



# Short and long term vegetative growth response to temperature, interpreted by the dynamics of a carbohydrate storage

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## ABSTRACT

Growth models are an important element of rational crop management. In an attempt to produce a model suitable for greenhouse environmental-control, we further develop an available model with variable storage of non-structural carbohydrate (NSC). The model considers the supply and demand of carbohydrate and can simulate the daily storage cycle as well as long term transient acclimation processes. Model predictions agree qualitatively rather well with whole-plant experimental correlations between NSC content and growth, and with measured growth as a function of temperature. The model also mimics successfully both the short- and the long-term effects of temperature on respiration. This is achieved by expressing growth respiration as a product of (1) a function of the NSC content (representing the long-term effect of temperature), and (2) a function of the current temperature (representing the short-term effect). The use of the model as a control tool by the grower is outlined.

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## 1. Introduction

Models of crop growth are an essential element of rational crop management in general and of greenhouse environmental control in particular. Traditional crop models integrate gross-photosynthesis and maintenance-respiration over the daily cycle, and use these integrals to calculate the daily growth. A common scheme of the daily calculations (Spitters et al., 1989, page 147; Seginer et al., 1991, Equation 6; Dayan et al., 1993, Eq. 13) is

$$W = \varepsilon(P - M), \quad (1)$$

where  $W$  is daily growth,  $P$  is daily gross photosynthesis,  $M$  is daily maintenance-respiration, and  $\varepsilon$  is the conversion efficiency from carbon in photosynthate (mostly carbohydrate) to carbon in structure (protein, lignin etc.; Penning de Vries et al., 1974). Equation (1) is commonly expressed in  $\text{g[DM]}/(\text{m}^2[\text{ground}]\text{d})$  or in  $\text{g[DM]}/(\text{g[DM]d})$ , where DM is acronym for dry matter, the former

indicating ‘absolute’ dry matter growth and the latter – ‘relative’ growth.

Alternatively, Eq. (1) may be written as a carbon balance

$$P = M + G + W, \quad (2)$$

where  $G$  is daily growth-respiration. This follows a long-standing modeling paradigm which divides total (dark) respiration into two components: maintenance and growth (Amthor, 2000; Cannell and Thornley, 2000). Elimination of  $P - M$  between Eqs. (1) and (2) shows that  $G$  and  $W$  are proportional to each other (Amthor, 1989, Eq. 2.10; Bertin and Gary, 1993):

$$G = \left( \frac{\varepsilon}{1 - \varepsilon} \right) W. \quad (3)$$

Note that in this traditional growth model all the supply of carbohydrate is utilized on the same day, so that an explicit storage compartment is not required.

Equation (1) is appropriate for cases where the supply of carbohydrate by photosynthesis is the growth-limiting factor. It is not appropriate, however, for situations where the limiting factor is the demand (requirement) of the plants for carbohydrate, for instance when metabolism (processing rate) is slow due to cool temperature. In that case the daily surplus of carbohydrate must be stored in some storage compartment.

The amount of carbohydrate in storage varies not only from day to day, but also along each day, typically reaching a maximum in the late afternoon and a minimum in the early morning

Abbreviations: DAS, days after sowing; DM, dry matter; NSC, non-structural carbohydrate; PAR, photosynthetically active radiation; RGR, relative (specific) growth rate; SGT, Seginer–Gary–Tchamitchian 1994 model; TDM, total dry matter, structural and non-structural.

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## Nomenclature

### List of symbols

Most rates are given in both 'absolute' (per ground area) or 'relative' (per total dry matter) terms.

Curly brackets, {}, are used exclusively for arguments of functions. Square brackets are used for unit descriptors.

