Ecological Modelling, 53 (1991) 1–26
Elsevier Science Publishers B.V., Amsterdam

A demographic model of assimilation and allocation of carbon and nitrogen in grapevines

B. Wermelinger and J. Baumgärtner

Division of Plant Sciences/Phytomedicine, Swiss Federal Institute of Technology ETH,
8092 Zürich, Switzerland

A.P. Gutierrez

Division of Biological Control, University of California, Berkeley, CA 94706, U.S.A.

(Accepted 7 May 1990)

ABSTRACT

Wermelinger, B., Baumgärtner, J. and Gutierrez, A.P., 1991. A demographic model of assimilation and allocation of carbon and nitrogen in grapevines. *Ecol. Modelling*, 53: 1–26.

A dynamic crop model is presented for grapevine (*Vitis vinifera* L.) dry matter and nitrogen (N) assimilation and allocation with distributed developmental times and age structures of the plant subunits. The model forms a basis for future analyses in the vineyard ecosystem. A flowchart of the daily computations is presented and the corresponding mathematical structure is described.

In the model, the plant is divided into annual populations of fruit, leaves, shoots and roots which develop on a perennial frame. In general, these populations are age-structured and have the attributes of numbers, dry matter and N mass, and their dynamics are simulated as a time-invariant distributed delay process with attrition. Growth occurs per degree-day above the developmental threshold of 10 °C. The seasonal N dynamics is the net result of the processes of new tissue formation with high N concentrations and the constant proportional export of N from ageing parts to reserves. The latter process commences immediately after tissue formation. The mean concentration of N in a population of plant subunits is determined by the ratio between young N-rich zones and ageing N-exporting tissues.

Simulations were used to assess the patterns and magnitudes of photoassimilate allocation to the three sinks: maintenance respiration, reproductive growth and vegetative growth. In summer, roughly one-third of the assimilate available daily is allocated to each.

INTRODUCTION

A great number of crop models using various approaches have been described in the literature. Among them are simulation models which may

0304-3800/91/$03.50

be divided into engineering and demographic models (Baumgärtner and Gutierrez, 1988). The model presented here is a dynamic systems model with demographic structure. This model structure was first proposed by Gutierrez et al. (1984b) for cotton and later extended for cassava (Gutierrez et al., 1988a). From a theoretical point of view, this paradigm provides a link between crop physiology and population theory, and facilitates the structuring of multitrophic models of plant/herbivore interactions. This model type has the remarkable advantage of being readily adapted to other plant species and phytophagous arthropod pests, as well as predators or parasites (Gutierrez et al., 1987). The common structure permits the use of the same demand-driven acquisition function for plant, herbivore and antagonist species. These features enable the analyses of complex ecosystems by connecting the submodels of the respective species to one another (e.g. Gutierrez et al., 1984a; Gutierrez et al., 1988a, b, c).

A canopy model of grapevines (*Vitis vinifera* L.) (VIMO, *vi*ne *mo*del) was developed to quantify plant assimilation and allocation, and to provide a basis for evaluating interactions with associated herbivores, in particular spider mites. Previous uses of this approach in apple trees, based solely on dry matter (i.e. carbon) acquisition and allocation, revealed serious limitations (Zahner and Baumgärtner, 1988). Gutierrez et al. (1985) developed a deterministic model of grape growth and development, but unlike the present model it did not include nitrogen. Nitrogen (N) has proven to be very important for both plant and herbivore population growth in experimental (Wermelinger et al., 1985) as well as in multitrophic simulation studies (Gutierrez et al., 1988a, b, c). For this reason, a nitrogen submodel was introduced following the approach of Gutierrez et al. (1988a). In previous models of this kind, the mathematical framework was emphasized (e.g. Gutierrez et al., 1984b; Gutierrez et al., 1985; Baumgärtner et al., 1986; Baumgärtner et al., 1987; Gutierrez et al., 1988a, b, c), while in this publication the structure of the simulation model is stressed. The model was developed for the cultivar 'Pinot Noir' in Northern Switzerland, but it can be easily adapted to other varieties and for other regions. The long-term goal of this research is to provide insight into this multitrophic system rather than to predict yields.

GENERAL MODEL STRUCTURE

Physiological time

In our model, assimilation, i.e. photosynthesis and N uptake, as well as fruit and frame growth are modelled on a daily basis. Growth and ageing of leaves, shoots, and roots, however, are modelled on physiological time and are expressed in degree-days (DD). A linear relationship between developmental rates and temperature seems reasonable for most of the season. The degree-days are thus calculated by integrating the area above the developmental threshold of 10 °C reported for grapevine (Winkler et al., 1974; Gutierrez et al., 1985) and below a sine wave through the daily temperature minima and maxima (Frazer and Gilbert, 1976). The accumulation of DD > 10 °C starts on 1 January to produce the yearly heat sum (physiological time). The driving variables of the model are daily temperature extremes (°C) and radiation (MJ m^{-2}) obtained from a local weather station.

Mathematical framework of plant structure and growth

The plant is structured as a perennial frame, comprised of trunk, canes and woody roots, and the subunits of annually growing populations of leaves, shoots, white roots and fruit (inflorescences). Leaves, shoots and roots are age-structured populations that vary in developmental time (life span). Knowing the age distribution of the populations at any time t is important because of its influence on maintenance respiration and arthropod damage. Since fruit are all of approximately the same age, the growth of grape berries is modelled in a deterministic non-age-structured way. The three population attributes of numbers, dry matter, DM (g), and N mass (g) are modelled for leaves and grape berries; only DM and N mass are computed for shoots and roots. The simulation starts at 1 January with a perennial frame (Fr in Table 1).

