

A model of growth and sugar accumulation of sugar beet for potential production conditions:

SUBEMOpo

I. Theory and model structure

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Abstract

SUBEMOpo (SUGar BEet MOdel potential production) is a mechanistic simulation model to simulate sugar beet growth and sugar accumulation for potential production conditions. Under those conditions sugar beet growth and sugar accumulation are entirely controlled by the prevailing weather (radiation, temperature) and by the crop characteristics (plant density). The only site characteristic required for modelling the potential production is the latitude. Dry matter and sugar accumulation are calculated from the CO₂ assimilation of the crop, taking into account the respiration losses and a teleonomic mechanism for the allocation of the carbohydrates to the different plant organs and to sugar storage. A functional balance, consisting of source and sink terms, is thereby used. The computer code of SUBEMOpo is written in the FORTRAN 77 standard. The model structure consists of a main program and 11 subprograms which describe processes occurring in sugar beet plants, such as, assimilation, respiration, transpiration, growth, development and ageing or deal with the initialization of state variables and fluxes and with the translation of daily weather data into hourly data. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Simulation model; Potential production; Sugar beet

1. Introduction

The primary aim of this modelling research is to increase insight in the processes of growth, sugar accumulation and internal sugar beet quality. SUBEMOdel integrates quantitatively the current knowledge on development and growth of sugar

beet plants. SUBEMO is an acronym for SUGar BEet MODEL. SUBEMOpo is the version of SUBEMO that simulates potential growth and sugar accumulation for optimal conditions, where water and nutrient supplies are adequate and pests, diseases and weeds do not hinder growth and yield. Because nutrients are not considered to have a limiting effect, the po-version of SUBEMO only simulates sugar content to characterize internal beet quality.

SUBEMOpo is a dynamic, mechanistic simulation model. It is a typical state-variable model with integration of diurnal variation in control of growth and other considered processes. SUBEMOpo predicts the response of the sugar beet crop to the prevailing weather conditions and crop characteristics.

The basis for the calculations is the rate of CO₂ assimilation of the canopy. That rate depends on the radiant energy absorbed by the canopy, which is function of incoming radiation and crop leaf area. From the absorbed radiation and the photosynthetic characteristics of individual leaves, the rate of gross CO₂ assimilation of the sugar beet crop is calculated. Part of the carbohydrates produced is used to maintain existing biomass (maintenance respiration). The remaining carbohydrates are converted into structural dry matter of leaves, tap roots and fibrous roots, and into sugar storage. In the process of conversion, part of the weight is lost in growth respiration. Growth and partitioning are done according a teleonomic mechanism.

For the development of the SUBEMOdel, parts of published models were selected on the basis of one of the following criteria: (1) the theoretical concept and level of process description; and/or (2) the overall performance of the model component. SUBEMO is based on the models CROPPHOT (Goudriaan and van Laar, 1978) and its sequential improvements (Spitters, 1986; Spitters et al., 1986), on SUBGRO I and II (Fick, 1971) and SUBGOL (Hunt, 1974). Some of the relations and parameters are derived from the literature. This paper describes the processes involved in growth and sugar accumulation of sugar beet in the same sequence as they are described in the SUBEMOpo model.

1.1. Theory and conceptual background of SUBEMOpo

SUBEMOpo models sugar beet growth and the accumulation of sugar in a dynamic way in response to the daily weather variables: global solar radiation, maximum and minimum air temperatures, total wind speed and rainfall. A hourly time step is used in the model to calculate plant growth. The hourly values of the output variables are integrated over 24 h.

The production of dry matter and sugar is based on the daily CO₂ assimilation of the crop and the respiration losses. A teleonomic mechanism is used to distribute the daily production of carbohydrates over the different plant organs, including sugar storage. The processes controlling growth in the model are discussed in the following sections: (1) Light interception; (2) Gross CO₂ assimilation; (3) Respiration; (4) Partitioning and growth; and (5) Development and ageing. The environmental factors and the internal plant factors defining these processes are described in a separate section.

1.2. Description of the growth processes

1.2.1. Light interception

Light or, more exactly, the photosynthetically active radiation (PAR) supplies the plants with the energy for CO₂ assimilation. Daily values of global irradiance are input for the SUBEMOdel. The global radiation is partitioned into a direct and diffuse flux based on the approach of Spitters et al. (1986) using the fraction of the total radiation transmitted through the atmosphere. The atmospheric transmission is determined as the ratio between measured daily irradiance of the earth surface and the calculated radiation outside the atmosphere. The diurnal variations for total, diffuse and direct radiation are derived from the daily totals by applying a modified sinusoidal function over the day.

1.2.2. Gross CO₂ assimilation

Canopy photosynthesis is calculated from: (1) the amount of PAR absorbed by the canopy; (2) the assimilation — light response of a single leaf; and (3) the leaf area index (LAI).

The amount of PAR absorbed by the canopy is based on the light profile within the canopy for the different radiation components. This light profile approximates an exponential decrease of light intensity with LAI. Before calculating the light profile, the incoming total, direct and diffuse light at the top of the canopy are adjusted for canopy reflection. On the basis of the light profile, light absorption can be derived for any depth within the canopy. Substitution into the assimilation–light response of a leaf gives the assimilation per unit leaf area.

The assimilation–light response curve is described in the model as an asymptotic exponential relationship, which according to Peat (1970) and Spitters (1986) appears to be the most satisfactory response function. The response is characterized by its slope at low light intensity and its maximum rate at light saturation (P_{\max}). The instantaneous assimilation per canopy layer is obtained by substituting the absorbed amount of light energy into this assimilation–light response curve. This is done separately for the shaded and the sunlit leaves. The assimilation rate per unit leaf area, averaged over a canopy layer, is then calculated as the sum of the assimilation rates of sunlit and shaded leaves. The fraction sunlit leaf area in a canopy layer is thereby equal to the fraction of the direct light beam reaching that layer. A detailed description of the assimilation per canopy layer and of the several sources of variation in illumination intensity of the leaves accounted for in the model, is given by Spitters (1986).

