for potato, tomato, and field bean; and KIP 9010, Koito Seisakusyo, Tokyo, Japan, for the remaining crops). *Pₛₑₐₜ* was measured at photon saturation: namely, at [μmol m–² s–¹] 1 000 to 1 500 (rice, winter wheat, maize, soybean, and fodder beet), 740 (field bean), 1 300 (tomato), and 740 (potato). Leaf was irradiated by a reflection lamp for field bean, tomato, and potato, and by a halogen lamp (Kenko Co., KTS-100R) for the remaining crops. In maize, though the photosynthesis was saturated at around 3 000 μmol m–² s–¹, due to the limit of the facility, *Pₛₑₐₜ* was estimated at around 1 500 μmol m–² s–¹, at which *Pₛₑₐₜ* is about 90% of the value at photon saturation. Thus, for all crops examined, *Pₛₑₐₜ* was estimated at or near the maximum rate. In the chamber, air temperature was 20 to 25 °C, relative humidity 40-50%, and CO₂ concentration 350-370 g m–³. The air flow rate was 16.7 cm² s–¹ for LIA-2 and 8.3 cm² s–¹ for KIP 9010 for the measurement of *Pₛₑₐₜ* and *R₀*. *R₀* was measured by covering the leaf with aluminium foil after *Pₛₑₐₜ* had been measured, and the rate was adjusted at 25 °C, assuming that the Q₁₀ value was 2 (James 1953).

The measured whole single leaf blade was sampled. Leaf area was determined using a leaf area meter (Hayashi Denki Co., model AAC-400). Then it was dried in an air-forced oven at 80 °C for 48 h to determine leaf dry mass and N content. Leaf mass area (LMA) was calculated as leaf dry mass per leaf area.

Measurement of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBPCO): RuBPCO was extracted according to Osaki et al. (1993). 200 mg of lyophilised leaves were homogenised in 100 mM Tris-HCl (pH 7.8), containing 1 mM EDTA, 10 mM mercaptoethanol, 10 mM MgCl₂, 1 mM monoiodoacetate, 10 μM leupeptine, and 12 500 cm³ m⁻³ glycine, in a chilled mortar with a pestle with acid-washed quartz sand. The homogenate was centrifuged at 3 000×g for 15 min at 4 °C. The precipitate was re-extracted two times with 5 cm³ of the same buffer. Obtained supernatants were mixed, made up to 25 cm³ with the same buffer, and 1 cm³ of it was centrifuged at 15 000×g for 20 min at 4 °C. Polypeptides in the extracted sample were further separated by SDS-PAGE according to Laemmli (1970). The gel was dried and then the RuBPCO concentration was determined by a densitometric method using NIH image software after the gel image was obtained by scanner (EPSON 7000G) with purified spinach RuBPCO (Sigma) as standard.
ONTGENETIC CHANGES OF PHOTOSYNTHESIS

Chemical analysis: Nc was determined by the Kjeldahl method (Hind 1993). Sugar was extracted from 200 mg of lyophilised sample by the addition of 25 cm3 of 80 % hot ethanol, then centrifuged at 6 000 x g, and starch was extracted by 30 cm3 of 30 % perchloric acid using the residue after sugar extraction. Each procedure was repeated 3 times. The solution that contained sugar was concentrated on a water bath (100 °C) to remove ethanol. The contents of sugar and starch were determined colorimetrically by an anthron method (Trevelyan and Harrison 1952), and expressed on a glucose basis.

Statistical analysis: All values were collected primarily by using the duplicate plantings, and were expressed as the average value. Nc after full leafing was adapted in the current paper by the following equation at 1% significance level:

\[ Nc = (Nc_0 - Nc_d) \exp(-Nc f) + Nc_d \]  

(1)

where \( Nc_0 \) is the initial value of \( Nc \), \( Nc_d \) is the \( Nc \) of dead leaves, \( Nf \) is a coefficient, and \( t \) is the number of days after leafing. All values were subjected to statistical analysis by SPSS (1994).

