A carbohydrate supply and demand model of vegetative growth: response to temperature and light

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ABSTRACT

Photosynthesis is the limiting factor in crop growth models, but metabolism may also limit growth. We hypothesize that, over a wide range of temperature, growth is the minimum of the supply of carbohydrate from photosynthesis, and the demand of carbohydrate to synthesize new tissue. Biosynthetic demand limits growth at cool temperatures and increases exponentially with temperature. Photosynthesis limits growth at warm temperatures and decreases with temperature. Observations of tomato seedlings were used to calibrate a model based on this hypothesis. Model predictions were tested with published data for growth and carbohydrate content of sunflower and wheat. The model qualitatively fitted the response of growth of tomato and sunflower to both cool and warm temperatures. The transition between demand and supply limitation occurred at warmer temperatures under higher light and faster photosynthesis. Modifications were required to predict the observed non-structural carbohydrate (NSC). Some NSC was observed at warm temperatures, where demand should exceed supply. It was defined as a required reserve. Less NSC was found at cool temperatures than predicted from the difference between supply and demand. This was explained for tomato and sunflower, by feedback inhibition of NSC on photosynthesis. This inhibition was much less in winter wheat.

Key-words: law of the minimum; non-structural carbohydrate; photosynthesis inhibition; respiration; structural growth.

INTRODUCTION

Mathematical models that include simple representations of physiological processes have been used in agriculture and ecology to explain or predict the effect of environment on plant growth. Most crop production models are driven by the effect of shoot environment on gross photosynthesis and maintenance respiration over the daily cycle. Daily structural growth, \( s \), is daily gross photosynthesis, \( p \), minus daily maintenance respiration, \( m \), times a conversion efficiency, \( \varepsilon \), from carbon in photosynthate to carbon in structure (Spitters, van Keulen & van Kraalingen 1989, Seginer et al. 1991; Dayan et al. 1993).

\[ s = \varepsilon (p - m) \]  

This can also be represented by a carbon balance, where \( p - m \) is equal to \( s - g \), where \( g \) is growth respiration. The concepts of growth and maintenance respiration come from modelling respiration (Amthor 2000; Cannell & Thornley 1999; Frantz, Cometti & Bugbee 2004).

Gross photosynthesis controls growth when the supply of carbohydrate is limiting. However, the demand of plants for carbohydrate may limit growth, due to various factors, including small size of the growing organs, low temperature, and scarcity of nutrients or water. We somewhat arbitrarily equate supply with gross photosynthesis minus maintenance respiration, while we equate demand with potential growth plus the corresponding growth respiration, plus any additional carbohydrate required as a reserve. We distinguish between potential and actual supply and demand. When growth is limited by supply, supply is said to be at its potential level, while the demand is at its actual level, and vice versa. Potential demand is similar to the concept of potential growth rate or potential capacity to accumulate assimilates (Marcelis 1996).

At cool temperatures, in the range of 0 to 20 °C, the potential demand for carbohydrate may be less than the potential supply, resulting in surplus carbohydrate. Under high light and cool temperatures, plants accumulate excess non-structural carbohydrate (NSC), mostly in the form of starch and sugars (Gent 1986; Huang & Gao 2000). Annual crop plants can be divided into starch- and sugar-accumulators. Tomato is an example of the first group, while lettuce is an example of the second (Frantz et al. 2004). The accumulation of NSC in the form of either sugar or starch is evidence of a surplus of carbohydrate supply over demand. Plants photosynthesize during daylight hours and accumulate NSC which is partially or fully consumed by biosynthetic assimilation in the dark. This pattern has been observed in diverse species of plants (Chatterton & Silvius 1979; Gent 1984; Gerhardt, Stitt & Heldt 1987; Riens et al. 1994; Burner & Belesky 2004). The NSC available at the end of the light period is positively correlated with growth (Thornley & Hurd 1974), while that still available at dawn is negatively correlated with growth (Acoc, Acoc & Pasternak 1990).
We denote any NSC observed at dawn under warm temperatures, above 20 °C, as a carbohydrate reserve. This NSC has been observed in several studies. When expressed as a fraction of total dry matter (TDM), warm root-zone temperatures depleted starch to not less than 60 mg g\(^{-1}\) [TDM] in leaves of tomato seedlings (Hurewitz & Janes 1983). A similar minimum amount of starch was found in potato grown at warm air temperature (Lafta & Lorenzen 1995). The minimum was about 30 mg g\(^{-1}\) [TDM] for melon leaves grown at various temperatures and CO\(_2\) levels (Acock et al. 1990), and 15 to 25 mg g\(^{-1}\) [TDM] for starch in cucumber grown under low light (Verkleij & Challa 1988).

The temperature and light response of accumulation of dry matter in plants can be determined from growth and photosynthesis measurements. To measure growth, plants are subjected to an environmental treatment long enough to measure accumulated biomass. Growth is often expressed per unit plant biomass, namely, relative growth rate (RGR). In photosynthesis experiments, dry matter accumulation is calculated from the rate of specific net photosynthesis measured over a short time, such as minutes. While plants in a growth experiment acclimate to the environment imposed by the treatment, photosynthesis measurements are so brief that plants are not acclimated.

The temperature response of growth is qualitatively different than that of photosynthesis at cool temperatures. The growth rate increases exponentially with temperature (convex downward), with a sensitivity denoted by \(Q_{10}\), the factor by which the process rate is multiplied over a span of 10 °C. The growth response of lettuce in the range from 10 to 25 °C was exponential with a \(Q_{10} = 3.3\) (Scaife 1973). The extension of wheat leaves had a similar exponential response with a \(Q_{10}\) from 2.5 to 3.5 (Kemp & Blacklow 1980). Growth of tomato seedlings had a \(Q_{10} = 2\) (Paul, Hardwick & Parkers 1984). The rate of growth reaches a maximum at warm temperatures, and decreases at higher temperature for tomato (Went 1945), lettuce (Verkerk & Spitters 1973) and several other species (Rajan, Betteridge & Blackman 1973). At warm temperatures, the optimal temperature for growth increases as light increases, while growth at cool temperatures is not necessarily sensitive to light intensity (Rajan et al. 1973).

Net photosynthesis first increases and then decreases with increasing temperature, but the response curve is concave downward throughout the temperature range (Yamori et al. 2010). The maximum of the temperature response increases in magnitude and occurs at a warmer temperature under increasing light intensity. This behaviour has been observed for grasses and legumes (Ludlow & Wilson 1971), maize (Kim et al. 2007) and even for mosses (Stålfelt 1937).

