An eco-physiological model for interspecific competition, applied to the influence of Chenopodium album L. on sugar beet. I. Model description and parameterization

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Received 13 August 1991
Revised version accepted 31 March 1992

Summary: Resume: Zusammenfassung

An eco-physiological simulation model is presented in which competition between crop and weeds is simulated. The procedure is based upon the underlying physiological processes of distribution of the resources light and water over the species and the manner in which the species utilize the amounts taken up for dry matter production. On the basis of the leaf area of the competing species and its distribution over the height of the canopy, the absorbed radiation in relationship to plant height is calculated. Using the CO$_2$ assimilation light response of individual leaves, the profile of CO$_2$ assimilation in the canopy is calculated. The daily rate of CO$_2$ assimilation of the species is obtained by integration over height and daylight period after subtraction of losses for maintenance and growth. Effects of drought are taken into account by a simple water balance in which the available amounts of soil moisture during the growing season are monitored. Soil moisture is allocated to the competing species, in proportion to their demands. The model was parameterized for the crop sugar beet (Beta vulgaris L.) and Chenopodium album L. These parameter values were partly derived from literature data and partly from our own experimental data obtained from monocultures. In a subsequent paper (Kropff et al., 1992), evaluation of the model with experimental data will be presented as well as an evaluation of important species characteristics and strategies for weed control.

†Deceased.
most of these models have a static character: they describe the outcome of competition at a single time with some regression equation. In studies on crop weed interactions these models generally relate yield loss of the crop to weed density (cousens, 1985; spitters et al., 1989b). Such regression models provide a simple and precise description of the competition effects in a particular experiment in which only weed density is varied. However, regression coefficients may vary strongly among experiments due to factors other than weed density, e.g. the relative time of weed emergence (håkansson, 1983; cousens et al., 1987). Another disadvantage of these models is that they do not give insight into the competition process per se. Analysis of the causes of variation in coefficients is, therefore, only possible by performing laborious and expensive empirical studies.

Competition can be defined as the growth reduction of a plant brought about by the capturing of growth-limiting resources by its neighbours. These resources can be light, water and nutrients. This indicates that competition is a dynamic process that can be understood on the basis of the distribution of the limiting resources between the competing species and the efficiency with which each species uses the amounts taken up. Such a mechanistic approach may provide insight into the processes underlying competition effects observed in field experiments, and may aid manipulation of competitive relationships, such as those between crop and weeds.

In this study, a mechanistic model for cropweed competition (spitters & aerts, 1983; kropff et al., 1984; kropff 1988a) was further developed and used to analyse competition between sugar beet (beta vulgaris L.) and Chenopodium album L. the major improvements are the simulation of canopy photosynthesis, seasonal leaf area dynamics, transpiration, evaporation and the water balance of the soil. The model (programmed in a structured way in FORTRAN) and its list of variables is available upon request. Preliminary summarized results were presented by kropff (1988a, b, c). This paper gives a detailed description of the principles of the model, the mathematics underlying it, and its parameterization. In a subsequent paper (kropff et al., 1992) the evaluation of the model will be discussed.
Special attention is paid to the procedures used to estimate the parameters required for the competition model. The parameter values were partly derived from the results of three field experiments, and partly from published data. These parameter estimates may be seen as quantitative summary of the relevant growth characteristics of the species.

In the present paper, only information from the monocultures is used. In Kropff et al. (1992), the growth pattern of the species in monoculture and mixture are analysed with the model using a single set of parameter values, showing the extent to which the growth in competition can be explained by the model. An analysis of the contribution of species characteristics to the competitive ability of the species is also described.

Materials and methods
Model description

General structure. Under favourable growth conditions, light and temperature are the main factors determining the growth rate of the crop and its associated weeds. From the leaf area index of the species and the vertical distribution of their leaf area, the light profile within the canopy is calculated. On the basis of the photosynthesis characteristics of single leaves, the photosynthesis profile of each species in the mixed canopy is obtained. Integration over the height of the canopy and over the day gives the daily assimilation rate for each species. After subtraction of respiration requirements, the net daily growth rate (in kg dry matter ha\(^{-1}\) day\(^{-1}\)) is obtained. The dry matter produced is partitioned among the various plant organs. The phenological development rate is monitored in the model as a function of ambient daily average temperature. When the canopy is not yet closed, leaf area increase is calculated from daily average temperature. When the canopy closes, the increase in leaf area is obtained from the increase in leaf weight. Integration of daily growth rates of the organs and leaf area results in a dry weight increase during the growing season.

To account for the effects of drought stress, a simple water balance for a free draining soil profile is coupled to the model, tracking the available amount of soil moisture in due time. Transpiration and growth rates of the species are reduced when the available soil moisture drops below a certain level. Competition for water is thus closely linked to above-ground competition for light, because transpiration is driven by the absorbed amount of radiation by the species and the vapour pressure deficit inside the canopy.

Input requirements of the model are as follows: geographical latitude, standard daily weather data, soil physical properties, crop and weed density, date of crop and weed emergence and parameter values that describe the morphophysiological characteristics of the plant species. The time step of integration is one day.