Table 1. Outline of the cultivation conditions for estimating the photosynthetic rate. Data collectors were undergraduate and graduate students in the Laboratory of Plant Nutrition, Faculty of Agriculture, Hokkaido University. Exceptions: *Date of transplanting. **High-yielding cultivars or experimental lines; other cultivars were standard yield cultivars for farmers. ***Ammonium sulfate + coated urea (commercial name: LP coat) + coated N, P, and K (commercial name: Long). Tomato was transplanted in mid June to the field. In field bean additional top dressing with N was used.

<table>
<thead>
<tr>
<th>Species</th>
<th>Cultivar or line</th>
<th>Hill spacing [cm]</th>
<th>Plant number per hill</th>
<th>Fertiliser ( N : P_2O_5 : K_2O )</th>
<th>Planting date</th>
<th>Year</th>
<th>Collector</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rice</td>
<td>Joiku 404**</td>
<td>30±15</td>
<td>3</td>
<td>(40+80+160)***:200:200</td>
<td>May 26*</td>
<td>1992</td>
<td>T. Kaneda</td>
</tr>
<tr>
<td>Maize</td>
<td>Pioneer 3540**</td>
<td>40±30</td>
<td>1</td>
<td>(40+110+200)***:200:200</td>
<td>May 12</td>
<td>1992</td>
<td>T. Kaneda</td>
</tr>
<tr>
<td>Soybean</td>
<td>Tsununamuse**</td>
<td>50±20</td>
<td>2</td>
<td>(40+160)***:214.5:200</td>
<td>May 18</td>
<td>1992</td>
<td>T. Kaneda</td>
</tr>
<tr>
<td>Field bean</td>
<td>Gintebou</td>
<td>25±5</td>
<td>2</td>
<td>(40+20):32:40</td>
<td>May 21</td>
<td>1973</td>
<td>K. Kimiizuka</td>
</tr>
<tr>
<td>Potato</td>
<td>Norin 1</td>
<td>70±10</td>
<td>1</td>
<td></td>
<td>Apr. 28</td>
<td>1977</td>
<td>K. Kimiizuka</td>
</tr>
<tr>
<td>Tomato</td>
<td>Fukuju No. 2</td>
<td>90±50</td>
<td>1</td>
<td>30±30</td>
<td>mid Apr.</td>
<td>1972</td>
<td>K. Kimiizuka</td>
</tr>
<tr>
<td>Fodder beet</td>
<td>Sugarmanagold**</td>
<td>50±25</td>
<td>1</td>
<td>(40+160+200)***:200:200</td>
<td>Apr. 28*</td>
<td>1992</td>
<td>T. Kaneda</td>
</tr>
</tbody>
</table>

Results

Ontogenetic changes of \( Nc \), \( P_{sat} \), and \( R_D \). After leaf emergence, \( Nc \) decreased gradually with growth, and subsequently \( Nc \) decreased exponentially. As this \( Nc \) tendency was similar to our previous finding (Osaki 1995), we do not show the values here. \( Nf \) (estimated from Eq. 1) was high in maize and soybean, low in tomato, potato, and fodder beet (Table 2).

Generally, \( P_{sat} \) was low at the leafing, and increased with growth until the full leaf expansion was reached (Fig. 1). After \( P_{sat} \) had reached its maximum value, or after the first measurement of \( P_{sat} \) it decreased continuously with growth. For example, \( P_{sat} \) was low at high \( Nc \) (at a very early stage) at \( L_1, L_2 \), and \( L_5 \) in field bean; at \( L_{11} \) and \( L_{18} \) in fodder beet; and at \( L_{19}, L_{15} \), and \( L_{20} \) in potato.

On the other hand, the value of \( R_D \) was generally high in the early growth stage of leaves, then decreased (Fig. 2). However, in some crops or at some leaf positions, \( R_D \) increased slightly at a late growth stage of leaves. Thus, the changes of \( P_{sat} \) were significantly different from the changes of \( R_D \), indicating that it is difficult to derive a simple relationship between \( P_{sat} \) and \( R_D \) in individual leaves.