Gross photosynthesis can be obtained by adding respiration measured in the dark to net photosynthesis measured at the same temperature in the light. The temperature response of dark respiration often has \(Q_{10} = 2\) (Ryan 1991). At warm temperatures, gross photosynthesis is less sensitive to temperature than net photosynthesis, because dark respiration contributes to the decrease in net photosynthesis. One model of gross photosynthesis as a function of temperature follows a parabola shape for C\(_3\) plants, indicating a loss of about 5% of the maximum rate at a ±5 °C deviation from the optimal temperature (Spitters, van Keulen & van Kraalingen 1989; Jones & Luyten 1998, Verdoort, van Ranst & Ye 2004).

When the supply of carbohydrate from photosynthesis is greater than the demand for growth, the surplus could be stored as NSC, adding to total biomass but not to structural mass, or it may inhibit photosynthesis, largely preventing its own accumulation. We denote the difference between potential supply and potential demand of carbohydrate as \(\text{surplus}\), while \(\text{excess}\) refers to the actual accumulation of NSC. Surplus photosynthate may partially inhibit photosynthesis (Marcelis, Heuvelink & Goudriaan 1998). In a literature review, Stitt (1991) stated: ‘photosynthesis is inhibited when demand for photosynthetic… is decreased’. He referred to this as ‘sink regulation of photosynthesis’. The source/sink terminology is often associated with the carbohydrate-producing and absorbing organs (Dreccer, Grashoff & Rabbinge 1997), where leaves are source organs that differ from the sink organs, such as growing fruit. We consider the vegetative plant as a single organ for which the supply/demand terminology and associated flux of carbohydrate is essentially equivalent to the terms source-strength and sink-strength (Marcelis 1996; Marcelis et al. 1998).

We hypothesize that over a wide temperature range, growth is governed by the minimum of the supply of carbohydrate from photosynthesis, and the demand of carbohydrate to synthesize new tissue. We developed a model based on this hypothesis to predict the effect of temperature and light on vegetative plants growing exponentially under a constant environment, and applied it to published data sets for tomato, sunflower and wheat. These data cover a wide range of light and temperature that includes both supply- and demand-limited growth regimes.

Plants acclimate to new environments, such as a change in light, temperature or CO\(_2\) concentration. Acclimation changes some traits, such as the rate of specific leaf photosynthesis and leaf area ratio (LAR). The process of acclimation is dynamic, and can take days or weeks to complete. The time course of this transition could be modelled, if appropriate dynamic data were available. However, our objective is to predict growth of acclimated plants. The values we assign to some model parameters may differ for plants grown under different light or temperature conditions.

**MODEL DEVELOPMENT**

**Growth from carbohydrate balances**

All equations of the model refer to daily changes per unit structural dry matter (SDM). The starting point is a daily (dawn to dawn) carbohydrate balance in which each symbol is a rate or amount per 24 h, g g\(^{-1}\) [SDM] d\(^{-1}\) (see Appendix for variable definitions and units):

\[
\begin{align*}
\dot{p} - \dot{m} &= s + g + r + e + i.
\end{align*}
\]
where \( \hat{p} \) is daily potential gross photosynthesis, \( \hat{m} \) is maintenance respiration, \( s \) is structural growth, \( g \) is growth respiration, \( r \) is a required minimum NSC observed at dawn, \( i \) is inhibited photosynthesis. The hatted symbols are potential rates that can be calculated as functions of the environment alone. Un-hatted symbols represent actual rates. We further assume that \( g \) and \( r \) are proportional to \( s \), either actual or potential. The conversion coefficient \( \epsilon \) relates \( g \) and \( s \) and is assumed not to change due to acclimation.

\[
g = \frac{1 - \epsilon}{\epsilon} s. \tag{3}
\]

We assume a proportionality between \( r \) and \( s \) that varies according to light, \( L \),

\[
r = \frac{\phi(L)}{\epsilon} s. \tag{4}
\]

Therefore, from Eqns 2, 3 and 4, the potential demand for carbohydrate is defined as

\[
\hat{d} = \hat{s} + \hat{g} + \hat{r} = \frac{1 + \phi(L)}{\epsilon} \hat{s}. \tag{5}
\]

We define the potential supply of carbohydrate as

\[
\hat{\sigma} = \hat{p} - \hat{m}. \tag{6}
\]

If \( \hat{\sigma} - \hat{d} < 0 \), growth is considered supply-limited, while if \( \hat{\sigma} - \hat{d} > 0 \), growth is demand-limited. Therefore, a unified expression for structural growth would be

\[
s = \frac{\epsilon}{1 + \phi} \min\left\{ \hat{\sigma}, \hat{d} \right\} = \min\left\{ \frac{\epsilon}{1 + \phi} (\hat{p} - \hat{m}), \hat{s} \right\}. \tag{7}
\]

where the difference between \( s \) and \( \hat{s} \) should be noted. A similar minimum scheme was used to describe partitioning of carbohydrate to several competing sink organs (Marcelis et al. 1998; Heuvelink 1999). In general, the structural-growth Eqn 7 requires the specification of \( \hat{p}, \hat{m} \) and \( \hat{s} \) as functions of the environment (here temperature and light).

We assume that maintenance respiration is an exponential function of temperature:

\[
\hat{m}(T) = m_0 \exp(\theta T), \tag{8}
\]

where \( T \) is temperature and \( m_0 \) and \( \theta \) are constants. The demand for potential growth, \( \hat{s} \), is also formulated as an exponential function

\[
\hat{s}(T) = s_0 \exp(\zeta T), \tag{9}
\]

where \( s_0 \) and \( \zeta \) are constants, and \( \zeta \) may differ from \( \theta \).