The LAI of the sugar beet crop, as calculated in the shoot growth section of the SUBEMOdel, is used to generate the canopy assimilation. The interval in canopy depth is a leaf layer of LAI=1. The output of the CO₂ assimilation process is added in the SUBEMOdel to a metabolic pool of carbohydrates (Fig. 1), which in turn is an input to subprocesses such as respiration, growth and sugar accumulation.

1.2.3. Respiration

The respiration section of the SUBEMOdel is a two-component coupled respiration model, with growth respiration coupled to the rate of biomass increase (dW/dt), and maintenance respiration related to the amount of biomass (W).

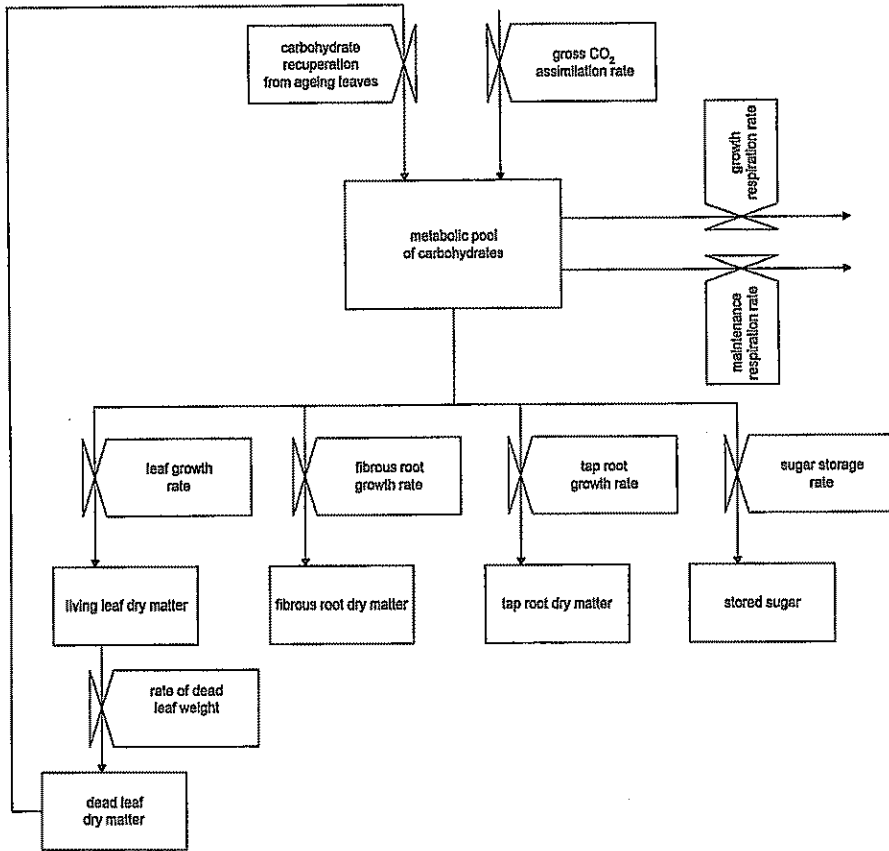


Fig. 1. Relational diagram showing the partitioning of carbohydrates to respiration, structural dry weight and sugar storage, in the simulation model SUBEMOpo (Vandendriessche, 1989). Symbol convention after Forrester.

$$R = G_R(dW/dt) + M_R W \quad (1)$$

The respiratory coefficients for growth (G_R) and maintenance (M_R) are taken from Penning de Vries (1972) and Stout and Smith (1950). The total respiration rate (R) of a component of the plant (leaves, tap roots, fibrous roots) is taken as the sum of the temperature-dependent maintenance respiration and the growth respiration. The maintenance respiration is thereby calculated as the maintenance respiratory coefficient, corrected for temperature and multiplied by the weight of the plant component (weight of the plant component = structural components, excluding accumulated assimilates such as sucrose in the tap root). The growth respiration is calculated as the growth rate of the plant component, including storage of assimilates multiplied by the growth respiratory coefficient.

1.2.4. Partitioning and growth

Carbohydrate partitioning in the plant is managed in SUBEMOpo by a double teleonomical partitioning mechanism (Thornley and Johnson, 1990). The goal-direc-

ted behaviour of the partitioning mechanism includes: (1) a regulation of priorities among the various plant organs for carbohydrate allocation; and (2) a controlling functional equilibrium between shoots and roots so that within a given environment, new material is allocated to the shoot and to the root in such a way that the plant attains an optimal specific growth rate. Fick (1971) and Fick et al. (1975) tested this functional equilibrium hypothesis and the priority concept in his SUBGRO model with good results for the partitioning between root and shoot structural material during vegetative growth of sugar beet.

The integration of this interdependency of plant parts in SUBEMO results in a balanced response to environmental changes. Root growth, for example, is dependent upon carbohydrates from the leaves, but leaf growth in turn is dependent upon the amount of fibrous roots and the water and nutrients which they acquire. Because SUBEMO_{po} supposes an ample supply of water and nutrients, the root:shoot functional balance and the priorities among organs are based on the water and carbohydrate status of the plant. The water status is derived from the relative leaf water content of the plant (RWC).

The teleonomic approach for partitioning in the SUBEMO_{po} model is shown in Fig. 1. The sugar beet plant is divided into: (1) three parts of structural dry matter (leaves, tap root, fibrous roots); and (2) two parts of non-structural dry matter (metabolic pool of carbohydrates, stored sugar). The metabolic pool is replenished by CO₂ assimilation and by recuperation of carbohydrates from ageing leaves, and is depleted by respiration, growth and sugar storage.