$a$	intercept of $\hat{m}$ , $g[DM]/(m^2[ground]s)$ or $g[DM]/(g[TDM]s)$
$b$	slope of $\hat{m}$ on $T$ , $g[DM]/(m^2[ground]sK)$ or $(g[DM]/g[TDM])/(sK)$
$C$	NSC content, $g[DM]/m^2[ground]$ or $g[DM]/g[TDM]$
$c$	rate of change of $C$ , $g[DM]/(m^2[ground]s)$ or $g[DM]/(g[TDM]s)$
$G$	daily growth respiration, $g[DM]/(m^2[ground]d)$ or $g[DM]/(g[TDM]d)$
$g$	growth respiration rate, $g[DM]/(m^2[ground]s)$ or $g[DM]/(g[TDM]s)$
$L$	light flux, $mol[PAR]/(m^2[ground]s)$
$M$	daily maintenance respiration, $g[DM]/(m^2[ground]d)$ or $g[DM]/(g[TDM]d)$
$m$	maintenance respiration rate, $g[DM]/(m^2[ground]s)$ or $g[DM]/(g[TDM]s)$
$P$	daily gross photosynthesis, $g[DM]/(m^2[ground]d)$ or $g[DM]/(g[TDM]d)$
$p$	gross photosynthesis rate, $g[DM]/(m^2[ground]s)$ or $g[DM]/(g[TDM]s)$
$Q_{10}$	temperature quotient: ratio of reaction rates at 10 K difference dimensionless
$S$	structural material, $g[DM]/m^2[ground]$ or $g[DM]/g[TDM]$
$s$	structural growth rate, $g[DM]/(m^2[ground]s)$ or $g[DM]/(g[TDM]s)$
$T$	temperature, K, °C
$t$	time, period, s, d, h
$W$	daily growth, $g[DM]/(m^2[ground]d)$ or $g[DM]/(g[TDM]d)$
$\gamma$	$\equiv \varepsilon/(1 - \varepsilon)$ dimensionless
$\varepsilon$	carbon (growth) conversion efficiency dimensionless
$\theta$	potential ratio of growth to maintenance respiration dimensionless
$\pi$	photosynthesis response to $C$ dimensionless
$\rho$	growth-respiration response to $C$ dimensionless
$\tau$	time as fraction of 24 h day s/d dimensionless

### Subscripts

$A$	acclimation (growth)
$c$	critical value
$D$	dark period (night)
$d$	processing (depletion) period
$E$	short exposure
$e$	NSC reserve
$g$	growth respiration
$i$	intercept
$L$	light period ('day')
$p$	photosynthesis
$r$	at end of dark period ('sunrise')
$s$	at end of light period ('sunset')
$x$	maximum value
$H$	high light level
$L$	low light level

### Superscripts

$\hat{\phantom{x}}$	'potential' value (function of environment)
*	first approximation

(Madsen, 1968, Fig. 1; Gent, 1986, Fig. 4; Stutte et al., 1996, Fig. 3; de Groot et al., 2001, Fig. 5; Huanosto-Magaña et al., 2009, Fig. 2). Modeling this diurnal variation, as well as long-term transient processes, such as acclimation, requires the introduction of a variable carbohydrate storage,  $C$ . A simple model of this kind (Seginer et al., 1994) was originally used to predict growth of greenhouse tomato for a range of temperatures, and more recently (Seginer and Gent, 2012), also to predict the accumulation of non-structural carbohydrate (NSC) when the temperature, and hence the demand, are low. In that simple dynamic model, photosynthesis is inhibited abruptly when the carbohydrate storage reaches its capacity,  $C_x$ , and growth stops abruptly when the storage becomes empty. This paper presents and discusses several cases where the simple 'abrupt' dynamic model makes predictions which are qualitatively in agreement with available experimental data, and extends the model to cases where photosynthesis and respiration are affected more gradually by the NSC content.

Many different terms are used to describe the stored substance (photosynthate, carbohydrate, non-structural-carbohydrate, carbon,  $C$ , substrate) and the storage compartment (buffer, pool, storage, reserve, content). We refer to the compartment as 'storage', to the stored substance as 'non-structural-carbohydrate' (NSC), and to the current amount as 'content'. Thus, 'the current NSC content of the storage is  $C$ '.

## 2. A dynamic carbon-balance model

A minimal dynamic vegetative growth model considers the carbon balance of the plant as a whole, and has just two state variables (two compartments): structural biomass (phytomass),  $S$ , and NSC biomass (mostly starch and sugar),  $C$ . The model of Seginer et al. (1994), hence referred to as the SGT model, is an example of such a model, where, typically,  $S$  increases monotonically with time, while  $C$  exhibits diurnal fluctuations. The rates of photosynthesis and respiration are assumed to change abruptly when the NSC trajectory attaches to or detaches from the bounds of the storage ( $C=0$  and  $C=C_x$ ), while in between the bounds the rates are independent of  $C$ .

### 2.1. Potential rates

The two dynamic equations of the SGT model (with some notational differences) are

$$\frac{dS}{dt} \equiv s \quad (4)$$

and

$$\frac{dC}{dt} \equiv c = p - m - g - s \quad (5)$$

where  $s$  is structural growth rate,  $c$  is the rate of change of NSC storage,  $p$  is gross photosynthesis rate,  $m$  is maintenance respiration rate, and  $g$  is growth respiration rate. Assuming that  $s$  and  $g$  are proportional,

$$g = \left( \frac{1 - \varepsilon}{\varepsilon} \right) s \quad (6)$$

(as for the daily integrals in Eq. (3)), only three of the four fluxes on the right of Eq. (5) need to be further formulated. The model assumes that for a crop of a given size, when the NSC content is

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