An efficient model for handling the distribution in developmental times of individuals in a cohort was proposed by Manetsch (1976). This distributed-delay approach has been widely used to model insect phenologies (Croft and Knight, 1983) but only recently to include mortality (Gutierrez et al., 1984b). In that model, members of a cohort initiated at the same time will produce an Erlang distribution of developmental times depending on their mean developmental time T_j and parameter k_j (see below). The model utilizes constant mean developmental times in DD, hence the time-invariant delay model was used. The different plant subunits (populations, Q_j) are specified by the indices ($j =$ L, S, R) for leaves, shoots and roots, and are handled in vectors of length k_j. Each element $i \in [1, k_j]$ represents an age class of the pivotal age (iT_j/k_j) in DD containing individuals in the ith substage (see Fig. 1). The vector lengths (T_j) in DD correspond to the average longevity (maturation time) of the respective population members. The vector structure is depicted in Fig. 1, and the delay model is given in equation (1). The input x_j into the first substage is the initiation of new population members in numbers, dry matter or N mass units per DD. The outflow y_j from the last substage k_j may be interpreted as abscission of leaves or lignification of shoots and roots. Vansickle (1977) introduced premature attrition (losses) into the time-distributed delay model, which permitted the incorporation of population changes during development and thus the construction of population models (Gutierrez et al., 1984a). The parameter $\mu_{j,i}$, originally defined as attrition, includes both losses and gains (Gutierrez et al., 1984b; Severini et al., 1990b) and is used here in this

TABLE 1

Grapevine parameters used for model construction (DD = degree-days)

Parameter	Reference	Value	Source
Initial conditions			
Ω	*Setup*, 9, 11, 23	2.42 m^2 per plant	Wermelinger and Koblet (1990)
T_L	*Setup*	750 DD	Wermelinger and Koblet (1990)
T_S	*Setup*	600 DD	Field
T_R	*Setup*	150 DD	Estimate
t_{bb}	*Setup*	35.8 DD from 1 Jan.	Field
t_{bl}	*Setup*	336 DD from 1 Jan.	Field
Fr	*Setup*	865 g	Field
$Z(t=0)$	*Setup*	$0.1 \times \mathrm{Fr}$	Yang et al. (1980); Candolfi-Vasconcelos and Koblet (1990)
$n_S(t=0)$	*Setup*	14.2	Wermelinger and Koblet (1990)
$n_F(t=0)$	*Setup*	4700	Field, estimate
c_8	*Setup*	0.73%	Field
c_9	*Setup*	0.44%	Field, Alexander (1957)
$Z_N(t=0)$	*Setup*	2/3 of total frame N	Schaller et al. (1989)
$N_{soil}(t=0)$	*Setup*	1.7 g m^{-2} Ω	Field
h_{soil}	*Setup*	2.8%	Field
Constants			
c_1	3ii	0.004 g	Field
c_2	4i	1.1	Calibration value
c_3	4ii	0.1	Calibration value
c_4	4iii	0.1	Calibration value
c_5	4iv	0.7	Calibration value
c_6	6i	0.1	Calibration value
c_7	9, 11	0.75	Jackson and Palmer (1979)
c_{10}	17i, 17iii–vi	0.07	Field
c_{11}	17i, 21iv	0.02	Estimate
c_{12}	17ii	0.0044	Alexander (1957)
Q_{10}	*DM Demand*	2.3	Butler and Landsberg (1981)
β	7, 13ii–v	0.3	Penning de Vries and Van Laar (1982)
λ	10	0.6	Jackson and Palmer (1979)
α_1	12	0.02	Estimate
α_2	19	0.33	Estimate

TABLE 1 (continued)

Parameter	Reference	Value	Source
Age-specific constants			
SLA_i	11	$(8.26\mathrm{E}{-}3 + 1.74\mathrm{E}{-}4x$ $- 5.46\mathrm{E}{-}7x^2)\ \mathrm{m}^2\ \mathrm{g}^{-1}$ (age $x < 250$ DD) [a] $(1.95\mathrm{E}{-}2 - 5.37\mathrm{E}{-}6x)\ \mathrm{m}^2\ \mathrm{g}^{-1}$ (age $x > 250$ DD) [a]	Wermelinger and Koblet (1990)
LE_i	11	$1.43x/1.05^x$ (x = age/10 in DD) [a]	Kriedemann et al. (1970)
Rates			
ω	3i	$0.05\ \mathrm{DD}^{-1}$	Wermelinger and Koblet (1990)
$\delta_{\mathrm{L},i}$	3iii, 15iii, 21iv	$0.003\ \mathrm{g}\ \mathrm{DD}^{-1}$ (age < 250 DD) $0.0006\ \mathrm{g}\ \mathrm{DD}^{-1}$ (age > 250 DD)	Wermelinger and Koblet (1990)
δ_F	5ii	$(-2.0\mathrm{E}{-}3 + 6.15 - 6x$ $- 3.85\mathrm{E}{-}9x^2)\ \mathrm{g}\ \mathrm{DD}^{-1}$ (for $t > 536$ DD, x = time after budbreak)	Field
ϵ	*DM*, *N Growth*	$0.02\ \mathrm{d}^{-1}$ ($0\,°\mathrm{C}$ < Temperature < $10\,°\mathrm{C}$) $0.3\ \mathrm{d}^{-1}$ (Temperature < $0\,°\mathrm{C}$)	Calibration values
m_F	22i	$0.011\ \mathrm{DD}^{-1}$ (before bloom) $0.0038\ \mathrm{DD}^{-1}$ (after bloom)	Calibration values
$m_{\mathrm{L},i}$	22ii	$0.007\ \mathrm{DD}^{-1}$ (age < 300 DD) 0 (age > 300 DD)	Calibration values
m_S, m_R	22iii, 22iv	$0.05\ \mathrm{DD}^{-1}$	Calibration value

[a] x = pivotal age of age class i.

manner for both the dry matter and the N model. The different vectors j refer to the attributes of number, dry mass and N mass of the populations leaves, shoots and roots.