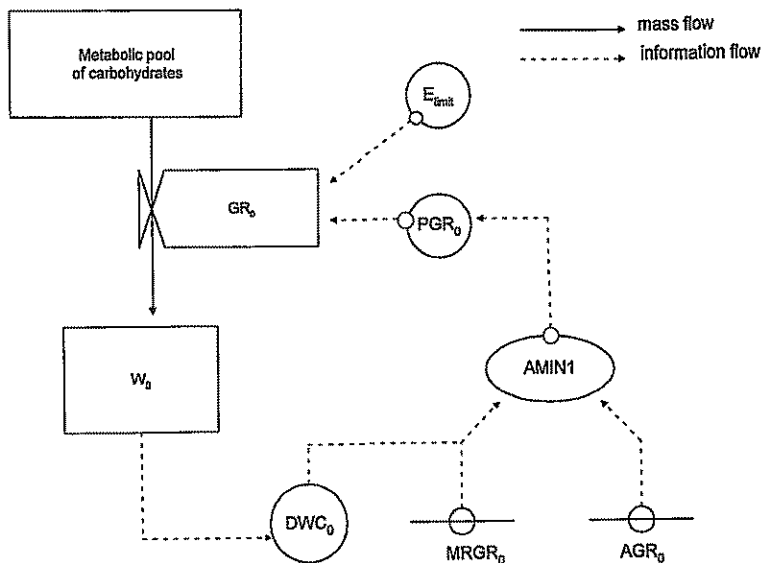


Fig. 2. Relational diagram for the growth of the various plant organs (structural dry matter increase and sugar storage, W_o) showing the sink activity and the transfer of carbohydrates from the metabolic pool with a rate equal to GR_o . This actual growth rate is calculated from the potential growth rate (PGR_o) by reducing it for the various defining factors (E_{limit}). PGR_o is computed as an absolute growth rate (AGR_o) or a relative growth rate ($DWC_o \times MGR_o$). Symbol convention after Forrester.

Whereas growth is modelled in terms of structural dry matter increase of leaves, tap roots and fibrous roots, the functional balance mechanism involves the calculation of activities of the various sinks for carbohydrates (Fig. 2). The sink activity of a plant component is defined as the rate of increase in organ weight. SUBEMO models this sink activity from the potential sink activity and growth defining factors. The potential sink activity is described in SUBEMO_{po} in terms of relative growth rate or absolute growth rate. Sugar storage is treated as a special case of growth, namely increase of non-structural dry matter in the tap root.

The hourly growth rates of the plant components are computed from these potential values by reducing them for the various defining factors. The growth rates as well as the various defining factors are described below. Thus, in SUBEMO_{po}, the growth of a plant component (GR_o) is modelled as:

$$GR_o = PGR_o \times E_{limit} \quad (2)$$

with

$$PGR_o = \text{MIN} (MRGR_o \times DWC_o, AGR_o), \quad (3)$$

where PGR_o is the potential growth rate of the plant component, which is taken as the lowest value of either absolute growth rate (AGR_o) or the maximum relative growth rate of the plant component ($MRGR_o$) multiplied by the dry weight of that part of that component which is able to grow (DWC_o). Defining factors (E_{limit}) have values between 0 and 1. When E_{limit} equals 1, actual growth equals potential growth. Methods to obtain the value of E_{limit} were discussed by Vandendriessche (1995).

Potential growth of a plant component is at least limited by two of these defining factors: air or soil temperature (Fig. 5), carbohydrate supply (Fig. 3), relative water content (Fig. 4) and the amount of stored sugar (see Defining factors for growth).

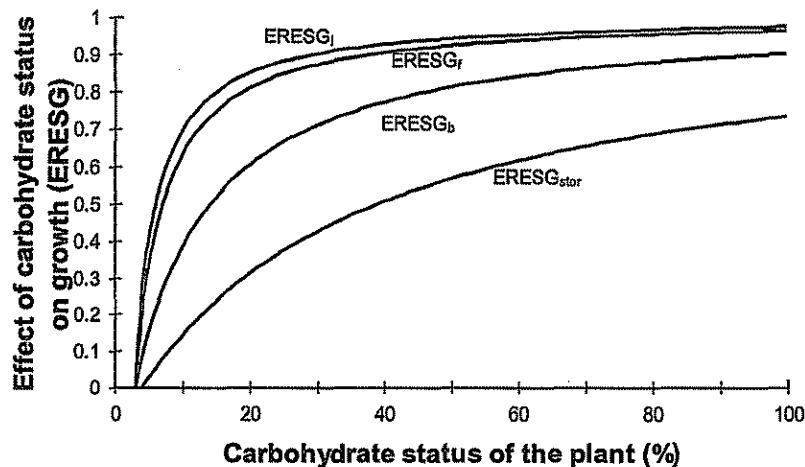


Fig. 3. Response curves showing the effect of carbohydrate status of the plant on the growth of the leaves ($ERESG_l$), the fibrous roots ($ERESG_f$), the tap roots ($ERESG_b$), and on sugar storage ($ERESG_{stor}$).