Incoming light flux. Measured daily total solar irradiation (wavelength 300–3000 nm) is input for the model. Only half of this incoming radiation is photosynthetically active (PAR, wavelength 400–700 nm). This visible fraction, generally called ‘light’, is used in the calculation procedure of the CO\(_2\) assimilation rates of the species. A distinction is made between diffuse skylight and direct sunlight because of the large difference in illumination intensity between shaded leaves, which receive only diffuse radiation, and sunlit leaves, which receive both direct and diffuse radiation. The proportion of diffuse light in the total incident light flux is derived from the atmospheric transmission, i.e. the ratio between actual solar irradiance and the quantity that would have reached the earth’s surface in the absence of an atmosphere, using an empirically determined relationship (Spitters et al., 1989a). Instantaneous flux densities of diffuse and direct light are inferred using a sinusoidal course of the irradiance intensity over the day.

Light profile within the canopy. The radiation fluxes attenuate approximately exponentially within the foliage with increasing leaf area:

\[
I_L = (1-\rho)I_o \exp(-\sum (k_j L_j))
\]

(1)

where \(I_L\) is the net flux at depth \(L\) (J m\(^{-2}\) ground s\(^{-1}\)), \(I_o\) is the flux at the top of the canopy (J m\(^{-2}\) ground s\(^{-1}\)), \(L_o\) is the cumulative leaf area index of species \(j\) (counted from the top of the canopy downwards) (m\(^2\) leaf m\(^{-2}\) ground), \(\rho\) is the reflection coefficient of the canopy and \(k_j\) is the extinction coefficient of species \(j\). The leaf areas \(L_j\), weighted by the extinction coefficients \((k_j)\), are summed over the \(j = 1...n\) plant species in the mixed vegetation. In this approach it is assumed that the leaves are horizontally
homogenously distributed. The diffuse and the direct flux have different extinction coefficients, giving rise to different light profiles within the canopy for diffuse and direct radiation.

The light absorbed by species $i$ at a depth $L$ in the canopy ($H_{L,i}$) is obtained by taking the derivative of Equation 1 with respect to the cumulative leaf area index:

$$H_{L,i} = \frac{dI_{L,i}}{dL} = k_i(1-p)L_i \exp[-\Sigma (k_i L_i)](2)$$

$CO_2$ assimilation rates of single leaves. The photosynthesis–light response of individual leaves follows a saturation type of function, characterized by the initial slope (the initial light use efficiency ($\epsilon_i$, kg CO$_2$ ha$^{-1}$ h$^{-1}$/(J m$^{-2}$ s$^{-1}$)) and the asymptote ($A_{mi}$, kg CO$_2$ ha$^{-1}$ h$^{-1}$)), and is described by the negative exponential function:

$$A_i = A_{m_i} [1-\exp(-\epsilon_i H_{L,i}/A_{m_i})] \quad (3)$$

where $A_i$ is the gross assimilation rate (kg CO$_2$ ha$^{-1}$ h$^{-1}$), $A_{m_i}$ is the gross assimilation rate at light saturation (kg CO$_2$ ha$^{-1}$ h$^{-1}$), and $\epsilon_i$ is the initial light use efficiency (kg CO$_2$ ha$^{-1}$ h$^{-1}$/(J m$^{-2}$ s$^{-1}$)). Substitution of the absorbed light intensity at depth $L$ ($H_{L,i}$ in Equation 2) gives the assimilation rate of species $i$ at that specific canopy depth. The assimilation rates are calculated for shaded leaf area and sunlit leaf area separately. The assimilation rate of species $i$ per unit leaf area in a canopy layer is the sum of its assimilation rates of sunlit and shaded leaves, taking into account the proportion of sunlit and shaded leaf area at that depth in the canopy.

Daily total $CO_2$ assimilation rate. The total daily rate of $CO_2$ assimilation of the species ($A_d$) is obtained by integrating the instantaneous rates of $CO_2$ assimilation ($A_{di}$) over the $LAI$ of the species and over the day. The integration is achieved by applying the Gaussian algorithm. This method specifies discrete points at which the value of the function to be integrated must be calculated. It also defines the weighting factors that have to be applied to these values to attain an accurate approximation compared to the analytical solution (Goudriaan, 1986). For integration of the instantaneous assimilation rates over the $LAI$ of the species, the 5-point method is generally satisfactory (C. Rappoldt & S. A. Weaver, personal communication), while the 3-point method performs very well for integration over the day (Goudriaan, 1986). Thus, at three selected times during the day, the assimilation rates at five selected depths in the canopy are calculated for each species. This subroutine was developed by S. A. Weaver and C. Rappoldt at the Department of Theoretical Production Ecology, Wageningen Agricultural University.

Dry matter growth rate from rates of $CO_2$ assimilation and respiration. The assimilated $CO_2$ is converted into carbohydrates (CH$_2$O). For every kg of $CO_2$ taken up, 30/44 kg of CH$_2$O are formed, the numerical values representing the molecular weights of CH$_2$O and $CO_2$, respectively. Part of the carbohydrate is respired to provide the energy for maintaining the existing biostructures. The remaining part is converted into structural plant dry matter. Thus, the daily growth rate equals:

$$G = C_t(A_d (30/44) - R_m) \quad (4)$$

where $G$ is the growth rate (kg dry matter ha$^{-1}$ d$^{-1}$), $C_t$ is the conversion efficiency (kg dry matter kg$^{-1}$ CH$_2$O), and $R_m$ is the maintenance respiration cost (kg CH$_2$O ha$^{-1}$ d$^{-1}$). If $R_m$ exceeds $A_{d_i}$ net growth is set to 0.