NSC

We chose simple linear functions to predict required and excess NSC. The required reserve, \( r \), is assumed to be a fraction of \( s \) (Eqn 4) that varies with light, \( L \), in a linear fashion. Where \( \phi_0 \) and \( \zeta \) are constants

\[
\phi(L) = \phi_0 + \zeta L. \tag{10}
\]

In the demand-limited regime, inhibition of gross photosynthesis, \( i \), is required to balance potential surplus and actual excess carbohydrate. We assume that a constant fraction, \( \beta \), of the potential surplus carbohydrate is inhibited.

\[
i = \beta (\hat{\sigma} - \hat{d}) = \beta \left[ (\hat{p} - \hat{m}) - \frac{1 + \phi(L)}{\epsilon} \hat{s} \right]. \tag{11}
\]

And the remaining excess carbohydrate, \( e \), is given by

\[
e = (1 - \beta)(\hat{\sigma} - \hat{d}) = (1 - \beta) i / \beta. \tag{12}
\]

Estimating carbon input from photosynthesis

Growth rates are expressed per unit dry mass per day, while photosynthesis is expressed as moles carbon per unit leaf area per second. To distinguish between the two, we use different fonts: \( p \) to represent a specific rate on a daily basis, in g[NSC] g\(^{-1}\)[SDM] d\(^{-1}\); while \( p \) represents an instantaneous rate in \( \mu \)mol[C] m\(^{-2}\) s\(^{-1}\). The conversion from the one to the other requires the structural leaf area ratio \( \lambda \) in m\(^2\)[leaf] kg\(^{-1}\)[SDM], and a conversion constant, \( C \), from seconds to hours in the photoperiod, and from moles CO\(_2\) to 30 g mol\(^{-1}\) [CH\(_2\)O]:

\[
p(L, T) = C p(L, T) \lambda. \tag{13}
\]

Following the lead of others (Seginer et al. 1986; Dayan et al. 1993; Thornley & France 2007), we predict gross photosynthesis as a product of two independent functions for the light and temperature responses

\[
p(L, T) = h_l[L] \cdot h_r[T] = \left[ \frac{\alpha L}{\gamma + L} \right] \left[ 1 - \kappa(T - T_*)^2 \right]. \tag{14}
\]

where \( h_l[L] \) is an asymptotic function, with parameters \( \alpha \) and \( \gamma \) and \( h_r[T] \) is a concave parabola with a maximum at temperature \( T_* \).

Qualitative behaviour of the model

A schematic view of the model is presented in Fig. 1. The top solid curve is a parabola, describing potential gross photosynthesis \( \hat{p} \) as a function of temperature for a given light level, Eqns 13 and 14. The next curve is the carbohydrate supply \( \sigma = \hat{p} - \hat{m} \), obtained by subtracting maintenance respiration, Eqn 8. In the supply-limited range, to the right of the dotted exponential curve, the carbohydrate supply is divided in fixed proportions from top to bottom, between \( g, r \) and \( s \), respectively, according to Eqns 3 and 4. In the demand-limited range, on the left, maintenance and
growth respiration, $\dot{m}$ and $\dot{g}$, follow the same rules as before, while the surplus, $s = \dot{g} - \dot{r}$, is divided between $e$ and $i$, according to Eqns 11 and 12. In this example, most of the carbohydrate surplus is inhibited.

**Parameter estimation**

We estimated parameter values for the model by minimizing the sum of differences squared between observations and model predictions for the data ranges most sensitive to each parameter. Altogether, the proposed model has 12 independent parameters (Table 1). Parameters were varied in the following order. Parameters for $p$ in Eqn 14 were determined by a least squares fit to data from measurement of gross photosynthesis of leaves. The resulting temperature dependence was used in the model to predict growth. However, the light response parameters were usually adjusted to improve prediction of growth. LAR usually reported per g [TDM] was transformed to $\lambda$ by using model predictions for NSC. Maintenance respiration, $m_s$, and its temperature dependence, $\theta$, were determined from observations of dark respiration. The values of parameters related to growth metabolism, $s_i$ and $\zeta$, were determined by fitting growth data at temperatures cooler than 20 °C. The parameters $\phi_i$ and $\zeta_i$ to predict reserve carbohydrate, were varied to optimize the fit between observed and predicted NSC at temperatures warmer than 20 °C. The parameter $\beta$ was chosen to optimize the fit between observed and predicted NSC at cool temperatures.

**EXPERIMENTAL METHODS**

We describe the experiments that were the sources of the data used to estimate parameters of the model, and to test its validity for several plant species. Experiments to measure growth are described first, and then those to measure photosynthesis.

**Tomato growth under two light intensities and a range of temperatures**

Gent (1986) examined the response of tomato seedlings (Solanum lycopersicon L.) ‘Sonato’ (Deruiter Zonen, Netherlands) to a wide range of temperatures under controlled environment conditions. Light and temperature were controlled and carbon dioxide concentration was in the range of 40–45 Pa. The experiment consisted of two parts: The main part had 11 experimental cycles, each at a different temperature, ranging from 9 to 36 °C. Day and night temperatures were the same, except in three cases, where day temperature was 10 °C higher than night temperature. Following previous findings (Miller & Langhans 1985, Bakker & van Uffelen 1988), we used mean daily temperature to analyse these cases. There were two light intensities with a 12 h photoperiod, about 110 and about 370 μmol m$^{-2}$ s$^{-1}$ photosynthetically active radiation (PAR). The environment was imposed 5 to 18 d after germination, first harvest was 2 to 5 d later, and final harvests were at dusk and dawn, 3 to 11 days following the first harvest. Total dry mass was determined for all harvests, and leaf area in the final harvest only. The RGR was determined from initial and final harvests. NSC equal to starch plus soluble carbohydrate per gram TDM was determined for both harvests on the final day of the experiment (Gent 1986). In an auxiliary experiment, plants were grown at 23 °C for 18 d under the two light levels. Both dry mass and leaf area were measured three times a week.

**Other growth experiments**

Data for growth of sunflower seedlings (Helianthus annuus L.) ‘Pole Star’ came from a study of the light and temperature response during vegetative growth of four species (Rajan et al. 1973). Plants were grown for 14 d in a controlled environment under one of six temperatures from 10 to 35 °C by 5 °C intervals and one of five light levels from 10 to 54 kLux. The RGRs over the growth interval were reported in their fig. 11 (Rajan et al. 1973), and final LARs at the end of the growth interval in their fig. 7. We used their table 2 (Rajan et al. 1973) to convert temperature set points to actual leaf temperatures, and their fig. 1 to convert light intensity in units of lux to PAR in the range 400 to 700 nm. We assumed the initial LAR for each treatment was 21.5 m$^{-2}$[leaf] kg$^{-1}$[TDM], based on germination conditions of 25 °C and 170 μmol m$^{-2}$ s$^{-1}$ PAR, and used this to calculate the mean leaf area for the growth interval.