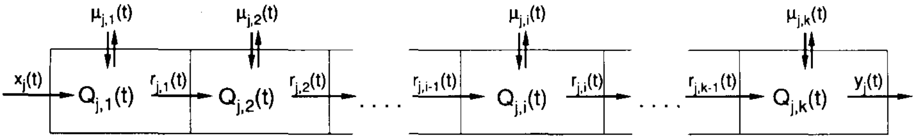

Fig. 1. Vector representing the populations and their dynamics. The symbols are explained in equation (1).

$$\begin{aligned}
\mathrm{d}Q_{j,1}/\mathrm{d}t &= x_j(t) - r_{j,1}(t) + \mu_{j,1}(t)\ Q_{j,1}(t)\\
\mathrm{d}Q_{j,2}/\mathrm{d}t &= r_{j,1}(t) - r_{j,2}(t) + \mu_{j,2}(t)\ Q_{j,2}(t)\\
&\vdots\\
\mathrm{d}Q_{j,i}/\mathrm{d}t &= r_{j,i-1}(t) - r_{j,i}(t) + \mu_{j,i}(t)\ Q_{j,i}(t)\\
&\vdots\\
\mathrm{d}Q_{j,k}/\mathrm{d}t &= r_{j,k-1}(t) - y_j(t) + \mu_{j,k}(t)\ Q_{j,k}(t) \qquad (1)
\end{aligned}$$

where i is the index denoting the substage ($1 < i < k$), k the number of substages of population j, j the index denoting the population, $r_{j,i}(t)$ the transition rate from substage i to substage $i+1$, $Q_{j,i}(t)$ the storage (mass or numbers) in substage i, $\mu_{j,i}(t)$ the age-specific proportional growth and/or loss rate, $x_j(t)$ the input in the first substage of population j (initiation of mass or numbers), and $y_j(t)$ the output out of the last substage of population j (mass or numbers).

For simulation purposes it is more convenient to write equation (1) as flow rates (Vansickle, 1977). Then, the vector elements are transition rates ($r_{j,i}$) that shift at a given rate from the first towards the last age class. The contents of the age classes ($Q_{j,i}$) in terms of numbers or mass are represented in the vectors by their transition rates ($r_{j,i} = Q_{j,i}k_j/T_j$). The simulation technique of the delay process is described in more detail by Manetsch (1976) and Vansickle (1977).

The variation in transition times (T_j) through the delay process is determined by the number of substages (k_j) which may be estimated from the mean longevity (T_j) and variance (s_j^2) (Manetsch, 1976):

$$k_j = T_j^2/s_j^2 \qquad (2)$$

The smaller k_j (less substages), the greater is the variance of the longevity. This means that at low k_j some individuals pass faster through the vector than the average and some pass more slowly thus living longer (Gutierrez et al., 1984b). The frequency distribution of output individuals depends also on $\mu_{j,i}$ (Vansickle, 1977; Schaub and Baumgärtner, 1989): the smaller k_j, the more the distribution is affected by attrition. A realistic estimate of k_j could be obtained from field data with the method of Severini et al. (1990a). In our model it was arbitrarily set to 30 for all populations, and this proved satisfactory for our purpose.

Metabolic-pool model

The metabolic-pool concept (Gutierrez and Wang, 1979) is illustrated in Fig. 2. The C and N assimilates (carbohydrates and nitrogenous compounds) available daily for distribution are viewed as pools augmented by the daily assimilation of carbon (C) and nitrogen (N) plus that remobilized from reserves. The contents of the carbohydrate and N pools are distributed according to a similar priority scheme. Conceptually, the allocation of assimilate to the various organ populations is determined by the current level of the pools and the 'outlet' levels to the respective demands. Maintenance respiration costs met only with carbohydrates have first priority. If this demand cannot be satisfied, at exhausted reserves, the plant dies. After blooming, when auxin production in the berries starts (Alleweldt, 1977), reproductive growth is given second priority for both carbohydrate and N allocation. The third priority is growth of vegetative parts (Sartorius, 1969; Taylor and Van den Ende, 1969; Ho et al., 1989). Reproductive and vegetative demands for C and N have equal priority before blooming. The last priority is accumulation or replenishing of plant reserves which are important during periods of shortfall, e.g. limited radiation at high temperatures, and as the energy source for early spring regrowth.

The Frazer and Gilbert (1976) function is used to estimate C and N acquisition (see *DM Supply*). A fundamental feature of this function is that assimilation is sink-driven, but may be limited by the availability of resources such as radiation and N in the soil. Thus the plant is able to react to increased demands resulting from internal or external stresses from insects or pathogens. Photosynthesis is leaf-age dependent and linearly related to N content of leaves (Williams and Smith, 1985; Field and Mooney, 1986). In the model, N deficiency lowers the carbohydrate demand of the plant, and indirectly affects photosynthesis.

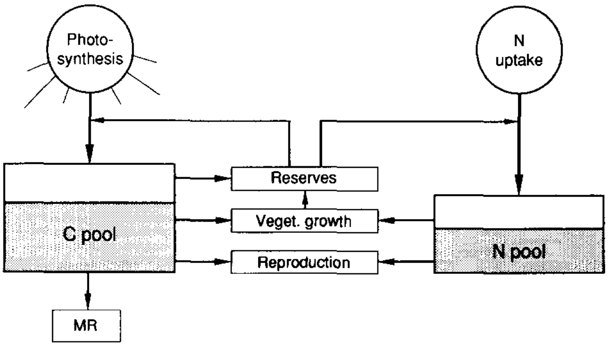

Fig. 2. Metabolic-pool model for carbohydrates (C) and nitrogen (N) (arrows indicate mass flows; MR, maintenance respiration).

Flow chart

The program was written in Turbo Pascal; its simplified flow chart is depicted in Fig. 3. The dry-matter (DM) model deals with the assimilation and allocation of carbon, while the parallel nitrogen submodel contains the processes involving N. The structure permits either running the DM model alone assuming unlimited N supply, or inclusion of the nitrogen submodel.

A short overview of the model is presented first, followed by a detailed explanation of each step. At the beginning of the program, crop parameters are read from a setup file and all state variables are initialized (procedure 'SETUP'). Subsequently the 'potential' daily DM and N demand rates (DEMAND) are calculated at the current daily thermal sum (Δt) in DD for all subunit populations assuming unlimiting conditions. In the next step (SUPPLY), the actual assimilation of C and N under the current weather and soil conditions are computed. Growth coefficients ($\Phi_j \in [0, 1]$) are computed (RATIOS) as the ratios of the acquired C and N mass (SUPPLY) and their potential for growth (DEMAND). These ratios scale the genetic potential demand rates to the actual growth rates of the population members, following the priority scheme outlined above. Dry matter is allocated to the population members on a thermal-sum (degree-day) basis, and each

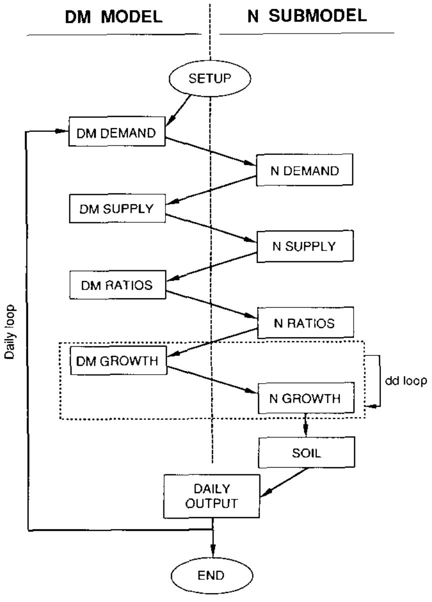

Fig. 3. Flowchart for the dry-matter (DM) and nitrogen (N) model (dd loop = computations with a time step of one degree-day).

cohort is aged (GROWTH). In the N submodel, available N in the soil is updated (SOIL). Eventually, a daily output is created (OUTPUT). The structure is identical for the DM and the N model. In the following description, reference to time t is omitted in the equations unless specifically required.