Maintenance requirements are approximately proportional to the dry weights of the plant organs to be maintained; the various plant organs differ in their maintenance coefficients. For leaves, stems, roots and storage organs, values of 0-030, 0-015, 0-015 and 0-010 kg CH$_2$O kg$^{-1}$ dry matter day$^{-1}$, respectively, are used as proportionality coefficients (Penning de Vries & van Laar, 1982). In this model a coefficient of 0-015 kg CH$_2$O kg$^{-1}$ dry matter day$^{-1}$ is used for the active tissue of the storage organ. No maintenance requirements are assumed for stored material. These values refer to a temperature of 25°C. With each 10°C temperature increase, these coefficients increase by a factor two ($Q_{10} = 2$).

The carbohydrates in excess of the maintenance costs are available for conversion into structural plant material (Equation 4). The weight of structural dry matter formed per unit weight of carbohydrates depends on the biochemical composition of the formed dry matter only. Typical values for leaves, stems, roots and storage organs have been presented by Penning de Vries et al. (1989).

Dry matter partitioning and phenological development. For each of the competing species, the total dry matter increase is partitioned among the various groups of plant organs
(leaves, stems, storage organs and roots) according to partitioning coefficients ($pc$ in kg dry matter organ/kg dry matter crop) defined as a function of the phenological development stage of the species. The growth rate of plant organ group $k$ ($Gk$) is thus obtained by multiplying the total growth rate ($G$, Equation 4) by the fraction allocated to that organ group ($pc_k$). Total dry weights of the plant organs are obtained by integrating their growth rates over time.

The rate of phenological development is mainly determined by temperature. Over a wide range of temperatures, the development rate increases more or less linearly with temperature, so the development stage is directly related to the temperature sum after seedling emergence.

**Leaf area dynamics.** Under optimum conditions, light and temperature are the environmental factors influencing the rate of leaf area expansion. Light intensity determines the rate of photosynthesis and hence the supply of assimilates to the leaves. Temperature determines the rates of cell division and extension.

In temperate climates, temperature is the overriding factor determining leaf area development during the early stage of plant growth. Because the total $LAI$ is small, all leaves absorb enough radiation to fulfill assimilate needs for leaf expansion in spring. Then, leaf area increases more or less exponentially in time, expressed as the temperature sum:

$$LAI_t = N' \cdot L_o \cdot \exp(R_t \cdot t)$$  \hspace{1cm} (5)

where $LAI_t$ is the leaf area index ($m^2$ leaf $m^{-2}$ ground) at time $t$ (°C d), $N'$ is the number of plants per $m^2$, $L_o$ is the initial leaf area per plant at seedling emergence ($m^2$ plant$^{-1}$), and $R_t$ is the relative leaf area growth rate (°C$^{-1}$ d$^{-1}$), which is introduced as a function of temperature. The exponential phase ends when the portion of assimilates allocated to non-leaf tissue sharply increases, or when mutual shading becomes substantial. As a yardstick for these events, one can use $LAI = 0.75$ as the end of the exponential growth period, since leaves start to overlap.

For the later stages, leaf area increase ($GLAI$) is calculated by multiplying the simulated daily leaf weight increase ($G_{lw}$) of the species by its specific leaf area:

$$GLAI = SLA \cdot G_{lw}$$  \hspace{1cm} (6)

To account for leaf senescence, a relative leaf death rate is defined, being a function of both the developmental stage of the species and the ambient temperature. Leaf death rate ($DLAI$ in $m^2$ m$^{-2} \cdot (°C \cdot d)^{-1}$) is then obtained by multiplying the green $LAI$ by this relative death rate ($R_s$, in (°C d)$^{-1}$):

$$DLAI = LAI \cdot R_s$$  \hspace{1cm} (7)

The amount of light absorbed by a species depends on the position of its leaf area within the multi-species foliage. The distribution of leaf area over plant height is described for each species by its leaf area density function, which relates the leaf area density ($m^2$ leaf $m^{-2}$ ground $m^{-1}$ height) to plant height, using a parabolic function as default, with plant height as the upper limit. The $LAI$ of the species measures the surface enclosed by this function. Plant height is introduced as a logistic function of the development stage. From the leaf area density functions of the various plant species, the cumulative leaf area index of the species above the selected plant height is calculated. Together with the incoming light flux at the top of the canopy, this determines the light absorption at the selected plant height and thus the assimilation rate at that height (Equation 3).

**Growth rates limited by soil moisture availability.** To account for water shortage, a simple moisture balance for a free-draining soil profile is included in the model. The daily change in soil moisture content in the rooted zone is calculated from the rainfall ($R$), transpiration by the vegetation ($T$), soil evaporation ($E$), and deep percolation ($DP$) as:

$$d\theta = R - T - E - DP$$  \hspace{1cm} (8)

where $d\theta$ is the change in soil moisture content expressed in kg $H_2O \cdot m^{-2} \cdot d^{-1}$. Daily data on rainfall (in mm) represent input for the model. Percolation is calculated as the amount of water in excess of field capacity, which drains below the rooted zone with a delay of a few days.