Growth data for wheat (Triticum aestivum L.) came from three publications (Gifford 1995; Hurry et al. 1995;
Leonardis et al. 2003). Winter wheat ‘Monopol’ plants were grown at 20/16 °C or 5/5 °C for a 16 h photoperiod under 250 μmol m⁻² s⁻¹ PAR irradiance and 37 Pa CO₂ (Leonardis et al. 2003). They reported data for non-acclimated plants at the 2nd leaf stage and acclimated plants at the 4th leaf stage, corresponding to 12 d, and then 25 d for warm-grown plants, or 75 d for cold-grown plants. Data for daily carbon balance in mg[Ç] g⁻¹[TDM] d⁻¹ were graphically interpolated from their fig. 1 (Leonardis et al. 2003), and converted to RGRs. Daily gross photosynthesis was corrected for daily respiration in the dark, assuming respiration per day was three times that measured for 8 h in the dark.

Winter wheat ‘Portal’ and spring wheat ‘Dragon’ plants were grown at 24/16 °C or 5/5 °C under 300 μmol m⁻² s⁻¹ PAR for a 17 h photoperiod (Hurry et al. 1995). Measurements were made on days 24 to 28 for warm-grown plants, or days 65 to 70 for cold-grown plants. We used RGRs and net assimilation rates reported in their fig. 1 (Hurry et al. 1995). LAR was determined from the ratio of net assimilation rate and RGR. Values for fructose, glucose and sucrose in mmol m⁻² leaf area reported in their fig. 6 (Hurry et al. 1995) were converted to g[hexose] g⁻¹[TDM] and summed to give NSC.

Spring wheat ‘Highbury’ was grown at 15, 20, 25 or 30 °C under 600 μmol m⁻² s⁻¹ irradiance and an assumed photoperiod of 16 h, and ambient CO₂ (Gifford 1995). RGRs and LARs were reported in his fig. 2 (Gifford 1995). These LARs were far less than in the other studies. We doubled the reported values to account for the photosynthetic activity of the sheath, in addition to that of the leaf blade.

**Photosynthesis measurements for tomato**

Photosynthesis was measured for tomato ‘Early Cascade’ (Johnny’s Select Seed, Winslow, ME, USA) plants grown for 60 d, until flowering but barely fruiting, in a greenhouse environment with 25/15 °C day/night temperature under sunlit conditions with average irradiance of 400–600 μmol m⁻² s⁻¹ PAR. Plants were measured in a laboratory where temperature was 25 °C and light level was approximately 10 μmol m⁻² s⁻¹ PAR. The terminal leaflet of the 5th expanded leaf from the apex was enclosed in a cuvette with controlled values for light and temperature, and a CO₂ concentration of 40 Pa. Gas exchange was measured using an LCpro portable photosynthesis system (ADC Bioscientific Ltd., Hoddeston, UK). The leaflet was exposed to the selected temperature for 10 min in the dark before any measurement was taken. Photosynthesis was then measured for 3 min at several light levels, starting in the dark (dark respiration) and stepping up to about 1500 μmol m⁻²[leaf] s⁻¹. The leaflet was given 1 to 2 min to adjust to each new light level. This sequence was repeated for four temperatures at 10 °C steps, and the whole procedure was repeated for eight different plants. Gross photosynthesis was determined from net photosynthesis by adding the respiration measured in the dark. The tomato cultivars used in the growth and photosynthesis experiments had similar photosynthetic characteristics. The photosynthetic parameters reported for ‘Sonato’ (Gent & Enoch 1983) gave a response to light and temperature that is similar to the response shown here for ‘Early Cascade’.

**Other photosynthesis measurements**

Two other datasets were used to determine the light and temperature response of photosynthesis of tomato. Sage & Sharkey (1987) reported the temperature response from 9 to 33 °C of tomato grown in the field. The plants were grown from May to September in Reno, NV in ambient temperatures that ranged from 4 to 37 °C. Ambient CO₂ was 31 Pa CO₂. Most days were cloud free with 80% of possible

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**Table 1. Values of the parameters of the model determined from minimizing the sum of squared deviations of measured and predicted values for the relevant data for each species**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Species</th>
<th>Tomato</th>
<th>Sunflower</th>
<th>Spring wheat</th>
<th>Winter wheat</th>
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<td>Gross photosynthesis</td>
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<tr>
<td>α</td>
<td>μmol[Ç] m⁻²[leaf] s⁻¹</td>
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<tr>
<td>γ</td>
<td>μmol m⁻²[leaf] s⁻¹</td>
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<td>201</td>
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PAR, photosynthetically active radiation; SDM, structural dry matter.
sunshine. Maximum irradiance would be approximately 1800 μmol m\(^{-2}\) s\(^{-1}\) PAR. Short-term measurements of individual leaves were made under light-saturating conditions. The data for net photosynthesis of tomato measured under 18 kPa O\(_2\) from their fig. 2 (Sage & Sharkey 1987) were converted to gross photosynthesis using the rates we measured for dark respiration.

Yamori et al. (2010) measured the response of net photosynthesis of individual tomato leaves at 5 °C intervals from 10 to 35 °C, under 1500 μmol m\(^{-2}\) s\(^{-1}\) irradiance. The plants were grown at either 30/25 °C or 15/10 °C day/night temperatures under 250 μmol m\(^{-2}\) s\(^{-1}\) PAR for an 8 h photoperiod. Net photosynthesis and dark respiration per unit area were reported in their supporting information fig. 1, panel D (Yamori et al. 2010). Data for net photosynthesis and dark respiration of both spring wheat and winter wheat grown under the same conditions were reported in their supporting information fig. 1, panels G and H, respectively (Yamori et al. 2010). Net photosynthesis was converted to gross photosynthesis using their rates of dark respiration.

Paul, Lawlor & Driscoll (1990) measured the temperature response of photosynthesis in sunflower cultivar ‘Asmer’ grown at either 13 or 30 °C under 400 μmol m\(^{-2}\) s\(^{-1}\) PAR for a 16 h photoperiod. Short-term measurements on recently expanded leaves were made at temperatures between 4 and 35 °C under 1000 μmol m\(^{-2}\) s\(^{-1}\) PAR. Net photosynthesis was graphically interpolated from their fig. 2a (Paul et al. 1990). Gross photosynthesis was determined by using values of dark respiration measured for sunflower at 25 °C (Szaniawski & Kielkiewicz 1982), and interpolating from 25 °C using a Q\(_{10}\) = 2. Concentrations of fructose, glucose and starch in mmol m\(^{-2}\), determined 1 h into the light period for plants grown at 13 and 30 °C and reported in their table 2 (Paul et al. 1990), were converted to g[NSC] g\(^{-1}\)[TDM] assuming an LAR of 20 g m\(^{-2}\).