Relationship between \( P_{sat} \) and \( Nc \) or saccharide content: At the very early leaf expanding stage, \( P_{sat} \) was negatively correlated with \( Nc \) (values in parentheses in Fig. 3). However, after full leaf expansion, \( P_{sat} \) was positively correlated with \( Nc \) as follows:

\[ P_{sat} = C f Nc + P_{sat0} \]  

(2)

where \( Cf \) and \( P_{sat0} \) are coefficients.
Fig. 1. Changes in photosynthetic rate of individual leaves at successive growth stages. The L numbers in the figure indicate leaf position counted from the bottom. Time after transplanting in rice, and time after wintering in winter wheat.

Fig. 2. Changes in respiratory rate of individual leaves at successive growth stages. The L numbers in the figure indicate leaf position counted from the bottom. Time after transplanting in rice, and time after wintering in winter wheat.

Fig. 3. Relationship between photosynthetic rate and nitrogen content. Values in parentheses (corresponding to the N content at very early leafing) were omitted for estimating the regression between the photosynthetic rate and nitrogen content for the reasons mentioned in the text. The L numbers in the figure indicate leaf position counted from the bottom. Regression coefficients are in Table 2.

The $P_{sat}$-Nc relation remained constant regardless of leaf position except for tomato (Fig. 3). Presumably because we expressed $P_{sat}$ and Nc on a dry mass basis and not on a leaf area basis. If $P_{sat}$ and Nc were expressed on a leaf area basis, the Cf value would differ considerably among the leaf positions (values not shown). Thus the effect of LMA on the Cf value was cancelled, because the $P_{sat}$-LMA relationship varied among the leaf position or with leaf ageing (Fig. 4). Therefore, we estimated Cf of each crop from all the data including possible leaf positions. The Cf variation among leaf positions was negligible in spite of the difference in growth condition as indicated by correspondingly low SE values (Table 2). The Cf value was very low in tomato, potato, and fodder beet, intermediate in rice, winter wheat, soybean, and field bean, and very high in maize. Since Cf was different among the crops, inter-specific differences in $P_{sat}$ could not be explained solely by the function of Nc. Other factors such as sugar and/or starch contents in leaves were not related to $P_{sat}$ (Fig. 5).

Relationship between $P_{sat}$ and concentration of N in RuBPCO: Although $P_{sat}$ was related to RuBPCO-N except in maize (Fig. 6), the regression coefficient was remarkably different among the C3 crops. The regression
Fig. 4. Relationship between photosynthetic rate and leaf mass per area. The L numbers in the figure indicate leaf position counted from the bottom.

Fig. 6. Relationship between photosynthetic rate and ribulose-1,5-bisphosphate carboxylase/oxygenase (RubPICO-N) based on nitrogen content. **significant at 1% level, *significant at 5% level.

Fig. 5. Relationship between photosynthetic rate and sugar, starch, and nitrogen contents. Arrows indicate the progression of growth from leafing to senescence of individual leaves.

coefficient was high in soybean, medium in winter wheat, and low in rice and fodder beet. Thus the difference in the \( P_{\text{max}} \) relationship among the crops was not associated with RubPICO-N.

Relationship between \( R_0 \) and \( N_c \) or saccharide content: \( R_0 \) decreased significantly with the decrease of \( N_c \) in maize, field bean, and potato (Fig. 7). In tomato, \( R_0 \) decreased with the decrease of \( N_c \) to approximately 30 g(N) kg\(^{-1}\), then increased with the decrease of \( N_c \). In fodder beet, \( R_0 \) increased slightly with the decrease of \( N_c \). Thus, \( R_0 \) among crops did not show a consistent relationship with \( N_c \).