Potential rates of transpiration and soil evaporation are derived from the reference evapotranspiration of a short grass cover ($ET_c$), calculated from the weather data using the Penman (1948) equation (evapotranspiration of short grass is about 0.8 times the evaporation of open water). Rates of transpiration and evaporation are approximately proportional to the amount of total solar radiation intercepted. The
radiation intercepted by the vegetation and that transmitted to the soil are derived from the exponential radiation profile (Equation 1). This gives the following for the potential transpiration of a canopy ($T_o$) (composed by $C_3$ species) as a function of the reference evapotranspiration ($ET_o$):

$$T_o = 1.3 \cdot ET_o \cdot (1 - \exp(-\Sigma[0.7 \cdot k_j \cdot LAI_j]))$$

(9)

and for the potential soil evaporation ($E_o$):

$$E_o = 0.9 \cdot ET_o \cdot \exp(-\Sigma[0.7 \cdot k_j \cdot LAI_j])$$

(10)

where 1.3 and 0.9 are empirical constants (Spitters, 1989, p. 209), $k$ is the extinction coefficient for PAR, and 0.7 is the ratio between the extinction coefficient for total solar radiation and that for PAR. LAIs are weighted to the species respective extinction coefficients and summed over the $j = 1...n$ species constituting the mixture. The potential transpiration rate of a species growing in mixture is assumed to be proportional to its relative amount of intercepted radiation, calculated in a similar way to the interception of PAR.

Water shortage reduces the rates of evaporation and transpiration. The actual value of the soil evaporation ($E_a$) is obtained by multiplying the potential value ($E_o$) by a factor that is a function of the moisture content of the top 2 cm of the soil. This content is also tracked in the model. The ratio between actual transpiration ($T$) and potential transpiration ($T_o$) decreases linearly with soil moisture availability when the actual soil moisture content ($\theta_a$) falls below a certain critical level ($\theta_c$) (Doorenbos & Kassam, 1979):

$$T / T_o = (\theta_c - \theta_w) / (\theta_c - \theta_wp); \ 0 \leq T / T_o \leq 1$$

(11)

where the critical soil moisture content is defined as:

$$\theta_c = \theta_wp + (1 - p)(\theta_fn - \theta_wp)$$

(12)

in which $\theta$ is the soil moisture content (kg H2O m$^{-2}$ ground or mm), subscripts denoting the critical value ($c$) and the values at wilting point ($w$) and field capacity ($f$), respectively. The soil moisture depletion factor ($p$) is dependent on plant species and evaporative demand, but for $C_3$ species it typically varies between 0.6 and 0.4 for an evaporative demand of 1 and 5 mm $d^{-1}$, respectively.

The reduction in growth rate is more or less proportional to the reduction in transpiration rate. Thus, the growth rate $G$, limited by soil moisture, is obtained by multiplying its potential value ($G_o$; Equation 4) by the factor $T / T_o$:

$$G = (T / T_o)G_o$$

(13)

The multiplication factor $T / T_o$ is also applied to the rate of plant height increase. Drought also affects rates of leaf expansion and senescence, the dry matter partitioning between above-ground and below-ground parts, and the photosynthetic capacity of the leaves.

**Experimental design**

Parameter values were mainly derived from three field experiments, where $C. album$ L. and sugar beet were grown in monocultures and mixtures in three consecutive years (1984–1986) on a sandy loam in Wageningen, The Netherlands. In these experiments, plants were harvested at regular intervals throughout the growing period. At each harvest, samples were dissected to the various plant organs, dried at 80°C and weighed.

In sugar beet, laminae, petioles (including crown and midribs) and tap root were separated. The midrib was separated from the lamina when plants were older than 5 weeks after plant emergence. The crown (i.e. hypocotyl and epicotyl) was separated from the tap root just below the lowest leaf mark, at the point where the concentric bundle rings are visible. In $C. album$ L., leaf laminae, stems (including petioles and flowering stalks) and fruits (i.e. perianth and seed) were separated. The area of green leaf blades was measured with an electronic planimeter. Dead leaves and seeds which fell off were collected, except in the 1984 experiment. Date of emergence of the species was characterized by the median of their frequency distribution, inferred from daily recordings of plant emergence in permanent quadrats.

The experiments were laid out according to a split-plot design with 4 replicates, populations as main plots and harvest dates as subplots. Here, only the data from the monospecies stands are used; the results of the mixtures are discussed in Kropff et al. (1992), where the weather data are also summarized. Experimental details of the monocultures are given in Table 1. The beets were sown with a precision drill at a high population density, and after emergence thinned back to the right spacing. $C. album$ L.
Model for interspecific competition