**RESULTS**

**Model parameters for photosynthesis**

The temperature response of gross photosynthesis of tomato under saturating irradiance was compared after growth and acclimation under different light and temperature conditions (Fig. 2). The results differed among these studies primarily due to acclimation to light that changed leaf thickness and biochemistry. However, a single quadratic temperature response, independent of the light intensity to which the leaves were acclimated, Eqn 14, accounted for most of the variation in response to temperature of plants grown under this wide range of light intensities (Fig. 2). The parameters \(T_\text{a} = 25\) °C and \(\alpha = 0.0013\) °C\(^{-2}\) gave the best fit to all three datasets simultaneously. These parameters predicted most of the variation due to temperature, even for plants acclimated to 13 and 30 °C (Yamori et al. 2010). The observed temperature response differed to some extent under different light levels, but a more complicated model with an interaction of effects of light and temperature would be needed to account for this. For all except tomato, we do not have the data to define the parameters of a more complex model of photosynthesis.

To determine the rate of photosynthesis under the growth irradiances, we measured the light and temperature response for tomato grown at 400–600 μmol m\(^{-2}\) s\(^{-1}\) at various irradiances from 92 to 1472 μmol m\(^{-2}\) s\(^{-1}\) (Fig. 3). When the parameters of Eqn 14 were optimized to fit these data, the temperature response was the same as that for the combined data sets in Fig 2. The optimum parameters to describe the light response were \(\alpha = 24\) μmol[CO\(_2\)] m\(^{-2}\)[leaf] s\(^{-1}\), and \(\gamma = 309\) μmol PAR m\(^{-2}\)[leaf] s\(^{-1}\). The predicted values for net photosynthesis after correction for dark respiration are compared with the data in Fig. 3. The decrease at warm temperatures was greater for net compared with gross photosynthesis, and the temperature of maximum net photosynthesis increased under higher light intensity.

Data for the temperature response of photosynthesis in sunflower were only available at saturating light (Paul et al. 1990). The best fit of these data to Eqn 14 required \(T_\text{a} = 30\) °C, and \(\kappa = 0.0012\) °C\(^{-2}\), indicating a warmer optimum and less sensitivity to temperature in sunflower than in tomato (data not shown).

We used two datasets to determine the temperature response of photosynthesis in wheat; measurements at saturating light over a range of temperatures (Yamori et al. 2010) and under the low irradiance of a growth experiment at cool and warm temperature (Leonardis et al. 2003) (data not shown). The optimum parameters to predict gross photosynthesis showed that wheat was relatively sensitive to
temperature, $\kappa = 0.0015 \, ^\circ\text{C}^{-2}$, and the optimum temperature was relatively low, $T^* = 24 \, ^\circ\text{C}$.

### Predicting growth and carbohydrate of tomato

Tomato seedlings exposed to a constant, or daily periodic, environment grew at a constant RGR, while maintaining roughly constant organ proportions and chemical composition (Gent 1986). The growth over 18 d was close to exponential, as shown by the straight lines in Fig. 4. While biomass and leaf area grew at the same relative rate under high light, the leaf area grew faster than biomass under low light, which resulted in thinner leaves over the course of the experiment. This indicated a gradual acclimation of LAR over the course of the growth. We found that the average of the LAR at the beginning and end of the growth period predicted growth better than the final LAR. The initial condition for all plants was 25 °C and low light. There was an increase in LAR as plants grew, because root and stem weight accounted for a greater fraction of total weight for the youngest plants. This increase was less for plant grown under high compared with low irradiance. Because of this gradual change in LAR, using the average LAR was appropriate.

Figure 5 summarizes the rates of growth and NSC observed for tomato grown under two irradiances and a range of temperatures. The symbols represent data obtained from Gent (1986). The temperature responses of growth rate and NSC at dawn both appear to change around 20 °C. This suggests two distinct growth regimes.
The model used the parameters defined by measuring photosynthesis (Fig. 3) along with measured values of temperature, light intensity and $\lambda$ in Eqns 13 and 14 to predict the supply of carbohydrate. Then parameters governing demand were varied to minimize the sum of squared deviations between observed and predicted values for growth. Growth at cool temperatures was predicted best with $s_1 = 0.03 \text{g}[\text{SDM}] \text{g}^{-1}[\text{SDM}] \text{d}^{-1}$ and $\xi = 0.110 \text{°C}^{-1}$. The exponential temperature response was equivalent to $Q_{10} = 3$. The model accounted for 0.72 of the variance in RGR. The smooth curves representing model predictions in Fig. 5 were created using values for $\lambda$ and irradiance that were averaged over all experiments under each of the two light levels. Qualitatively speaking, the model predicted that growth was similar under high and low light conditions at temperatures cooler than 20°, and then split, with faster growth under higher irradiance at warmer temperatures.

This dataset for tomato was complete in terms of variation of NSC with light and temperature. The ratio NSC/SDM was about 0.2 at the coolest temperature of 9 °C, and fell to about 0.05 above 20 °C, when the model predicted that growth was limited by carbohydrate availability. The parameters needed to predict this required reserve, $r$, were $\phi_b = 0.015 \text{g}[\text{NSC}] \text{g}^{-1}[\text{SDM}]$ in the dark, and $\xi = 0.00017 \text{g}[\text{NSC}] \text{g}^{-1}[\text{SDM}] \text{mol}^{-1} \text{m}^2 \text{s}^{-1}$ PAR. This required reserve was greater for plants grown under high compared with low irradiance (Fig. 5). Plants accumulated more NSC at cool temperatures. However, to prevent more accumulation of NSC than was observed, a substantial inhibition of photosynthesis was required: $\beta = 0.88$ of the potential surplus carbohydrate. Using these refinements, the model accounted for 0.63 of the variance in NSC. The optimum values for all model parameters are summarized in Table 1.

Once the parameters of the model describing growth and NSC were optimized, as described previously, the coefficients describing photosynthesis were varied again to optimize the fit of the model to growth and NSC (results not shown). The optimum values for the parameters describing the light response of photosynthesis derived from this procedure were $\alpha = 22.7 \text{mol m}^{-2} \text{s}^{-1}$ and $\gamma = 229 \text{mol m}^{-2} \text{s}^{-1}$. The temperature response parameters did not change. This second optimization increased slightly the fraction of the variance accounted for by the model for growth, 0.78 compared with 0.72, and for NSC, 0.70 compared with 0.63.