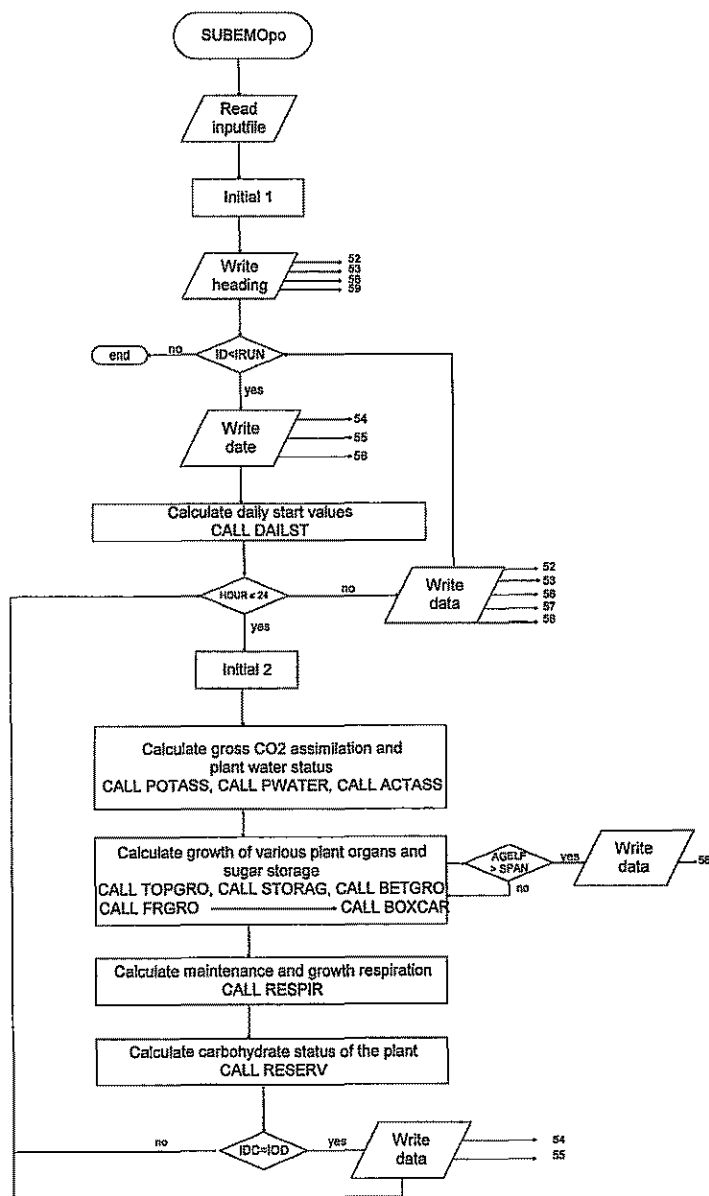


Fig. 4. Flowchart of the SUBEMOpo sugar beet crop simulation model for potential production conditions. The symbols are consistent with the American National Standard ANSI X 3.5-1970. SUBEMOpo is the main program from which all of the subprograms are called. The subprogram DAILST is called with time steps of 1 day. Within the daily loop, the model runs an hourly loop, calling the subprograms POTASS, P WATER, ACTASS, TOPGRO, STORAG, BETGRO, FRGRO, RESPIR, RESERV. The subprogram FRGRO calls on its turn the subprogram BOXCAR. The main program reads initial start data and weather data from the inputfile. Several outputfiles are created and filled in during the runtime of the model (file unit Nos. 52–59).

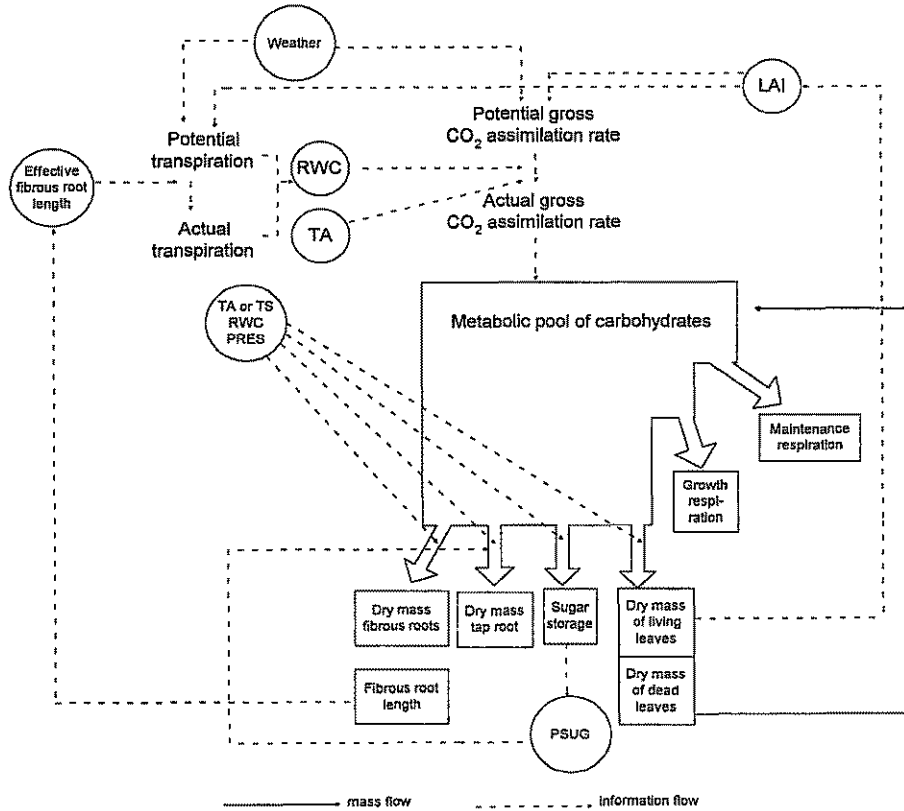


Fig. 5. General structure of SUBEMOpo. LAI, leaf area index; TA, air temperature; TS, soil temperature; RWC, relative water content of the leaves; PRES, carbohydrate status of the plant; PSUG, percentage sugar in the beet on fresh weight basis.