Table 1. Details of the field experiments with monocultures and mixtures of sugar beet and Chenopodium album L. carried out in three different years.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>1984</td>
<td>1985</td>
<td>1986</td>
</tr>
<tr>
<td>Sugar beet cultivar</td>
<td>Regina</td>
<td>Monohil</td>
<td>Salohil</td>
</tr>
<tr>
<td>Sowing date of sugar beet</td>
<td>17/4</td>
<td>24/4</td>
<td>18/4</td>
</tr>
<tr>
<td>Sowing date of C. album L.</td>
<td>—</td>
<td>14/5</td>
<td>6/5, 20/5</td>
</tr>
<tr>
<td>Plant emergence sugar beet</td>
<td>27/4</td>
<td>9/5</td>
<td>4/5</td>
</tr>
<tr>
<td>Plant emergence C. album L.</td>
<td>27/4</td>
<td>19/5</td>
<td>25/5, 3/6</td>
</tr>
<tr>
<td>Density sugar beet (plants m⁻²)</td>
<td>11-1</td>
<td>11-1</td>
<td>11-1</td>
</tr>
<tr>
<td>Density C. album L. (plants m⁻²)</td>
<td>22-2</td>
<td>11-1</td>
<td>11-1</td>
</tr>
<tr>
<td>Plant spacing sugar beet (m²)</td>
<td>0.30 x 0.30</td>
<td>0.30 x 0.30</td>
<td>0.50 x 0.18</td>
</tr>
<tr>
<td>Plant spacing C. album L. (m²)</td>
<td>0.30 x 0.15</td>
<td>0.30 x 0.30</td>
<td>0.50 x 0.18</td>
</tr>
<tr>
<td>Gross plot size (m²)</td>
<td>1.5 x 3.0</td>
<td>1.5 x 6.0</td>
<td>1.26 x 6.0</td>
</tr>
<tr>
<td>Net plot size (m²)</td>
<td>0.9 x 1.8</td>
<td>0.3 x 4.8</td>
<td>0.54 x 4.0</td>
</tr>
<tr>
<td>No. of replicates</td>
<td>4</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Fertilizer rate (kg ha⁻¹)</td>
<td>N 160</td>
<td>165</td>
<td>170</td>
</tr>
<tr>
<td></td>
<td>P₂O₅ 40</td>
<td>60</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>K₂O 100</td>
<td>200</td>
<td>280</td>
</tr>
<tr>
<td>Groundwater table (m)</td>
<td>0.7-1.0</td>
<td>0.7-1.8</td>
<td>1.2-1.4</td>
</tr>
</tbody>
</table>

* C. album L. 0.6 x 4.8 m.

Table 2. Summary of the parameter estimates for sugar beet and C. album L.

<table>
<thead>
<tr>
<th>Description</th>
<th>Symbol</th>
<th>Unit</th>
<th>S. beet</th>
<th>C. album</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light interception:</td>
<td>k</td>
<td>m²m⁻²</td>
<td>0.65</td>
<td>0.65</td>
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<tr>
<td>Photosynthesis and respiration:</td>
<td>e</td>
<td>kg CO₂ ha⁻¹ h⁻¹ (J m⁻² s⁻¹)</td>
<td>0.45</td>
<td>0.45</td>
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<tr>
<td></td>
<td>Aₘ</td>
<td>kg CO₂ ha⁻¹ h⁻¹</td>
<td>50</td>
<td>50</td>
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<tr>
<td>CH₂O requirements</td>
<td>Cₗ</td>
<td>kg CH₂O kg⁻¹ DM d⁻¹</td>
<td>Table 3</td>
<td>Table 3</td>
</tr>
<tr>
<td>Phenology:</td>
<td>Tₑ</td>
<td>°C d</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Tₘ</td>
<td>°C d</td>
<td>21</td>
<td>21</td>
</tr>
<tr>
<td>Dry matter distribution pattern:</td>
<td>pc</td>
<td>—</td>
<td>Fig. 1, 2</td>
<td></td>
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<tr>
<td>partitioning coefficients</td>
<td>Lₐ</td>
<td>m² plant⁻¹</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Leaf area dynamics:</td>
<td>Rₙ</td>
<td>m² plant⁻¹</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>relative growth rate of leaf area</td>
<td>Sₘ</td>
<td>m² leaf kg⁻¹</td>
<td>—</td>
<td>—</td>
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<tr>
<td>specific leaf area</td>
<td>Lₑ</td>
<td>m² leaf kg⁻¹</td>
<td>—</td>
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<tr>
<td>leaf senescence parameter</td>
<td>Rₛ</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Plant height:</td>
<td>Hₑ</td>
<td>m</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>height increase parameters</td>
<td>bₑ</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>s</td>
<td>°C⁻¹ d⁻¹</td>
<td>—</td>
<td>—</td>
<td>—</td>
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</tbody>
</table>

was sown by hand after pretreatment of the seeds with 0.005% gibberellic acid and 0.005% KNO₃ for 14 days at 4°C. In the 1984 experiment, the naturally established C. album L. population was thinned back to the right spacing. Weeding was done by hand.

Model parameterization

The parameter values used to characterize sugar beet and C. album L. are summarized in Table 2, and their estimation is discussed in the following sections.

**Light interception.** The extinction coefficient \( k \) in Equation 1 is estimated from measurements of the light intensity above and below a canopy (or canopy layer) with a known \( LAI \).

The estimate of \( k \) (Equations 1 and 2) presented in Table 2 refers to photosynthetically active radiation (PAR, wavelength 400-700 nm), the value for total solar radiation (300-3000 nm) being about 0.7 times that for PAR.
The extinction of direct solar radiation varies with solar elevation, which dependency is accounted for in the model (according to Goudriaan, 1977). Under a uniformly overcast sky all radiation is diffuse, the extinction coefficient for diffuse radiation being independent of solar elevation and, therefore, used as a model parameter.

The $k$ value of 0.65 for sugar beet was based on data from Clark & Loomis (1978). It fits with the value of 0.69 recorded by Tanaka (1983) and the value of 0.61 ± 0.04 measured on 4 July in the 1985 experiment.