DRY-MATTER MODEL

Setup

At the beginning of the program calculations, crop parameters, management practices and initial population attributes are defined. Among these are planting density (Ω), summer pruning and harvest dates, pruning losses, longevities of leaves (T_L), shoots (T_S) and roots (T_R), maximum leaf production rate per shoot (ω), growth rates ($\delta_{L,i}$) of leaves, initial bud number (n_S) and number of flowers (n_F), weight of the vine frame (Fr) (roots, trunk, canes) and number of degree-days required for budbreak (t_{bb}) and start of blooming (t_{bl}). The initial mass of reserves ($Z(t=0)$) is calculated from the frame mass. A detailed list of parameter values is given in Table 1.

DM Demand

The demand is defined as the genetically determined maximum (potential) growth rate (Gutierrez et al., 1987), and in most cases reasonable approximations can be obtained from field observations. Potential growth of each population per day is determined from growth rates of individuals in the population under non-limiting conditions of radiation and soil N supply.

Vegetative demand has the components leaves, shoots, roots, frame (= secondary growth of perennial roots, trunk and canes) and reserves. The potential *number* of new leaves (n_ω) is determined by the leaf production rate per shoot (ω), the number of shoots (n_S) and Δt (equation 3i). The DM demand for leaf *mass* has two components. First, the maximum number of new leaves (n_ω) and the weight of leaf buds (c_1) determine the demand (b_{L1}) for new mass entering the first substage (equation 3ii). Second, the demand for age-specific growth of individual expanding leaves (b_{L2}) depends on the number of leaves ($n_{L,i}$) in age class i, their respective potential growth rates ($\delta_{L,i}$) and the daily heat sum (Δt) (equation 3iii):

$$n_\omega = \omega \cdot n_S \cdot \Delta t \tag{3i}$$

$$b_{L1} = n_\omega \cdot c_1 \tag{3ii}$$

$$b_{L2} = \sum_{i=1}^{k_L} \delta_{L,i} \cdot n_{L,i} \cdot \Delta t \tag{3iii}$$

The further vegetative demands for shoots (b_S), roots (b_R), frame (b_{Fm}) and reserves (b_{res}) are proportional to leaf demand (cf. Gutierrez et al., 1988a; Wermelinger and Koblet, 1990):

$$b_S = c_2(b_{L1} + b_{L2}) \tag{4i}$$

$$b_R = c_3(b_{L1} + b_{L2}) \tag{4ii}$$

$$b_{Fm} = c_4(b_{L1} + b_{L2}) \tag{4iii}$$

$$b_{res} = c_5(b_{L1} + b_{L2}) \tag{4iv}$$

Thus demand for vegetative growth, excluding reserves, is:

$$b_{veg} = b_{L1} + b_{L2} + b_R + b_S + b_{Fm} \tag{5}$$

The reproductive demand (b_F) for inflorescences before berry set is proportional to total leaf demand (equations 3ii, 3iii). Thereafter, fruit demand is given by a quadratic function ($\delta_F(t)$) for individual berry demand and by the number of berries (n_F) and Δt(DD):

$$b_F = c_6(b_{L1} + b_{L2}) \qquad (t \leqslant 536\text{DD}) \tag{6i}$$

$$b_F = \delta_F \cdot n_F \cdot \Delta t \qquad (t > 536\text{DD}) \tag{6ii}$$

Growth respiration (β), part of the total demand for growth (equation 7), is the cost incurred in converting photoassimilate from primary carbohydrates to structural matter, and averages 30% of net assimilation (Penning de Vries and Van Laar, 1982). Accumulation of reserves has no conversion costs.

Daily maintenance respiration (b_{MR}) depends on the kind and the mass of the tissue. It is set to 1% for roots, fruit and reserves, to 1.5% for shoots, trunk and canes, and to 3% for leaves (Penning de Vries and Van Laar, 1982). These values, valid at 25 °C, are adapted to current temperatures using a Q_{10} of 2.3 (Butler and Landsberg, 1981). In roots, shoots, trunk and canes, only the living mass respires, therefore it is necessary to keep track of the lignification processes. Including maintenance and growth respiration, the overall daily demand (b_{tot}) is given by:

$$b_{tot} = (b_F + b_{veg})/(1 - \beta) + b_{res} + b_{MR} \tag{7}$$

If the N submodel is included, the above demands (equations 3, 4, 6) are multiplied by the respective N coefficients (Φ_{NV}, Φ_{NF}) computed in the N submodel (equations 20i, 20iii).