The growth rate of leaves is calculated from leaf appearance rate, cell expansion rate and cell division rate. The leaf appearance rate is modelled as an absolute growth rate with a maximum of 0.7 leaves per day. This ceiling value was calculated from data in the literature from experiments with different sugar beet varieties in controlled environments (Ulrich, 1955, 1956; Thorne et al., 1967; Fick, 1971) and in the field (Ng, 1980). Leaf appearance rate is temperature dependent and will only be at its maximum between 15 and 28°C air temperature. Besides temperature, the supply of carbohydrates from the metabolic pool determines leaf appearance rate.

Leaf growth is further modelled from cell division and cell expansion. Only a fraction of the total shoot weight is capable of growth by cell division and expansion and this fraction is dependent on leaf age. Modeling in this way is mimicking reality by expressing sink capacity for carbohydrates by growth of leaves in terms of meristematic activity. This is because physiologists recognize that growth and storage does not occur homogeneously in a plant, but at discrete sites (Hunt, 1974). However, division and expansion are limited by defining factors for growth.

The growth rate of the tap root was modelled in two ways, yielding a relative and an absolute growth rate, respectively (Fig. 2). Both growth rates are simulated simultaneously, and the model uses the minimum of both growth rates to update the weight of the tap root. The potential growth rate of the tap root [PGR_b in Eqs. (2) and (3)] is calculated as the product of the maximum relative growth rate [$MRGR_b$ is $0.437 \text{ g g}^{-1} \text{ day}^{-1}$, according to measurements on seedling shoots from growth chamber studies (Fick, 1971)] and the weight of the portion of the tap root capable of growth (DWC_b). The latter has an upper limit of 8.0 g plant^{-1} . Until this tap root weight is reached, DWC_b is the entire weight of the tap root (W_b) and growth rate is calculated as a relative growth rate model, relative to W_b . Once the tap root weight has reached 8 g plant^{-1} the growth rate is calculated as an absolute growth model with potential growth rate equal to $3.5 \text{ g plant}^{-1} \text{ day}^{-1}$ ($0.437 \text{ g g}^{-1} \text{ day}^{-1} \times 8.0 \text{ g plant}^{-1}$). This maximum absolute growth rate is close to the maximum observed in the experiments of Fick (1971).

The growth rate of the fibrous roots is also modelled as a combined relative growth rate and an absolute growth rate model (Fig. 2). To compute potential growth rate it is assumed that fibrous root growth rate has a maximum of $0.2 \text{ g plant}^{-1} \text{ day}^{-1}$. The fibrous root growth section of SUBEMO is a relative growth rate model until that rate is reached and an absolute growth rate model thereafter. The maximum relative growth rate ($MRGR_f$) is $0.437 \text{ g g}^{-1} \text{ day}^{-1}$ and the weight of the fibrous root capable of growth (DMC_f) depends on fibrous root age.

The growth rate of fibrous root length (GR_{fl}) is derived from the GR_f using the empirical relations derived from experiments of Brouwer and de Wit (1969) and Fick (1971). The computation of the GR_{fl} was simply taken from the SUBGRO model (Fick, 1971). GR_{fl} varies with soil temperature, resulting in roots having a smaller diameter at higher temperatures. The computation of root length is done to calculate water and nutrient uptake. In SUBEMOpo, water and nutrient supply are ample, but the uptake of water by the roots depends on the effective length of the fibrous root system. The effective length is a weighted summation of the total length based on reductions in water uptake capacity that occur with age because of suberization (see Development and ageing). The water uptake is one part of the calculation of the RWC of the leaves (see RWC).

In SUBEMOpo, the increase of sugar storage is treated similarly to the growth of the organs and modelled according to observations made by Giaquinta (1979). During the first 60–70 days after planting, Giaquinta (1979) observed that root fresh weight increased from 0.013 to 70 g, and by 120 days the beets weighed about 250 g. Concomitant with the increase in root weight, sucrose concentration increased to reach 40% sucrose on a dry weight basis (about 10% on a fresh weight basis) by 120 days. Sucrose storage commenced between 30 and 60 days (1–20 g beet weight). The onset of storage was accompanied by the appearance of sucrose synthetase activity (Giaquinta, 1979).

In SUBEMOpo the storage process is subdivided into two phases. During the pre-storage phase the carbohydrates are partitioned to structural material. From the moment the dry weight of the beet exceeds 0.1 g plant^{-1} , the storage phase starts with a storage rate relative to the growth rate of the beet structure corrected for the defining factors, soil temperature, relative water content of the leaves and carbohydrate supply.

1.2.5. *Development and ageing*

SUBEMOpo calculates the development and the age of shoots and fibrous roots by simple book-keeping during every time step of the simulation. SUBEMOpo keeps track of the number of living and the number that have died. When a certain leaf age is reached, the leaf dies. Based on pot experiments (Ng, 1980), successive leaves have a progressively larger life span but this life span decreases with increasing LAI. SUBEMOpo derives LAI from the specific leaf area (the ratio between leaf area and leaf dry weight). The dry weight of the leaves is computed by adding each time step the increase in dry weight. When a leaf dies, SUBEMO recuperates 25% of the dry weight of that leaf, by adding up this fraction to the metabolic pool of carbohydrates (Fig. 1). Experiments with carbon translocation in sugar beet are done by Giaquinta (1979) among others.

The time course of weight, length, age and suberization of fibrous roots is computed as in SUBGRO (Fick, 1971).

1.3. *Description of the growth defining factors*

1.3.1. *Gross CO₂ assimilation*

A review of the factors defining the CO₂ assimilation is given by Saugier (1983) and by Impens et al. (1992). The following factors are varied within the model: temperature, leaf age, the carbohydrate content of the leaves, the RWC. All others, e.g. CO₂ concentration and leaf nitrogen concentration, are considered constant. The way the varying factors control the CO₂ assimilation and how they are integrated in the SUBEMOdel are described below.