For *C. album* L., the same value of $k$ was used as for sugar beet. This is based on values for both species from the 1985 experiment: 0.61 ± 0.04 measured on 4 July in the 1985 experiment.

From measurements by Fukuda & Hayashi (1982), a value of 0.69 at 0.50 m plant height and 0.67 m height was inferred for *C. album* L. The value of 1.0 recorded by Monsi & Saeki (1953) is somewhat outside this range. This high value of Monsi & Saeki (1953) may be explained by light absorption by the flower stalks of *C. album* L. later in the season. At present, however, no estimate of their extinction characteristics is available.

**CO$_2$ assimilation.** In the model, canopy photosynthesis is calculated on the basis of the photosynthesis–light response of individual leaves. This response follows a saturation type of function, characterized by the initial slope (the initial light use efficiency ($\epsilon$, kg CO$_2$ ha$^{-1}$ h$^{-1}$/(J m$^{-2}$ s$^{-1}$)) and the asymptote ($A_m$, kg CO$_2$ ha$^{-1}$ h$^{-1}$)) (Equation 3).

For the initial light use efficiency ($\epsilon$), a constant value of 0.45 kg CO$_2$ ha$^{-1}$ h$^{-1}$/(J m$^{-2}$ s$^{-1}$) was selected, based on data of Ehleringer & Pearcy (1983).

The light-saturated photosynthesis ($A_m$), however, varies considerably, mainly as a function of leaf age and the environmental conditions to which the leaf has been exposed in the past. It is also influenced by genotype and plant species. For both species, $A_m$ was set at 50 kg CO$_2$ ha$^{-1}$ leaf $^{-1}$ as an average value for actively photosynthesizing foliage under favourable conditions. This value is within the wide range of values reported for sugar beet (Hall & Loomis, 1972; Hodanova, 1981; van der Werf, Department of Theoretical Production Ecology, Wageningen Agricultural University, unpublished data) and for *C. album* L. (Chu et al., 1978; Pearcy et al., 1981; van Oorschot & van Leeuwen, 1984) and our own data. No information was available on the photosynthesis characteristics of the flower stalks of *C. album* L.

In sugar beet, $A_m$ decreases toward the end of the season (Hodanova, 1981; van der Werf, unpublished data), probably due to increasing average leaf age and adaptation of the photosynthetic capacity to the lower temperature and radiation levels. This reduction is introduced by multiplying the above potential value of $A_m$ with a factor which is a function of time after plant emergence. Expressing time as a temperature sum, accumulated above a base of 2°C, this factor is assumed to decrease linearly from a value of 1.0 at 700°C d after plant emergence to 0.8 at 1700°C d, and thereafter to 0.6 at 3000°C d. For *C. album* L., no such reduction was applied because the plants mature earlier in the season and, moreover, they fall off when the leaves start to senesce.

**Respiration.** Dry matter growth rates are obtained from simulated CO$_2$ assimilation rates after subtracting respiration cost, the latter being divided into growth and maintenance requirements (Equation 4).

The maintenance requirements are more or less proportional to the biomass to be maintained; typical values for the various plant organs are given in Table 3. For the fruits of *C. album* L., a value of 0.01 kg CH$_2$O kg$^{-1}$ dry matter d$^{-1}$ was assumed, which is similar to values found for seed crops. For the storage beet, a storage component (sucrose) and a non-storage component are distinguished. The sucrose is metabolically inactive and does not require maintenance, whereas the maintenance coefficient of the non-storage component is assumed to be equal to that of the stem. With a sugar content of 80% on a dry weight basis, this means a beet maintenance coefficient of 0.80 × 0.01 = 0.003 kg CH$_2$O kg$^{-1}$ dry matter d$^{-1}$. Maintenance requirements decrease with the metabolic activity of the plant. In the model, this is accounted for by assuming plant maintenance respiration proportional to the fraction of the accumulated leaf weight that is still green (Spitters et al., 1989). In this way, the maintenance cost for sugar beet at final harvest is reduced to approximately 60% of its potential value, as defined by the coefficients in
Table 3. The maintenance coefficient of the storage beet is thus reduced to 0.0018 kg CO₂/kg d⁻¹, a value well in line with those measured 1 or 2 days after harvest (Koster et al., 1980) (assuming a reference temperature of 25°C, Q₁₀ = 2 and 24% dry matter in beet).

The primary assimilates in excess of the maintenance cost are converted into structural plant material. The amount of structural dry matter produced per unit of available carbohydrates depends on the chemical composition of the dry matter formed. Typical values of the glucose requirements (C₄) for various groups of compounds were derived by Penning de Vries & van Laar (1982), (modified by Penning de Vries et al., 1989). On the basis of their chemical composition, typical values have been derived for leaves, stems and roots (Table 3). The value for the storage beet was derived from its composition as given by Penning de Vries, van Laar & Chardon (1983), whilst that of C. album L. fruits was based on the measured chemical composition of the seeds.

Phenology. Phenological development is mainly determined by the temperature sum after plant emergence. The temperature sum is calculated on the basis of daily average temperatures. For sugar beet, a base temperature of 2°C is used, below which no development occurs, and a maximum temperature of 21°C above which the development rate is not further accelerated by increasing temperature. These cardinal points were inferred from temperature responses of leaf appearance rate (Terry, 1968; Clark & Loomis, 1978; Milford & Riley, 1980; Hodanova, 1981).