DM Supply

The function used to calculate photosynthesis is the functional-response model developed originally for insect predation (Frazer and Gilbert, 1976) and adapted to this purpose by Gutierrez et al. (1987, 1988a). The most important difference from other photosynthesis models is that assimilation is sink-driven. This implies possible stimulation of the photosynthetic rate by increased demands for carbohydrates:

$$S = b_{\mathrm{tot}}[1 - \exp(-a \cdot M/b_{\mathrm{tot}})] \tag{8}$$

The total demand (b_{tot}) represents the maximum possible growth rate at current Δt (i.e. the saturation level of the function). The variable M represents the C resources as a function of incident light. It is the carbohydrate equivalent (g m^{-2}) of a given radiation level, determined by the amount of quanta (I), their absorption, photorespiration and the theoretically possible conversion of quanta into carbohydrates (equation 9). Loomis and Williams (1963) calculate a potential daily productivity of 77 g m^{-2} at 500 cal cm^{-2} assuming 33% photorespiration. Modifying photorespiration to 25% (Penning de Vries and Van Laar, 1982) and adapting this productivity to the SI units, a conversion constant of 4.14 is used in the model to convert radiation (MJ m^{-2}) into carbohydrates (g m^{-2}). Accounting for planting density (Ω), the resources accessible to a single plant are:

$$M = 4.14 \cdot I \cdot c_7 \cdot \Omega \tag{9}$$

Although photosynthesis represents C assimilation, i.e. carbohydrate production, the Loomis and Williams (1963) productivity potential includes the associated inorganic compounds, and therefore carbohydrate allocation is referred to as dry-matter growth. The variable a is the light-interception rate obtained from the light-extinction coefficient (λ) and the leaf-area index (LAI) (Beer's Law):

$$a = 1 - \exp(-\lambda \cdot \mathrm{LAI}) \tag{10}$$

Since the model operates on a dry-matter (g) basis, the leaf area needs to be calculated from the leaf mass. Wermelinger and Koblet (1990) give a physiological-age-dependent specific leaf area (SLA_i) (m^2 g^{-1}). The effect of leaf age on photosynthetic activity (Kriedemann et al., 1970) is accounted for by inclusion of a leaf-age-specific coefficient of photosynthetic efficiency (LE_i) in the calculation of LAI:

$$\mathrm{LAI} = \sum_{i=1}^{k_{\mathrm{L}}} (Q_{\mathrm{L},i} \cdot \mathrm{SLA}_i \cdot \mathrm{LE}_i)/(c_7 \cdot \Omega) \tag{11}$$

where $Q_{\mathrm{L},i}$ is the dry mass of leaves in age class i, c_7 the proportion of the area shaded by the plant, and Ω is the planting density (m^2 per plant). With $\mathrm{LE}_{\mathrm{i}} = 1$ the actual LAI observed in the field is obtained. Note that all environmental and biotic factors are in the variables a, M and b_{tot}.

DM Ratios

The growth coefficients are calculated using allocation priorities (Fig. 2). The amount of carbohydrates (C_1) available in the metabolic pool for daily growth equals the sum of daily photosynthesis (S) and a fraction (α_1) of the reserves (Z):

$$C_1 = S + \alpha_1 Z \tag{12}$$

Maintenance respiration (b_{MR}) is subtracted first from this pool (13i). The index of C corresponds to the amount of assimilate available at the respective priority level (equation 13). For example, the index '1' refers to respiration with first priority. If $C_2 < 0$, additional reserves may be used; otherwise, after depletion of the reserves, the plant dies and the simulation is terminated. Since fruit has second priority, the remaining photosynthates (C_2) are used to compute the supply/demand ratio for the fruit growth coefficient (Φ_{F}). Once the amount used for fruit growth including growth respiration (β) is subtracted, the remaining supply (C_3) is available for vegetative growth (third priority). In an analogous way, the ratio supply/demand for the vegetative coefficient (Φ_{V}) is calculated and the corresponding dry mass subtracted from the metabolic pool. These coefficients are limited to a value between 0 and 1. The remaining photosynthates (C_4) are added to the reserves (Z). The computations are as follows:

$$C_2 = C_1 - b_{\mathrm{MR}} \tag{13i}$$

$$\Phi_{\mathrm{F}} = C_2/(b_{\mathrm{F}}/(1-\beta)) \qquad \Phi_{\mathrm{F}} \in [0, 1] \tag{13ii}$$

$$C_3 = C_2 - \Phi_{\mathrm{F}} \cdot b_{\mathrm{F}}/(1-\beta) \tag{13iii}$$

$$\Phi_{\mathrm{V}} = C_3/(b_{\mathrm{veg}}/(1-\beta)) \qquad \Phi_{\mathrm{V}} \in [0, 1] \tag{13iv}$$

$$C_4 = C_3 - \Phi_{\mathrm{V}} \cdot b_{\mathrm{veg}}/(1-\beta) \tag{13v}$$

Before blooming, both reproductive (inflorescences) and vegetative growth have the same priority level ($\Phi_{\mathrm{F}} = \Phi_{\mathrm{V}}$). After harvest, reserves take over the priority level of fruit (cf. Sartorius, 1969) so as to fill up reserves for winter respiration and sprouting next spring.

DM Growth

The demands of the various populations are scaled down to actual growth by the growth coefficients (Φ_{F} and Φ_{V}).

Growth per day. The daily mass increments of grapes (inflorescences) and frame can be simply expressed as:

$$\Delta Q_{\mathrm{F}} = b_{\mathrm{F}} \cdot \Phi_{\mathrm{F}} \tag{14i}$$

$$\Delta Q_{\mathrm{Fm}} = b_{\mathrm{Fm}} \cdot \Phi_{\mathrm{V}} \tag{14ii}$$

and they are added to current fruit and frame mass, respectively. If $\Phi_{\mathrm{F}} < 1$, i.e. if C stress occurs, fruit number and mass suffer a loss provided they are in a shedding window of 350 DD beginning at blooming. This is modelled by multiplying the fruit number (n_{F}) by the daily coefficient $0.8 \leq \Phi_{\mathrm{F}} \geq 1.0$.

Growth per degree-day. Once the above processes are calculated, growth and ageing of leaves, shoots, and roots are computed via the delay model (Fig. 1). The formation of new leaves, in terms of number and dry mass entering the first age class (initiation), is represented by x_{nL} and x_{L}, respectively. The proportional mass increase ($\mu_{\mathrm{L},i}$) is the expansion of existing leaves ($Q_{\mathrm{l},i}$) of age class i:

$$x_{\mathrm{nL}} = n_{\omega} \cdot \Phi_{\mathrm{V}}/\Delta t \tag{15i}$$

$$x_{\mathrm{L}} = b_{\mathrm{L1}} \cdot \Phi_{\mathrm{V}}/\Delta t \tag{15ii}$$

$$\mu_{\mathrm{L},i} = (\delta_{\mathrm{L},i} \cdot n_{\mathrm{L},i} \cdot \Phi_{\mathrm{V}}/Q_{\mathrm{L},i})/\Delta t \tag{15iii}$$

The time step for the population growth is 1 DD, hence, the delay process is performed Δt times per day. Consequently, the delay input into the first age class (equations 15i, ii) and into the subsequent age classes (equations 15iii) has to be divided by Δt for each pass. Leaves leaving the delay (y_{L}) are abscised from the grapevine, but 16% of the dry mass is reallocated as carbohydrates to reserves (data for apple leaves; Oland, 1963).