1.3.1.1. Temperature. The rate of CO₂ assimilation is zero at an air temperature of 0°C and increases linearly with temperature up to 10°C. Between 10 and 25°C it is assumed that the CO₂ assimilation rate is at its maximum. Above 25°C, the CO₂ assimilation rate decreases linearly to reach zero again at 35°C. The effect of air temperature on the CO₂ assimilation is described in the SUBEMOdel by multiplying the maximum rate of the assimilation–light response curve (P_{\max}) with an ‘effect of air temperature factor’ (ETTA) which has a value between 0 and 1. Between 10 and 25°C, ETTA equals 1, and P_{\max} has a maximum value of 40 kg CO₂ ha⁻¹ h⁻¹ for mature leaves at the top of the canopy.

1.3.1.2. Leaf age. Numerous field observations (Terry and Ulrich, 1973; Hodánová, 1979, 1981; Vandendriessche et al., 1990) have shown that P_{\max} rises to the stage of full leaf expansion, stays at its maximum for a period, and then declines until senescence. The occurrence of leaves of different age and photosynthetic capacity in the canopy is taken into account in the SUBEMOdel by making the P_{\max} value a function of the number of living leaves.

1.3.1.3. Carbohydrate content of the leaves. Several authors suggest that the CO₂ assimilation rate is a function of the accumulation of carbohydrates (soluble sugars, starch; Humphries, 1967; Neales and Incoll, 1968; Habeshaw, 1973). Other experiments

indicate that carbohydrates can be removed from the leaf, by translocation, respiration or incorporation into structural components, as fast as they are produced. Milford and Pearman (1975) concluded that it is unlikely that crops in the field experience sufficiently long periods (ca. 20 h) of photosynthetically saturating irradiances, which are necessary to attain inhibitory concentrations of carbohydrates in their leaves. Hence, in the SUBEMOdel the content of carbohydrates in the leaves is not taken into consideration as controlling factor in the CO₂ assimilation process. Carbohydrates produced in excess of the needs for respiration and growth are stored as sugar in the tap root of the beet. The latter is regulated by a teleonomic mechanism which allocates the carbohydrates to different plant organs and sugar storage.

1.3.1.4. RWC of the leaves. RWC can limit CO₂ assimilation. The RWC is a measure of the internal water status of the plant and is calculated from the ratio between actual transpiration rate (TRC) and potential transpiration rate (TRW). The latter is estimated with the generalized Penman combination formula. In fact, the RWC is the result of the balance between water uptake and transpiration. The effect of the RWC on the CO₂ assimilation is incorporated in SUBEMO_{po} by multiplying the maximum rate of the assimilation–light response curve with an ‘effect of RWC factor’ (ERWC) which has a value between 0 and 1. When the TRC equals the TRW, the value of the effect factor ERWC equals 1, and hence does not limit the CO₂ assimilation. The relation between ERWC and RWC is taken from Fick (1971).

1.3.2. Respiration

1.3.2.1. Temperature. For maintenance respiration a temperature dependency is calculated on an empirical basis. A Q₁₀ value of 2 is considered in the SUBEMOdel, with a reference temperature of 25°C. Hunt (1974) tested the respiration section of his SUBGOLmodel by calculating different temperature-dependent multipliers for the maintenance respiration. A Q₁₀ of 2 yielded the best results. A temperature dependency for G_R appears inappropriate according to Penning de Vries (1975).

1.3.2.2. O₂ supply. Several experiments indicate that the dark respiration (= maintenance and growth respiration) is unaffected by the O₂ concentration (Hofstra and Hesketh, 1969; Opik, 1980). Therefore, no effect of O₂ supply is considered in SUBEMO.

1.3.3. Partitioning and growth

The teleonomic behaviour of the sugar beet plant which is mimicked by SUBEMO_{po}, is to realize optimum growth in response to variation in the carbohydrate status of the plant and the RWC of the leaves. The response to a shortage of carbohydrates is to partition a greater proportion of growth to the shoot in order to acquire more carbohydrates. Similarly, the response to a low RWC is to partition a greater proportion of growth to fibrous roots to enlarge the root system for water uptake. In fact, the carbohydrate status of the plant and the RWC of the leaves are both internal factors defining growth, but both respond to external factors, such as light and water availability.

1.3.3.1. Carbohydrate status. The carbohydrate status of the plant is calculated in SUBEMOpo as the weight of the metabolic pool of carbohydrates, expressed as a percent of the total dry weight of the plant (structural dry matter and stored sugar). The defining effect of the carbohydrate status of the plant on the potential sink activity or potential growth rate, is incorporated in SUBEMOpo by multiplying potential growth rate with a 'factor of the carbohydrate status on growth' (ERESG_o), which has a value ranging between 0 and 1. The response of ERESG_o to the carbohydrate status follows Michaelis–Menten kinetics, obeying a linear response at low carbohydrate status, and saturating at high carbohydrate status. The response function is illustrated in Fig. 3 for leaf growth (cell expansion, cell division), tap root growth, fibrous root growth and sugar storage.

1.3.3.2. RWC of the leaves. The RWC of the leaves, which has a defining effect on the CO₂ assimilation, also defines the growth of leaves (cell expansion and division), fibrous roots and tap root. The effect of RWC on the growth of a plant component is also translated with a factor (ERWCG_o) having a value between 0 and 1. The impact of RWC is not the same for all the plant components. In the model the difference in effect is created by ranking plant components according to their sensitivity to the RWC.

The root:shoot functional balance is integrated in SUBEMOpo as a composed E_{limit} . The balancing is done by analogy to the reaction of real plants to water and carbohydrate stress. Thereby, shoot growth is more affected by water stress than root growth and root growth is more affected than shoot growth by deficiencies in the carbohydrate status.