For C. album L., a base temperature of 2°C was also assumed. This choice was inspired by the narrow range in base temperatures of 0-3°C encountered by Angus et al. (1981) for species originating from temperate regions. In the experiments presented, flowering of C. album L. started about 500°C d after seedling emergence. To account for photoperiodic effects on flowering in C. album L. (Ramakrishnan & Kapoor, 1973; Warwick & Marriage, 1982) as well as different temperature requirements between ecotypes, the development stage may be re-scaled to a dimensionless variable having the value 0 at seedling emergence, 1 at the onset of flowering, and 2 at ripeness. In that case, the developmental rate equals the reciprocal of the time, in photoperiodic °Cd, required to complete the unit of development.

Dry matter partitioning. In the model, the total daily dry matter increase is partitioned to the various plant organ groups according to factors that are a function of the developmental stage, the latter being expressed as °Cd after plant emergence. These factors are derived by analysing the fractions of new dry matter production allocated to the plant organs between two subsequent harvests. The total dry matter, daily produced, is first partitioned between 'shoots' (including beet tap root) and 'roots' (Fig. 1). The partitioning between the different 'shoot' organs is shown in Fig. 2. The dry matter distribution patterns in the various experiments corresponded closely with each other. In sugar beet, an increasing fraction of the newly formed dry matter is allocated to the tap root. In C. album L., the changes in the dry matter distribution pattern were associated with the appearance of flower stalks and with seed filling.

Leaf area. In the early phases, leaf area growth proceeds more or less exponentially, the
Fig. 1. The partitioning of current dry matter increases over 'shoots' (including beet tap root) and fibrous roots, as a function of the temperature sum after plant emergence. (a) Sugar beet: inferred from data of Boonstra (unpublished data). (b) C. album L.: guesstimate, partly based on the interrelationship of root and leaf growth. Relative growth rate being approximately linearly related to temperature (Equation 5). When leaf area per plant is plotted on a logarithmic scale against the temperature sum after emergence, a more or less linear relationship is therefore obtained (Fig. 3). The slope measures the relative leaf area growth rate ($R_L$ in cm$^{-1}$ d$^{-1}$) and the intercept the apparent leaf area at emergence. C. album L. had a smaller intercept ($L_0$, the initial leaf area per plant at seedling emergence) (m$^2$ plant$^{-1}$) than sugar beet because of smaller seed reserves. C. album L. showed a slightly greater $R_L$, mainly explained by a greater part of the assimilates allocated to the leaf blades (Fig. 2b). The exponential phase ended when an increasing portion of the assimilates was allocated to non-leaf tissue (Fig. 2b).

After this early exponential phase, leaf area growth is simulated by multiplying the leaf dry weight increase by the specific leaf area (SLA) (m$^2$ leaf kg$^{-1}$ leaf) of the newly formed leaves (Equation 6). SLA is plotted in Fig. 4 as a function of the development stage expressed in degree-days. For each harvest interval, the SLA of new leaves was calculated by dividing the increase in leaf area index ($GLA$) by the increase in leaf weight ($G_{lv}$) between subsequent harvests. In assessing the relationships in Fig. 4, the scatter in the data points was adjusted for by also considering the relationship of LAI/WL (weight of the leaves), which gives more stable values at later developmental stages.

In calculating SLA of sugar beet, the midrib was excluded from the leaf blade from 5 weeks (approximately 300°Cd, $T≥2°C$) after plant emergence onwards. The decrease in leaf area due to senescence was estimated from Fig. 5, where the green leaf area index is depicted.
relative to its maximum value in the experiment concerned (Equation 7). This procedure assumes that during the senescence phase there is no increase in new leaf area at all. This holds for *C. album* L. In sugar beet, however, this assumption is not entirely valid (Fig. 2), which biases the estimation of the relative death rate. However, this barely affects the simulation results of sugar beet yields because foliage senescence did not occur until late in the season. In *C. album* L., leaf senescence appeared much earlier in the 1984 experiment than in both the other experiments (Fig. 5), probably due to drought in this experiment. The 1984 data were therefore excluded when establishing the senescence function.

**Plant height.** The time course of plant height is described by a logistic function of the temperature sum after plant emergence (Fig. 6). The later data of the 1984 experiment were excluded, as plant height growth was reduced by drought stress.

**Plant-water relationships.** When water supply is limited, the ratio between actual transpiration ($T_a$) and potential transpiration ($T_o$) decreases linearly with soil moisture availability when the actual soil moisture content ($\theta_a$) falls below a certain critical level ($\theta_c$) (Equations 11 and 12). The soil moisture depletion factor ($\rho$) is dependent on plant species and evaporative demand (Doorenbos & Kassam, 1979).

In practice, drought stress reduces the relative rate of leaf area growth, the specific leaf area, leaf longevity, and the plant height increase as well. It also changes the dry matter partitioning in favour of the below-ground parts. At present, specific functions for sugar beet and *C. album* L. are lacking and, therefore, the general relationships referred to are applied.
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Fig. 5. Time course of the natural logarithm of green leaf area index (LAI) relative to its maximum value ($LAI_m$) for sugar beet (a) and C. album L. (b). Time ($t$) as temperature sum in °C d after plant emergence. Symbols as in Fig. 2; additional data for sugar beet from unpublished data of Sibma (Centre for Agrobiological Research, Wageningen). Slope of the drawn lines gives value of $R$, (relative death rate of leaves $[1/(°C \text{ d})]$) used in the model.