Shoot and root growth occur exclusively as inputs x_{s} and x_{R}, i.e. by initiation into the first age class:

$$x_{\mathrm{S}} = b_{\mathrm{S}} \cdot \Phi_{\mathrm{V}}/\Delta t \tag{16i}$$

$$x_{\mathrm{R}} = b_{\mathrm{R}} \cdot \Phi_{\mathrm{V}}/\Delta t \tag{16ii}$$

Thus, the leaf population consists of individual numbers and masses of leaves of different ages, but only mass age distribution is modelled for shoots and roots. All realized growth rates automatically include growth respiration. The ouflows y_{s} and y_{R} from the shoot and root vectors refer to lignification. One-third of this output mass is available as reserves, while two-thirds become an inactive part of the perennial system.

Mortalities per day. During the growing season, leaf and shoot mass/numbers are removed by pruning, but the number of shoots can increase (see section Parameterization and calibration) due to lateral shoots appearing after the loss of apical dominance. In late autumn, a daily mortality (ϵ) due to temperatures below the developmental threshold is applied outside of the delay process to model leaf-fall. Since ageing is degree-day driven and none is accumulated at the low temperatures of late autumn, the shedding of leaves cannot be accounted for by the regular delay procedure.

Daily output

At the end of the day, reserves are allocated to the storage organs such as shoots, frame and roots, in proportion to their mass, and the substages of all subunits are summed up to obtain numbers and mass of the populations. Numerical or graphical real-time output is created.

NITROGEN MODEL

The N submodel has the same structure as the DM model. The unit of N assimilation and allocation is (g per plant). The N mass is a population attribute contained in vectors in the same way as dry matter. Thus the leaf population has three attributes that are age-structured and may be represented by three vectors (numbers, dry matter, N mass) with a common age index. Shoots and roots have two age-structured attributes (dry matter and N mass). Potential or genetically defined N demand is assumed to be linearly related to DM growth. The dynamics of N in a subunit population is given by the following mechanism: the growth of new zones of tissue with a potential N concentration (demand) is scaled by an N-growth coefficient. Once this tissue is formed, N begins to be removed from it during its ageing process at a constant rate. This remobilized N mass is added to the common N reserve pool. The two processes of import and export overlap during the growth of the plant population members. The resulting balance between N-rich growing zones (e.g. shoot tips) and low-N ageing zones (e.g. lignifying shoot parts) determines the average N concentration of an organ population (e.g. mean shoot N).

Nitrogen assimilation occurs via a similar demand-driven acquisition function as used for carbohydrates. The resources are the nitrates in the soil, which are updated daily by the mineralization of organic matter and subsequent nitrification, input from the atmosphere and microorganisms, uptake by the plant, and other losses (leaching). Generally, the same variables are used as in the DM model, indexed by ‘N’.

Setup

If the nitrogen submodel is switched on, some additional initial values are read in the procedure 'SETUP': initial N concentration of perennial roots (c_8) and of the woody above ground frame (trunk and canes, c_9); initial N reserves ($Z_N(t=0)$) in spring; and the initial amount of N as nitrates in the soil ($N_{soil}(t=0)$). From the humus percentage (h_{soil}) the organic matter content (g m^{-2}) is calculated (Jones et al., 1974).

Nitrogen Demand

The demands of the different plant subunit members for N are proportional to their dry-matter growth (equations 14–16). The proportion is given by the potential N concentration of new growth of the respective population. Before blooming, the N demand of reproductive growth (bN_F) is the same as for vegetative growth but it is lower after blooming. Vegetative N demand is calculated via the common potential N concentration (c_{10}) for leaves, shoots and roots and c_{12} for the frame. Nitrogen demand of expanding leaves (bN_{L2}) is age-dependent. The calculations are made as follows:

$$bN_F = \Delta Q_F \cdot a \qquad \begin{array}{ll} a = c_{10} & \text{before blooming} \\ a = c_{11} & \text{after blooming} \end{array} \tag{17i}$$

$$bN_{Fm} = \Delta Q_{Fm} \cdot c_{12} \tag{17ii}$$

$$bN_{L1} = x_L \cdot c_{10} \tag{17iii}$$

$$bN_{L2} = \sum_{i=1}^{k_L} \delta_{L,i} \cdot n_{L,i} \cdot \Phi_V \cdot c_{10} \cdot \Delta t \tag{17iv}$$

$$bN_S = x_S \cdot c_{10} \tag{17v}$$

$$bN_R = x_R \cdot c_{10} \tag{17vi}$$

$$bN_{veg} = bN_{Fm} + bN_{L1} + bN_{L2} + bN_S + bN_R \tag{17vii}$$

The plant has no N demand for respiration. Total N demand (bN_{tot}) therefore is the sum of the above components ($= bN_F + bN_{veg}$).

Nitrogen Supply

The N acquisition function (equation 18) is analogous to equation (8) and needs only brief explanation. In order to limit accumulation of N reserves, the maximum N uptake (bN) is the total demand (bN_{tot}) diminished by a fraction (1/3) of the available N reserves of the plant. The search rate (a) is the ratio of the current mass of white roots to the maximum amount of these roots usually reached during a season. This assumes that, when living root mass is greatest, the plant has access to all nitrates in the soil (N_{soil}) at time t:

$$N_{\text{uptake}} = bN\left[1 - \exp(-a \cdot N_{\text{soil}}/bN)\right] \tag{18}$$

Nitrogen Ratios

In analogy to the DM model, a fraction of the N reserves (Z_{N}) is allowed to be used. This is very important for sprouting in spring (Taylor and May, 1967):

$$N_1 = N_{\text{uptake}} + \alpha_2 \cdot Z_{\text{N}} \tag{19}$$

The priority scheme for N is identical to that for dry matter, except that no respiration costs for N are subtracted. Φ_{NF} and Φ_{NV} denote the N coefficients for fruit and vegetative parts, respectively. Before blooming, reproductive and vegetative demands have the same priority ($\Phi_{\text{NF}} = \Phi_{\text{NV}}$):

$$\Phi_{\text{NF}} = N_1/bN_{\text{F}} \qquad \Phi_{\text{NF}} \in [0, 1] \tag{20i}$$

$$N_2 = N_1 - (bN_{\text{F}} \cdot \Phi_{\text{NF}}) \tag{20ii}$$

$$\Phi_{\text{NV}} = N_2/bN_{\text{veg}} \qquad \Phi_{\text{NV}} \in [0, 1] \tag{20iii}$$

$$N_3 = N_2 - \left(bN_{\text{veg}} \cdot \Phi_{\text{NV}}\right) \tag{20iv}$$

The remaining N_3 is allocated to N reserves. The reproductive and vegetative N growth coefficients are used to scale N allocation (equations 21, 22) and dry-matter demand (equations 3, 4, 6).