1.3.3.3. Temperature. Air temperature (TA) is considered as having an effect on leaf growth and soil temperature (TS) on fibrous root growth, tap root growth and sugar storage. Potential leaf growth is assumed between 21 and 27.5°C air temperature and root growth and sugar storage are not inhibited between 21 and 27.5°C soil temperature (Lundegardh, 1927; Ulrich, 1952). Between these specified temperature intervals the effect factor for temperature on growth has a value of 1.

1.3.3.4. Stored sugar. The sugar which is already stored is modelled as an internal factor having an influence on tap root growth rate. It implies that structural beet growth must occur before sugar can be stored, but also that a certain amount of sugar must be stored in existing cells before new cells can be produced. The forgoing is supported by observations of a relatively high sucrose concentration in the vascular cambial rings (Teranishi et al., 1956; Loomis and Ulrich, 1962; and many others). SUBEMO models the response of tap root growth rate on sugar content (ESCBG) by filling up the 'reservoir for sugar storage' to 2.5% of sugar on a fresh weight basis. As long as the threshold level of 2.5% sugar is not reached, no structural tap root growth will occur (ESCBG = 0). When the sugar content exceeds 8% on a fresh weight basis, the sugar content will no longer have a limiting effect on tap root growth (ESCBG = 1). Within the range of 2.5–8% ESCBG is computed by linear interpolation. In relation (2) ESCBG is one element of E_{limit} .

1.4. Model parameters

The values of model parameters and rate variables are most often derived from published experimental data. Most of the published data are derived from controlled environmental experiments and sometimes from field experiments. Table 1 gives a review of the model parameters and rate variables used in the model.

2. The SUBEMOpo model structure

The computer code of SUBEMOpo is written in FORTRAN 77. The model structure consists of a main program (SUBEMOpo) and several subprograms (DAILST, POTASS, P WATER, ACTASS, TOPGRO, STORAG, BETGRO, FRTGRO,

Table 1
Parameters and rate variables used in SUBEMOpo

Parameter or rate variable	Value	Unit	Reference
DWC _b , maximum dry weight of tap root capable to grow	8.0	g plant ⁻¹	Fick, 1971
EFF, initial light use efficiency for individual leaves	0.50	kg CO ₂ ha ⁻¹ h ⁻¹ (J m ⁻² s ⁻¹) ⁻¹	
FMFDL, fraction of a leaf's dry weight that is remobilized at leaf death	26	%	Ng, 1980
G _R , growth respiratory coefficient	0.25		Penning de Vries, 1972
KDIF, extinction coefficient for leaves	0.60	ha(ground) ha ⁻¹ (leaf)	
Maximum absolute growth rate of fibrous roots	0.2	g plant ⁻¹ day ⁻¹	Fick, 1971
Maximum leaf appearance rate	0.7	leaf day ⁻¹	Ulrich, 1955, 1956 Thorne et al., 1967 Fick, 1971 Ng, 1980
M _R , maintenance respiratory coefficient	0.00019583		Stout and Smith, 1950
MRGR _o , maximum relative growth rate of an organ	0.437	g g ⁻¹ day ⁻¹	Fick, 1971
P _{max} , CO ₂ assimilation rate of a leaf at light saturation (value depending on leaf age)	20–50	kg CO ₂ ha ⁻¹ h ⁻¹	Hodánová, 1979, 1981 Vandendriessche et al., 1990
SCV, scattering coefficient of leaves for photosynthetically active radiation	0.20	—	

RESPIR, RESERV, BOXCAR), each of which treats a different process. Extension of the model with other subprograms can easily be done; e.g. to allow for water or nutrient stress. SUBEMOpo works with a time step of 1 h.

2.1. Description of the main program

The main program of the model fulfils several tasks: (1) standard declarations; (2) reading input; (3) initialization; (4) organizing output; and (5) calling subprograms.

The standard declarations is the first task of the main program according to the definition of the FORTRAN 77 language. Arithmetic constants and variables (real, integer) are defined, arrays are declared, and data initialization statements are placed. Running the model requires data concerning the prevailing weather conditions and site and sugar beet specific information. The main program reads these data from an external inputfile. An overview of the necessary input for SUBEMOpo is given in Table 2.

The initialization of subprocesses is organized by the main program. To initialize crop- and site-specific variables, data of the external inputfile are used. Initialization of derived variables and of model parameters is directly done in the main program by simple assignments. Rates are set to zero explicitly to save the value of the state variables at the first integration.

After initialization the main program starts with the dynamic part of the model by calling a sequence of subprograms according to a daily and an hourly time scheme.

The organization of the model output is partly done in the initialization section of the main program and partly in the dynamic section. In the initialization section the information in the inputfile is subdivided into two outputfiles. One of these files gives a summary of the weather data (WEATHOUT), and the other file provides a listing of the initial crop data and site-specific information (INIOUT). In the dynamic section of the main program two different types of outputfiles are created. The first type contains hourly output data which are written to the files (EFFOUT, EFFGROUT) on the request of the user by specifying at which time interval hourly output is requested. The second type contains daily output midnight values (SINK-OUT, DRYWOUT, LEAFOUT). Besides, the outputfile LFDIEOUT contains information about death leaves. This information is written every moment a leaf is dying during the simulation run. A summary of the outputfiles of SUBEMOpo is given in Table 3. The outputfiles are ASCII files which can be used by a broad range of software (worksheets, statistical packages, graphical software . . .) for post-processing of the results.