Acknowledgements

We are grateful to Frits van Evert, Sanderine Nonhebel, Winand Smeets, Jan Geertsema, Lammert Bastianns, Barbara Habekotte, Harmke van Oene, Rob Werner, Hans Peelen, Jaap Stroet and Yvonne Vlaswinkel, who carried out the experiments as part of their MSc research. Part of this work was funded by the EC (EV4C-0020-NL). We would like to thank Gon van Laar, who edited and commented on the manuscript.

References


Appendix 1

Symbols used

\( A_d \) daily CO\(_2\) assimilation rate of a canopy (kg CO\(_2\) ha\(^{-1}\) ground d\(^{-1}\))

\( A_L \) CO\(_2\) assimilation rate at canopy depth \( L \) (kg CO\(_2\) ha\(^{-1}\) leaf h\(^{-1}\))

\( A_m \) maximum CO\(_2\) assimilation rate (at light saturation) (kg CO\(_2\) ha\(^{-1}\) leaf h\(^{-1}\))

\( C_t \) conversion factor (kg dry matter kg\(^{-1}\) CH\(_2\)O)

\( DLAI \) leaf area death rate (m\(^2\) m\(^{-2}\) (C d\(^{-1}\)) or (m\(^2\) m\(^{-2}\) d\(^{-1}\))

\( DP \) deep percolation (kg H\(_2\)O m\(^{-2}\) d\(^{-1}\)) or (mm d\(^{-1}\))

\( E \) soil evaporation (kg H\(_2\)O m\(^{-2}\) d\(^{-1}\)) or (mm d\(^{-1}\))

\( ET \) reference evapotranspiration of a short grass cover (kg H\(_2\)O m\(^{-2}\) d\(^{-1}\)) or (mm d\(^{-1}\))

\( \varepsilon \) initial light use efficiency (kg CO\(_2\) ha\(^{-1}\) leaf h\(^{-1}\))(J m\(^{-2}\) leaf s\(^{-1}\))

\( G_o \) potential growth rate of the crop (kg dry matter ha\(^{-1}\) d\(^{-1}\))

\( G \) actual growth rate of the crop (kg dry matter ha\(^{-1}\) d\(^{-1}\))

\( GLAI \) leaf area growth rate (m\(^2\) m\(^{-2}\) d\(^{-1}\))

\( H \) plant height (m)

\( H_L \) absorbed amount of radiation (PAR) at depth \( L \) (J m\(^{-2}\) leaf s\(^{-1}\))

\( I_o \) radiation flux at the top of the canopy (J m\(^{-2}\) ground s\(^{-1}\))
$I_L$, net flux of radiation ($\text{PAR}$) at depth $L$ ($\text{J m}^{-2} \text{ground s}^{-1}$)  
$k_j$, extinction coefficient for $\text{PAR}$ of species $j$ ($\text{m}^{-1}$)  
$\text{LAI}$, leaf area index ($\text{m}^2 \text{leaf} \text{m}^{-2} \text{ground}$)  
$L_j$, the cumulative leaf area index of species $j$ counted from the top of the canopy downward ($\text{m}^2 \text{leaf} \text{m}^{-2} \text{ground}$)  
$L_o$, the initial leaf area per plant at seedling emergence ($\text{m}^2 \text{leaf plant}^{-1}$)  
$N$, the number of plants ($\text{m}^{-2}$)  
$p$, the soil moisture depletion factor ($-$)  
$pc_k$, partitioning coefficient ($\text{kg dry matter (plant organ} k) \text{kg dry matter crop}$)  
$\text{PAR}$, photosynthetically active radiation (wavelength 400–700 nm) ($\text{J m}^{-2} \text{ground s}^{-1}$)  
$\theta_a$, actual soil moisture content ($\text{kg H}_2\text{O m}^{-2}$)  
$\theta_c$, critical soil moisture content ($\text{kg H}_2\text{O m}^{-2}$)  
$\theta_w$, soil moisture content at field capacity ($\text{kg H}_2\text{O m}^{-2}$)  
$\theta_r$, soil moisture content at permanent wilting point ($\text{kg H}_2\text{O m}^{-2}$)  
$R$, rainfall ($\text{kg H}_2\text{O m}^{-2} \text{d}^{-1}$) or ($\text{mm d}^{-1}$)  
$R_L$, relative growth rate of leaf area ($\text{C}^{-1} \text{d}^{-1}$)  
$R_o$, relative death rate of leaves ($\text{C}^{-1} \text{d}^{-1}$)  
$R_m$, maintenance respiration ($\text{kg CH}_2\text{O ha}^{-1} \text{d}^{-1}$)  
$\rho$, reflection coefficient of the canopy ($-$)  
$\text{SLA}$, specific leaf area ($\text{m}^2 \text{leaf kg}^{-1} \text{leaf}$)  
$T$, actual transpiration by the vegetation ($\text{kg H}_2\text{O m}^{-2} \text{d}^{-1}$) or ($\text{mm d}^{-1}$)  
$T_o$, potential transpiration of a canopy ($\text{kg H}_2\text{O m}^{-2} \text{d}^{-1}$) or ($\text{mm d}^{-1}$)