\( R_0 \) was not explained by a pattern of simple regression in the case of sugar or starch contents (Fig. 8). Since the starch concentration increased with the decrease of \( N_c \) and \( P_{\text{max}} \), starch probably accumulated due to the low rate of saccharide translocation, especially during the late growth stage of leaves (starch accumulation was estimated from Figs. 1, 2, and 5). Since the decrease of
Fig. 8. Relationship between respiratory rate and sugar or starch contents. Arrows indicate progression of growth from leafing to senescence of individual leaves.

Nc was caused by the degradation of protein from leaves, it indicates that respiration, which utilizes storage substances, was promoted by the decrease of Nc in some crops.

Relationship between $R_D$ and $P_{sat}$: If values at very early leafing stage were eliminated as shown in Fig. 3, $R_D$ was positively correlated with Nc in maize, field bean, and potato (Fig. 9). In rice, winter wheat, soybean, and fodder beet, $R_D$ remained constant regardless of $P_{sat}$. In tomato, at the early stage, $R_D$ decreased with the decrease of $P_{sat}$, then remained constant, and finally increased with the decrease of $P_{sat}$.

Discussion

Regulating factors of leaf $P_N$: At the early leafing stage, Nc was high, while $P_{sat}$ was very low due to low contents of chlorophyll and RuBPCO (Osaki et al. 1993, 1995a). In the current study, $P_{sat}$ increased with the decrease of Nc during the leafing stage (values in parentheses of Fig. 3), but after the leafing stage they decreased linearly with the decrease of Nc. At the early leafing stage, the leaf mass was too small to evaluate $P_{sat}$ values at this stage can therefore be omitted from discussion on productivity. Thus, based on the ontogenetic changes of $P_{sat}$ and Nc, a general model of the $P_{sat}$-Nc relationship was derived (Eq. 2) (Fig. 3).

LMA, a parameter related to the amount of air space of leaf (Koike 1988), regulates the diffusion rate of CO$_2$ (Nobel 1977, Björkman 1981). In previous studies; leaf mass per area (LMA) increased with the progression of growth, indicating a positive relationship between LMA and $P_{sat}$ (Jurik 1986, Oren et al. 1986). However, this relationship was not applicable when data on various tree species were compiled (Koike 1988). In the current report, $P_{sat}$ was not related to LMA (Fig. 4), indicating that at least in field crops, the difference of $P_{sat}$ per unit of Nc (estimated from CF) cannot be explained by the leaf structure, particularly by its thickness. On the other hand, the low distribution ratio of total N to RuBPCO-N tended to give a low regression coefficient of $P_{sat}$-Nc (e.g., Evans and Seemann 1989), and that the distribution ratio of total N to RuBPCO-N may account for the fact that the $P_{sat}$-Nc regression varied among species. However, in our observations the coefficient of regression between $P_{sat}$ and RuBPCO-N was markedly different among the species (Fig. 6). This means that CF differences among crops were not ascribed to the N distribution to functional proteins and that chlorophyll content (which forms the light-harvesting-pigment-protein complex) did not explain the CF difference among crops. Other factors such as sugar and/or starch contents in leaves are probably related to $P_{sat}$ (Krapp and Stitt 1995), while $P_{sat}$ in the
current report was not related at all to the sugar or starch contents (Fig. 5). Although it was difficult to determine the physiological factors responsible for the difference in CF among species, we assumed that CF is primarily regulated by the efflux rate of C and N compounds from leaves, as discussed by Osaki and Shinano (2001).

Since Nc in individual leaves decreased with the progress of growth, it was supposed, based on ontogenetic factors (Tanaka 1961), that N in old leaves is re-translocated to newly growing organs. The Nc change after leaf expansion is described in Eq. 1. These facts indicate that Nc is strictly regulated by inherited ontogenetic programs in leaves. On the other hand, since leaf senescence is accelerated by shading or mutual shading (Hirose et al. 1988, 1989), it is assumed that N re-translocation is also affected by environmental factors. In the current report, Nf was very similar among leaf positions, except for legume crops (soybean and field bean). This suggests that Nf is regulated more by ontogenetic factors than by environment, based on the following: (1) SC value of Nf among the leaf positions was low (Table 2). (2) Irradiation of each leaf changed considerably according to canopy growth. Our previous results (Osaki et al. 1995b) also support this assumption, because even if the sink (ears) of cereal crops is cut, Nn continues to be translocated from leaves to stem. The accumulation of N in the stem indicates that N translocation from leaves of cereal crops is regulated mainly by an autonomous mechanism in leaves.