Predicting growth and carbohydrate of sunflower

The model was applied to predict growth of sunflower under a wide range of light intensities (Rajan et al. 1973) using the model parameters for growth demand and carbohydrate suitable for tomato. When the parameters for the light response of photosynthesis of sunflower were optimized to minimize the squared deviations between the observed and predicted growth, the model accounted for 0.90 of the variance in growth rates. Figure 6 compares measured growth rates to those predicted by the model. The smooth curves for each light level were created using values of $\lambda$ and irradiance that were averaged over all experiments under each light level. The major difference in growth due to light was between the lowest three light levels of 85, 170 and 250 $\text{mol m}^{-2} \text{s}^{-1}$ PAR. Higher light intensities did not further enhance growth. These data showed growth was limited by demand at temperatures cooler than 16° and irradiance above 100 $\text{mol m}^{-2} \text{s}^{-1}$. Carbohydrate supply from photosynthesis was more limiting than demand for growth metabolism only at the lowest light of 85 $\text{mol m}^{-2} \text{s}^{-1}$.

The limited data for NSC of sunflower at dawn (Paul et al. 1990) were 0.26 and 0.07 $\text{g}[\text{NSC}] \text{g}^{-1}[\text{SDM}]$ when plants were grown at 13 or 30 °C and sampled 1 h into the photoperiod. The model predicted values of 0.20 and 0.12 for these conditions, using the growth demand parameters suitable for tomato. A relatively high inhibition of photosynthesis, $\beta = 0.88$, moderated the accumulation of NSC at cool temperatures. It was not necessary to change any of the parameters related to growth demand and NSC when applying the model to tomato or sunflower (Table 1).

Predicting growth and carbohydrate of wheat

Data for growth of winter and spring wheat were available at specific cool and warm temperatures, but not over as wide a range of light and temperatures as for sunflower. Table 2 compares the observed values and predictions of the model, after the parameters were optimized for growth of wheat (see Table 1). These predictions used LAR...
measured at the end of the growth interval. It was assumed this LAR was appropriate for the duration of growth, as these plants were acclimated for 12 d or more before measurement. The optimum light response coefficients of photosynthesis to predict growth were $\alpha = 25.1 \mu$mol[C] m$^{-2}$ s$^{-1}$ and $\gamma = 306 \mu$mol m$^{-2}$ s$^{-1}$ PAR. The response of growth demand to temperature was less for wheat than for the other two species, $\zeta = 0.088$ compared with 0.110 °C$^{-1}$. With these parameters, the model predicted 0.67 of the variance in RGR of three experiments, which when combined included a wide range of light and temperatures.

Winter wheat accumulates a remarkable fraction of NSC at cool temperatures, while spring wheat does not (Hurry et al. 1995). Spring wheat has a higher LAR than winter wheat when grown at cool temperatures, so the model predicted more photosynthesis per unit mass, and more NSC in spring than in winter wheat, all other parameters being similar. We derived the parameter $\lambda$, which converts photosynthesis per unit area to per unit SDM, from the reported LAR by correcting for NSC predicted by the model. Using a high NSC adjusted $\lambda$ sufficiently to predict the RGR and NSC that were observed. This adjustment from LAR to $\lambda$ was greater than two-fold for winter wheat at 5 °C (Table 2). The inhibition of photosynthesis by NSC in winter wheat had to be low, $\beta = 0.2$, to allow accumulation of excess NSC. We assumed that photosynthetic inhibition of spring wheat was similar to that in other species, $\beta = 0.88$. Thus, the model could predict high NSC in winter wheat, but the predictions were ambiguous, because they depended on a high initial value of NSC to calculate $\lambda$ from LAR. The lack of inhibition of photosynthesis by NSC in winter wheat seems to be a critical difference, compared with spring wheat.

### DISCUSSION

#### Inhibition of photosynthesis

The central focus of this model is the calculation of the surplus or deficit of carbohydrate supply on a daily basis with respect to the demand of growth metabolism. Without refinement, such a model would predict a large fraction of NSC at cool temperatures, and no NSC at warm temperatures. Comparing the model predictions to observations showed that feedback inhibition of photosynthesis was important at cool temperatures, and some NSC was retained at warm temperatures. Only a small fraction of the potential surplus photosynthesis predicted from the model was observed as excess NSC at cool temperatures (Fig. 1). The rest was suppressed via inhibition of photosynthesis. Other studies support such an inhibition. Insensitivity to $O_2$ is an indication of feedback inhibition of photosynthesis, and field-grown tomato showed $O_2$ insensitivity up to 20 °C, but not at higher temperatures (Sage & Sharkey 1987). If all except one source leaf was shaded, tissue sucrose declined and photosynthesis increased by 57% in sugarcane, a species with high NSC (McCormick, Kramer & Watt 2008). Elevated CO2 stimulated photosynthesis of $C_3$ plants in the short term, but there was less response over the long term, due to accumulation of excess carbohydrate (Stitt 1991).

The parameter value for inhibition of photosynthesis, $\beta$, depends on the definition of excess carbohydrate, $e$. A required reserve, $r$, was needed to predict the NSC observed at warm temperatures. However, we cannot distinguish experimentally between reserve and excess NSC at cool temperatures. If the reserve is not required, then a smaller value of $\beta$ would predict the observed $e$ at cool temperatures. We also assume that $r$ does not inhibit photosynthesis.