Nitrogen Growth

On a daily basis, N increments of fruit (inflorescences, ΔN_{F}) and frame (ΔN_{Fm}) are calculated, but growth and ageing of the other populations are performed per DD as in the dry-matter model.

$$\Delta N_{\text{F}} = bN_{\text{F}} \cdot \Phi_{\text{NF}} \tag{21i}$$

$$\Delta N_{\text{Fm}} = bN_{\text{Fm}} \cdot \Phi_{\text{NV}} \tag{21ii}$$

$$x_{\text{NL}} = bN_{\text{L1}} \cdot \Phi_{\text{NV}}/\Delta t \tag{21iii}$$

$$g_{\text{NL},i} = (\delta_{\text{L},i} \cdot n_{\text{L},i} \cdot \Phi_{\text{V}} \cdot c_{10} \cdot \Phi_{\text{NV}}/Q_{\text{NL},i})/\Delta t \tag{21iv}$$

$$x_{\text{NS}} = bN_{\text{S}} \cdot \Phi_{\text{NV}}/\Delta t \tag{21v}$$

$$x_{\text{NR}} = bN_{\text{R}} \cdot \Phi_{\text{NV}}/\Delta t \tag{21vi}$$

The constant N extraction rates (m_j) per DD are tissue-specific, and are divided at N deficiency by the respective N coefficients (Φ_{NF}, $\Phi_{NV} \in [0.5, 1]$. Thus, if Φ_{NF} and Φ_{NV} are less than 1, the extraction rates are increased. The daily net N accumulation of fruit is the balance of N acquisition and remobilization (equation 22i). Exports of N from leaves, shoots and roots are computed per degree-day in the delay process, with the loss rates having the opposite sign to the growth rates. The net growth rate of leaves $\mu_{NL,i}$ per DD, given by growth $g_{NL,i}$ and loss (m_L/Φ_{NV}), corresponds to the attrition $\mu_{j,i}$ in equation (1). For shoots and roots, only proportional losses ($\mu_{NS,i}$ and $\mu_{NR,i}$) are modelled via attrition:

$$N_F(t) = (N_F(t - \Delta t) + \Delta N_F)(1 - m_F/\Phi_{NF}\,\Delta t) \qquad \Phi_{NF} \in [0.5, 1] \qquad (22i)$$

$$\mu_{NL,i} = g_{NL,i} + m_{L,i}/\Phi_{NV} \qquad \Phi_{NV} \in [0.5, 1] \qquad (22ii)$$

$$\mu_{NS,i} = m_S/\Phi_{NV} \qquad \Phi_{NV} \in [0.5, 1] \qquad (22iii)$$

$$\mu_{NR,i} = m_R/\Phi_{NV} \qquad \Phi_{NV} \in [0.5, 1] \qquad (22iv)$$

Before leaves are abscised, 50% of leaf N is remobilized (Oland, 1963; Taylor and Van den Ende, 1969) and translocated to the N reserves. In reality this process takes 3–4 weeks, but for simplicity it was modelled via the outflow (y_{NL}) in equation (1). The same summer pruning and frost mortalities are applied as in the DM model.

Soil

Soil N dynamics is modelled in a very simple way on a per-plant basis. The nitrates in the root zone of a plant are considered to be in a container to which the plants has access depending on its relative root mass. This available N is updated by mineralization (N_{OM}): 4% of the N in organic matter (5% N) becomes available to the plant in a 160-day season (Jones et al., 1974). An average daily amount (N_{fix}) based on an annual 9 g m^{-2} is imported from atmospheric deposition and biological fixation. In addition to the extraction by the plant (N_{uptake}) there is a daily N loss (N_{loss}) (leaching, volatilization) given by an annual export of 5 g m^{-2}. These values were calculated for the year 1987 in Switzerland (Stadelmann, 1988), but are typical for many regions in Europe. Ω corrects for planting density. Daily N [g m^{-2} Ω] available to a plant is therefore:

$$N_{soil}(t) = N_{soil}(t - \Delta t) + N_{OM} - N_{uptake} + \Omega(N_{fix} - N_{loss}) \qquad (23)$$

Daily output

Nitrogen from the reserves pool is counted with the populations as in the DM model. Nitrogen concentrations of the subunit populations are calculated, and graphical output similar to that shown in Fig. 4 is created.