Regulating factors of RO: RO is related to Pn or Nc (e.g., Amthor 1989). Moreover, it is often suggested that saccharide content is related to RO (e.g., Azez-Biuto and Osmond 1983, Azez-Biuto et al. 1983, Hrbec et al. 1985, Baydorfer et al. 1987, Williams and Farrar 1990, Farrar and Williams 1991), but several reports indicated no clear relationship between the saccharide content and RO (Challa 1976, Farrar 1980, Journo et al. 1986, Brouquiss et al. 1991, Douce et al. 1991, Noguchi et al. 1996). We found that saccharide (sugars and/or starch) content was not the determinant factor (Fig. 8). According to McCree (1974), RO = kPn + cM, where Pn is gross photosynthetic rate, k and c are constants, and M is dry matter. Pn/M is expressed as Pn + 0.5 RO, assuming that RO during a light period (half day) is the same as that during a dark period. Therefore, the above equation can be rewritten as RO = k/1 - 0.5 k) Pn + c/(1 - 0.5 k), which was discussed by Heskesth et al. (1971). If this equation can be applied to ontogenetic data, RO must be related linearly to Pn. However, a significant relationship of RO and Pn was found in maize, field bean, and potato, while there was no significant relationship in other crops (Fig. 9).

Thus, in rice, winter wheat, soybean, tomato, and fodder beet, RO was not explained by Pn or Nc because RO remained constant or increased with the decrease of Pn or Nc (Figs. 7 and 9). RO/Pn will increase with the decrease of Nc because of contribution of storage substance or reconstruction of structural compounds at late growth leaf stage. Consequently, it is assumed that RO in leaves is not regulated solely by photosynthesis (substrate supply), and cannot therefore be represented by the equation of McCree (1974) for all species. Also, RO had significant relationship with Nc only in maize, field bean, and potato (Fig. 7), which relationship was similar with the relationships between RO and Pn. Therefore, we tested various models on RO/Pn and Nc parameters. Among these models we found that the RO/Pn ratio of various crops increased exponentially with the decrease of Nc, the RO/Pn ratio could be described by the following equation:

\[
\text{RO/Pn} = \text{a exp}(b \text{Nc})
\]
where a and b are coefficients (Fig. 10). $R_D$, then, could be estimated from the following equation:

$$\ln(R_D) = \ln(a P_{sat}) + b Nc$$

(3'). Thus, the regulation of $R_D$ by $P_{sat}$ and Nc is essential in rice, winter wheat, soybean, tomato, and fodder beet. Coefficients a and b were estimated among crops (Table 3). The regression coefficient b was markedly different among the species. However, in maize, field bean, and potato, the regression was not significant in this equation (Table 3). At the late stage of leaf development, owing to the low rate of saccharide translocation, the starch content may increase with the decrease of Nc, and protein is degraded due to re-translocation from leaves. This suggests that the usage of storage substances will be enhanced by the decrease of Nc. Therefore, $R_D/P_{sat}$ increased with the decrease of Nc in many crops except for maize, field bean, and potato.

Consequently, $P_{sat}$ of each species was explained by Nc function. $R_D$ was explained by Nc (or $P_{sat}$) function in maize, field bean, and potato, and by $P_{sat}$ and Nc function in rice, winter wheat, soybean, tomato, and fodder beet, because storage substance contribution was presumably different among crops.

References


Hirose, T., Weger, M.J.A., Pons, T.L., Van Rheenen, J.W.A.:


McCree, K.J.: Equations for the rate of dark respiration of white clover and grain sorghum, as functions of dry weight, photosynthetic rate, and temperature. – Crop Sci. 14: 509-514, 1974.