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**Table 2.** Model predictions compared with measured relative growth rate (RGR) and non-structural carbohydrate (NSC) of wheat grown under various light levels and temperatures

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Leaf area ratio</th>
<th>RGR</th>
<th>NSC</th>
<th>Measure</th>
<th>Predict</th>
<th>Measure</th>
<th>Predict</th>
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<tr>
<td>Temperature</td>
<td>Light</td>
<td>μmol m$^{-2}$ s$^{-1}$</td>
<td>TDM</td>
<td>SDM</td>
<td>g g$^{-1}$ d$^{-1}$</td>
<td>g [NSC] g$^{-1}$ [SDM]</td>
<td>g [NSC] g$^{-1}$ [SDM]</td>
</tr>
<tr>
<td>Day/Night °C</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
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<td>250</td>
<td>16.9</td>
<td>18.4</td>
<td>0.13</td>
<td>0.10</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>5/5</td>
<td>250</td>
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<td>14.6</td>
<td>0.09</td>
<td>0.04</td>
<td>0.14</td>
</tr>
<tr>
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<td>250</td>
<td>16.6</td>
<td>18.0</td>
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<td>0.10</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>5/5</td>
<td>250</td>
<td>8.9</td>
<td>9.7</td>
<td>0.06</td>
<td>0.02</td>
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<td>Hurry et al. (1995)</td>
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<tr>
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<td>0.13</td>
<td>0.15</td>
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<td>0.49</td>
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<td></td>
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<td>0.16</td>
<td>0.17</td>
<td>0.16</td>
<td>0.17</td>
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</table>

Leaf area ratio on a total dry matter (TDM) basis, converted to $\lambda$ on structural dry matter (SDM) basis, using predicted NSC.
while e does do so. If photosynthesis inhibition were sensitive to r, and r proportional to light, a high value for \( \beta \) would greatly reduce the difference in photosynthesis among light levels at warm temperatures. A value \( \beta < 0.6 \) would be required in order to predict the differences in growth observed for tomato under two light levels.

We did not include a light \( \times \) temperature interaction to predict gross photosynthesis in Eqn 14. Datasets to determine the parameters of this interaction were not available, except for tomato. In fact, photosynthesis is limited more by cold temperature under high light or CO\(_2\) than under low light or CO\(_2\) (Bunce 2000). This interaction is due to the complexity of the biochemistry of photosynthesis. For tomato grown at 30/25 °C, carboxylation rate limited photosynthesis through most of the temperature range from 10 to 35 °C except at very low temperatures, while for plants grown at 15/10 °C there was a combination of limitations due to carboxylation and Rubisco regeneration (Yamori et al. 2010). Our simplifications in the model overestimate photosynthesis at high light and low temperature, and result in a large excess NSC, unless \( \beta = 0.88 \). To some extent, the degrees of freedom in the model represented by the parameters used to predict e and r compensate for some deficiencies in the prediction of photosynthesis.

**Normalizing photosynthesis to predict growth**

Specific photosynthesis varies with acclimation to light, as shown in Fig. 2. It also varies with acclimation to temperature (Paul et al. 1990; Yamori et al. 2010). How can specific photosynthesis be normalized to predict growth under various light and temperature conditions? Acclimation to temperatures of 15/10 or 30/25 °C affected neither photosynthesis per unit mass nor nitrogen content per unit mass, but it did affect photosynthetic nitrogen use efficiency (Yamori et al. 2009). Many C\(_3\) species acclimated to light by adjusting LAR, so the light-saturated rate of photosynthesis per unit leaf mass was not affected by growth irradiance (Evans & Poorter 2001). We found the final values of \( \lambda \) measured for tomato, averaged over all temperatures, were 46.0 and 27.4 m\(^2\)[leaf] kg\(^{-1}\)[SDM], under 110 and 370 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) PAR, respectively. These values would diminish the predicted differences in photosynthesis and growth per unit biomass. The gradual change in LAR, shown over the time course of Fig. 4, would eventually eliminate any difference in photosynthesis per unit mass. Thus, the rate of photosynthesis per unit mass, scaled for LAR, appears to be most appropriate to predict carbohydrate supply for plants acclimated to a wide range of light and temperature.

**Temperature dependence of growth metabolism**

The temperature response of carbohydrate demand in our model does not reflect that observed in short-term studies of dark respiration of plants as a function of temperature, namely \( Q_{10} = 2 \). The optimum for the model was equivalent to \( Q_{10} = 3 \), and various studies of plant growth under relatively low temperatures are compatible with this response (Scaife 1973; Kemp & Blacklow 1980). Scanning calorimeter studies of tomato cell cultures implied an exponential response of metabolism with \( Q_{10} = 2.8 \) (Hansen et al. 1994). The short-term temperature response of dark respiration had \( Q_{10} = 2 \), for various plant species grown and acclimated either at 15/10 or 30/25 °C (Yamori et al. 2010). However, at any given temperature, respiration was two to three times faster for plants acclimated to the cool compared with the warm temperature. Thus, the temperature response of metabolism leading to growth is not simply related to the temperature response of short-term measurements of dark respiration.

**Validity of the model**

That our model fits the data is no proof that it is a correct representation of reality. Several physiological arguments support the supply–demand hypothesis, which is the basis for our model. However, the tomato growth data were fitted to a simple polynomial function of light and temperature (Gent 1986, Fig. 1) as well as by the model developed here. Equation 7 is reminiscent of Liebig’s law of the minimum (Berck & Helfand 1990; Frank, Beattie & Embleton 1990) that states one influencing factor cannot substitute for the insufficiency of another. If substitution is possible between factors, a product scheme is sometimes used (Paris 1992), which in the present context may be written as

\[
s \propto \sigma \cdot \delta. \tag{15}\]

The product scheme was used to predict growth by multiplying NSC, representing supply, and respiration rate, representing demand (Gent & Enoch 1983; Gent 1986). Fleisher & Timlin (2006) used a similar scheme to model leaf expansion. Both Eqns 7 and 15 result in an overall concave downwards relationship. If \( \sigma (T) \) and \( \delta (T) \) are descending and ascending linear functions of temperature, the minimum scheme predicts the response of \( s (T) \) is shaped as a triangle, and the product scheme predicts a concave downwards parabola. The choice of different models by Seginer, Gary & Tchamitchian (1994) and by Gent (1986) resulted in predictions (their fig. 7 and fig. 1, respectively) reminiscent of these two basic shapes. More comprehensive datasets would be required to choose between the minimum scheme and the product scheme, because it would require distinguishing between linear and non-linear responses.

**Possible model extensions**

The model could be extended beyond light and temperature as growth limiting factors. Consider nitrogen supplied to plants at a rate which is less than the demand for that nutrient at the optimal temperature for growth (Ingestad & Ågren 1988). The factors limiting growth would then be metabolism or respiration at low temperatures, nutrient supply around the optimal temperature,
and photosynthesis at high temperatures. Such a model would require a variable to represent the nutrient, in addition to the variables describing structural and non-structural material (Seginer 2004). The composition of the plants is likely to acclimate to the different environmental conditions. If carbohydrate replaced nitrate as an osmotic solute in the cell sap of nitrate-accumulating plants, nitrate content would be low at cool temperatures, where there is excess carbohydrate, and high at warm temperatures (Seginer 2003).