2.2. Description of the subprograms

The main program of the SUBEMOpo model is extended with 11 subprograms. Most subprograms describe processes occurring in sugar beet plants, such as assimilation, respiration, transpiration, growth, development and ageing. Other subprograms deal with the initialization of state variables and fluxes and with the translation of daily weather data into hourly data. A flowchart of the model is shown in Fig. 4. The

Table 2
Overview of the necessary input for SUBEMOpo

Input description	Units
<i>Meteorological data: daily values of</i>	
Maximum air temperature	°C
Minimum air temperature	°C
Precipitation	mm day ⁻¹
Mean wind speed (height: 2 m)	m s ⁻¹
Relative humidity	%
Daily global radiation	J cm ⁻² day ⁻¹
<i>Site-specific information</i>	
Latitude	Degrees
Longitude	Degrees
<i>Information about planting and crop management</i>	
Sowing date (in days from 1 January)	–
Emergence date (in days from 1 January)	–
Harvest date (in days from 1 January)	–
Growing season (year)	–
Plant density	No. of plants m ⁻²
<i>Initial crop information</i>	
Number of living leaves per plant	–
Age of the living leaves	g m ⁻²
Total dry weight of the living leaves	g m ⁻²
Total dry weight of the tap roots	g m ⁻²
Total dry weight of the active fibrous roots	g m ⁻²
Total sugar yield	g m ⁻²
Total fresh weight of the tap root	g m ⁻²
Percentage of carbohydrates on total plant weight	%
<i>Simulation time period</i>	
Starting day of the simulation (in days from 1 January)	–
The number of days to run the program	Days
Time interval for diurnal output	Days

flowchart shows the links between the main program and the subprograms, and the way input and output are processed. Fig. 5 depicts partitioning of carbohydrates over the several subprocesses and indicates the possible effect of defining factors on it.

3. Discussion

A recent review of mechanistic sugar beet models (Vandendriessche and van Ittersum, 1995) showed that the process of sugar storage is either not described in simulation models or is incorporated as a simple mathematical expression yielding poor simulation results. Therefore, further information is still needed on the processes

Table 3
Summary of the outputfiles of SUBEMOpo

Name (and number) of outputfile	Content of the outputfile	Frequency of writing during a single-season run of the model
INIOUT (52)	Site specific information Information about planting and crop management Simulation time period	Once at start of simulation, after initialization
SINKOUT (53)	Sink terms for carbohydrates State variables concerning tap roots: dry and fresh weight; sugar content on dry and fresh weight basis	Writing output every day of the simulation run (midnight values)
EFFOUT (54)	Values of the defining effect factors for CO ₂ assimilation, respiration, and sugar storage	Writing output every hour on a day requested by the user
EFFGROUT (55)	Values of the defining effect factors for leaf appearance, leaf cell division and leaf cell expansion, tap root growth, and fibrous root growth	Writing output every hour on a day requested by the user
LFDIEOUT (56)	The day when the leaf died The number of the leaf which died The dry weight (*) of the dead leaves (g pl ⁻¹) The total dry weight (*) of all dead leaves (g m ⁻²) (*) After recuperation of carbohydrates	Writing output every hour of the simulation run that a leaf is dying
DRYWOUT (57)	State variables: dry weight of total plant, leaves, fibrous roots and the tap roots; sugar content on fresh weight basis; shoot: root ratio Rate variables: CO ₂ assimilation rate; maintenance and growth respiration; transpiration rate	Writing output every day of the simulation run (midnight values)
LEAFOUT (58)	State variables concerning leaf development: leaf area index; number of leaves per plant; number of dead leaves	Writing output every day of the simulation run (midnight values)
WEATHOUT (59)	Daily weather data: minimum and maximum air temperature (°C); precipitation (mm); wind speed (ms ⁻¹); relative humidity (%); daily global radiation (J cm ⁻² day ⁻¹).	Writing output every day of the simulation run

associated with the sucrose translocation and storage in sugar beet. Also in previous versions of SUBEMO, where the process of sugar storage was treated as in SUBGOL (Hunt, 1974) the evolution of the sugar storage is poorly simulated (Vandendriessche, 1989).

4. Conclusions

In the version of the SUBEMOdel simulating potential growth of sugar beets it is assumed that the level of carbohydrates (assimilates) is the major defining factor for growth, yield and sugar accumulation. The calculation of the structural dry matter accumulation and of sugar storage is based on the carbon balance, being the total of the gross CO₂ assimilation minus the respiration losses for maintenance and growth. Dry matter partitioning among the various plant components, and sugar accumulation is modelled in terms of sources and sinks according to a root:shoot functional balance. This teleonomic partitioning mechanism results in an interdependency of plant parts as a response to environmental changes. Development is related to the life cycle of leaves and fibrous roots, reflecting physiological age and suberization.

The shoot section of the model consists of a number of subsections for the calculation of leaf appearance, leaf growth by cell division and expansion, leaf ageing, leaf death and the calculation of LAI. Also the defining factors for these processes are estimated and the impact of those on the leaf status is done by book-keeping.

In the fibrous root section of SUBEMOpo fibrous root growth is computed in terms of dry weight and fibrous root length. The fibrous roots are divided into different age classes. Physiological ageing and suberization of the fibrous roots is calculated for every age class. Potential fibrous root growth is reduced for the defining effect of soil temperature, relative water content of the leaves and the carbohydrate status of the plant.

The growth rate of the tap root is modelled as a combination of a relative growth rate and an absolute growth rate model, and will be determined by soil temperature, carbohydrate status, relative water content of the leaves and the amount of stored sugar.

To compute sugar storage, SUBEMOpo distinguishes a prestorage stage during which no sugar is stored, and a storage stage starting from the moment the dry weight of the beet exceeds 0.1 g plant⁻¹.

The sugar beet model SUBEMOpo, written in the FORTRAN77 standard, consists of a main program and 11 subprograms. The structure of the model allows to extend it easily with other subprograms like for example a water or a nutrient balance. The inputfile consists of data and plant and site-specific information which are not too complicated to be gathered from new or historical field trials. The outputfiles are structured and organized in ASCII files, which allows post processing of the simulation results by a broad range of software.

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