Our model partitions carbon into structure with a daily time step, based on the supply and demand of carbohydrate for the entire day. A dynamic version of the model could mimic the variation of carbohydrate over the diurnal cycle, and the effect of this variation on growth (Gent & Enoch 1983; Seginer et al. 1994). One requirement for modelling the diurnal variation in growth is conservation of some carbohydrate until dawn. This could be achieved by setting growth proportional to available carbohydrate. Plants can modulate metabolism based on carbohydrate content. When bean or tomato plants grown in the light were exposed to a prolonged period of darkness, dark respiration remained rapid for a certain period, before declining when carbohydrate was depleted (Breeze & Elston 1978; Gary et al. 2003). Photosynthesis inhibition may vary within a day, due to variation in NSC.

CONCLUSION

The range of traditional growth models was extended by considering both the supply and demand of carbohydrate. We assumed the following in a daily-step model of vegetative growth:

1 Seedlings are acclimated to repetitive daily environmental cycles.
2 Plant growth is limited by either the supply of carbohydrate via photosynthesis, or by the demand of carbohydrate for biosynthesis leading to growth.
3 The temperature response of gross photosynthesis is parabolic with a maximum within the temperature range of acclimation, while the temperature response of growth demand increases exponentially.
4 Thus, carbohydrate supply is limiting at warm temperature, while demand is limiting at cool temperature.
5 The excess NSC that accumulates under cool temperature partially inhibits photosynthesis. This model predicted that the response of growth to increasing temperature is convex at cool temperatures and concave at warm temperatures, and that growth is only sensitive to light at warm temperatures.

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REFERENCES


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**APPENDIX**

### Notation

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<tr>
<th>Symbol</th>
<th>Meaning</th>
<th>Units</th>
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<tr>
<td>(C)</td>
<td>conversion constant</td>
<td>g[CHO] g[SDM] (\cdot) [TDM] (\cdot) d (\cdot) (\mu)mol (\cdot) [C]</td>
</tr>
<tr>
<td>(e)</td>
<td>daily growth of excess carbohydrate</td>
<td>g[CHO] g[SDM] (\cdot) d (\cdot) (\mu)mol</td>
</tr>
<tr>
<td>(g)</td>
<td>daily growth – respiration</td>
<td>g[CHO] g[SDM] (\cdot) d (\cdot) (\mu)mol</td>
</tr>
<tr>
<td>(h_L)</td>
<td>response to light of gross photosynthesis</td>
<td>(\mu)mol[C] m (\cdot) [leaf] s (\cdot)</td>
</tr>
<tr>
<td>(h_T)</td>
<td>response to temperature of gross photosynthesis</td>
<td>(\mu)mol m (\cdot) [leaf] s (\cdot)</td>
</tr>
<tr>
<td>(i)</td>
<td>daily photosynthesis inhibition</td>
<td>g[CHO] g[SDM] (\cdot) d (\cdot)</td>
</tr>
<tr>
<td>(L)</td>
<td>light flux above canopy</td>
<td>g[CHO] g[SDM] (\cdot)</td>
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<tr>
<td>(m)</td>
<td>daily maintenance-respiration</td>
<td>g[CHO] g[SDM] (\cdot)</td>
</tr>
<tr>
<td>(m_0)</td>
<td>m at (T = 0^\circ C)</td>
<td>g[CHO] g[SDM] (\cdot)</td>
</tr>
<tr>
<td>(p)</td>
<td>short-term gross photosynthesis</td>
<td>g[CHO] g[SDM] (\cdot)</td>
</tr>
<tr>
<td>(P)</td>
<td>daily gross photosynthesis</td>
<td>g[CHO] g[SDM] (\cdot)</td>
</tr>
<tr>
<td>(Q_{10})</td>
<td>factor of growth-rate-increase over 10 (^\circ C)</td>
<td>g[CHO] g[SDM] (\cdot)</td>
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<td>(r)</td>
<td>daily growth of non-structural reserve</td>
<td>g[CHO] g[SDM] (\cdot)</td>
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<td>(s)</td>
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<tr>
<td>(T)</td>
<td>air temperature</td>
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<td>inhibited fraction of surplus carbohydrate</td>
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<td>coefficient in (h_L[T])</td>
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</tr>
<tr>
<td>(\varepsilon)</td>
<td>conversion efficiency from photosynthate to structure</td>
<td>(\mu)mol m (\cdot) [leaf] s (\cdot)</td>
</tr>
<tr>
<td>(\zeta)</td>
<td>temperature coefficient in the demand function</td>
<td>(\mu)mol m (\cdot) [leaf] s (\cdot)</td>
</tr>
<tr>
<td>(\theta)</td>
<td>temperature coefficient in the dark respiration function</td>
<td>(\mu)mol m (\cdot) [leaf] s (\cdot)</td>
</tr>
<tr>
<td>(\kappa)</td>
<td>temperature coefficient in (h_T[T])</td>
<td>(\mu)mol m (\cdot) [leaf] s (\cdot)</td>
</tr>
<tr>
<td>(\lambda)</td>
<td>‘structural’ leaf area ratio (LAR)</td>
<td>m (\cdot) [leaf] kg (\cdot) [SDM]</td>
</tr>
<tr>
<td>(\xi)</td>
<td>light coefficient in (\phi[L])</td>
<td>g[CHO] m (\cdot) [leaf] s g (\cdot) [SDM] (\mu)mol (\cdot) PAR</td>
</tr>
<tr>
<td>(\sigma)</td>
<td>daily supply of carbohydrate</td>
<td>g[CHO] g[SDM] (\cdot)</td>
</tr>
<tr>
<td>(\phi)</td>
<td>ratio of non-structural reserve to structural matter</td>
<td>g[CHO] g[SDM] (\cdot)</td>
</tr>
<tr>
<td>(\phi_0)</td>
<td>ratio (\phi[L]) for (L = 0)</td>
<td>g[CHO] g[SDM] (\cdot)</td>
</tr>
</tbody>
</table>

### Superscripts

- \(^{\wedge}\) potential rate

### Acronyms

- **CHO** carbohydrate at 30 g mol \(\cdot\) C
- **LAR** leaf area ratio
- **NSC** non-structural carbohydrate
- **PAR** photosynthetically active radiation
- **RGR** relative growth rate
- **SDM** structural dry matter (biomass)
- **TDM** total dry matter (biomass)

### Other symbols

[] Enclose arguments of a function