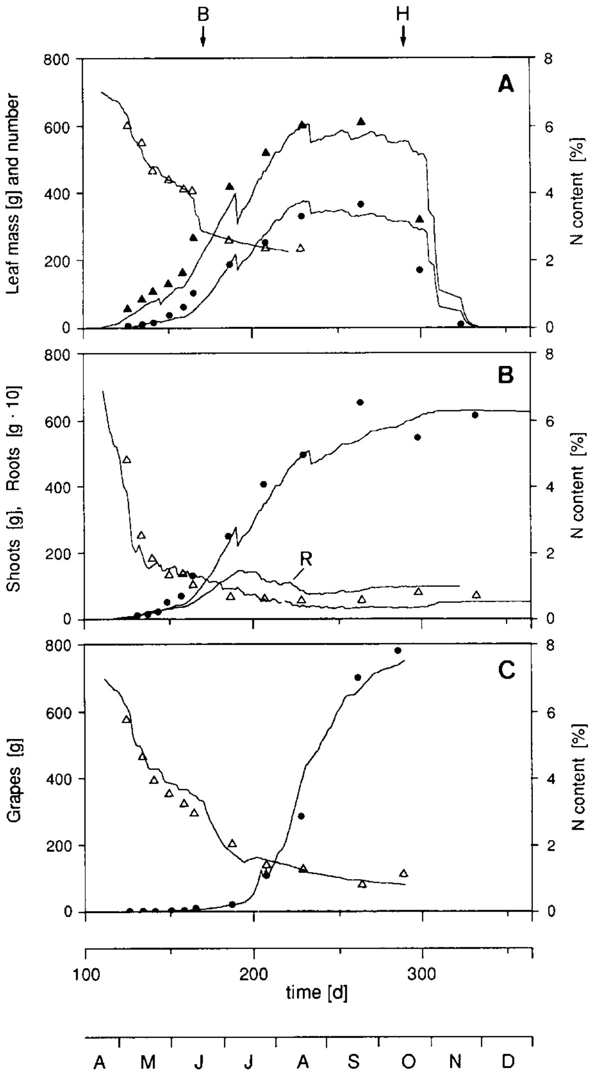

Fig. 4. Simulated (lines) and observed data (symbols) of grapevine development on a per-plant basis during the growing season 1988 at Wädenswil, Switzerland (time in Julian days; B, blooming; H, harvest): mass (●), number (▲) and N content (△) of leaves (4A); living root mass (*R*) and shoot mass (●) and N content (△) of shoots (4B); mass (●) and N content (△) of grapes (4C).

PARAMETERIZATION AND CALIBRATION

Most parameter values were estimated in 1988 in a 'Pinot Noir' vineyard in Wädenswil near Zürich, Switzerland. The sampling techniques and the field data are presented elsewhere (Wermelinger and Koblet, 1990). Other data were extracted from literature sources on vine or other deciduous plants where appropriate. All parameter values are listed in Table 1.

Dry-matter model

No calibration was necessary for the leaf dry-matter growth patterns. The constant proportionality factors ($c_2 - c_6$) for other vegetative growth were calibrated to meet the field data. To some extent, the summer pruning losses could be used to adjust the magnitude of leaf and shoot production, but this did not affect the production patterns. Pruning losses of leaves and shoots were estimated in the field from counts of the number of leaves per shoot before and after pruning. Summer pruning losses were set to 25%, 25%, and 10% on 25 May, 10 July, and 23 August, respectively. The multiplication of growing shoots after pruning, caused by lateral shoot production, was set to 1.7, 1.0, and 1.0.

Nitrogen submodel

It was not possible to estimate the rates of the postulated overlapping processes of N import and export in young growing zones in the field. Therefore, the extraction rates (m_j) of N out of the ageing tissues had to be calibrated to meet the slopes of the population N concentrations. The extraction rate per DD was kept constant during the whole season, which implies a higher turnover of proteins and, therefore, a higher N remobilization on warm days. Fruit had two different basic rates (m_F) of N extraction: before blooming it was 0.011 DD^{-1} and after blooming 0.0038 DD^{-1}. Leaf N was extracted at a rate (m_L) of 0.007 DD^{-1} up to a leaf age of 300 DD (Wermelinger and Koblet, 1990), the rate being zero until abscission when an additional fraction of the leaf N mass (see N submodel) was translocated to the N reserves. For shoots and roots the export of N to reserves occurred from all age classes, the remobilization rates (m_s and m_R) being 0.05 DD^{-1} each. The above estimates form the base rates which are increased during N deficiency by the coefficients Φ_{NF} and Φ_{NV}. Proportional pruning losses are the same as for DM.

SIMULATION RESULTS

As a verification of the model (Dent and Blackie, 1979), the logical correctness of the computer program and the adequacy of the description of the biological mechanisms were checked by comparing the simulations with the field data. In Fig. 4, the simulated DM and N development of the populations leaves, shoots, roots and fruit are presented with the corresponding field data (Wermelinger and Koblet, 1990). Leaf number and mass (Fig. 4A) are slightly underestimated at the beginning of growth. This can be explained by the simultaneous appearance of 2–3 leaflets at budbreak in the field, while the model operates on the basis of a constant leaf production rate per DD. The decline in leaf number and mass in late May, mid July and late August is caused by the summer prunings. The simulation of leaf area is not included, but it follows in magnitude (in dm^2) and shape the curve for leaf numbers. The line indicating leaf N represents the N concentration of a leaf initiated at the beginning of the season. By mid August these leaves have reached the end of their average life-span and are shed. Shoot mass (Fig. 4B) continues to increase until the end of the season, reduced only by the summer prunings. The N concentration declines sharply in early season but stabilizes as the shoots are increasingly lignified. The slight increase in shoot N in early November is in response to the reallocation of N reserves from the abscised leaves to the woody tissues. The simulated development of white, unlignified roots (Fig. 4B) lacks corresponding field data. However, the shape corresponds to the description of root growth in the literature (Champagnol, 1984), except that the decrease in living roots in the autumn in the field is not matched, because low temperatures hinder the ageing process using the linear degree-day model. Unfortunately, data to construct an appropriate non-linear development-rate model are not available. Root growth is known to start later than shoot growth in spring (Freeman and Smart, 1976). In Fig. 4C, the development of grape growth and N content is depicted. The fluctuations of DM at the end of July reflect the shedding of grape berries after blooming during a period of assimilate shortage.

In addition, the model was used to evaluate the daily proportional distribution of photoassimilate to the three sinks, respiration, reproductive growth and vegetative growth. Fig. 5B shows the daily gross photosynthesis expressed as carbohydrates produced, given by the abiotic factors, solar radiation (Fig. 5A) and temperature (Fig. 5C). Respiration (Fig. 5D) remains at a low level in winter and early spring, subsequently rising as the respiring plant mass and temperature increase. The effect of harvest, i.e. the removal of a considerable amount of respiring tissue, is visible on day 292. Relevant fruit increments (Fig. 5E) are restricted to a short period during the season, whereas vegetative growth occurs during the whole growing season. The magnitude of the daily peaks in summer is similar for all three sinks, i.e. the daily carbon gain is distributed in roughly equal parts to respiration, reproduction and vegetative growth, provided radiation and N uptake are not limiting. Thus, roughly one-third of the daily assimilation of a grapevine in summer is respired by living tissue. The effect of the allocation priority levels is visible in the extent of the daily fluctuations. Respiration, having top priority and depending only on temperature, is not

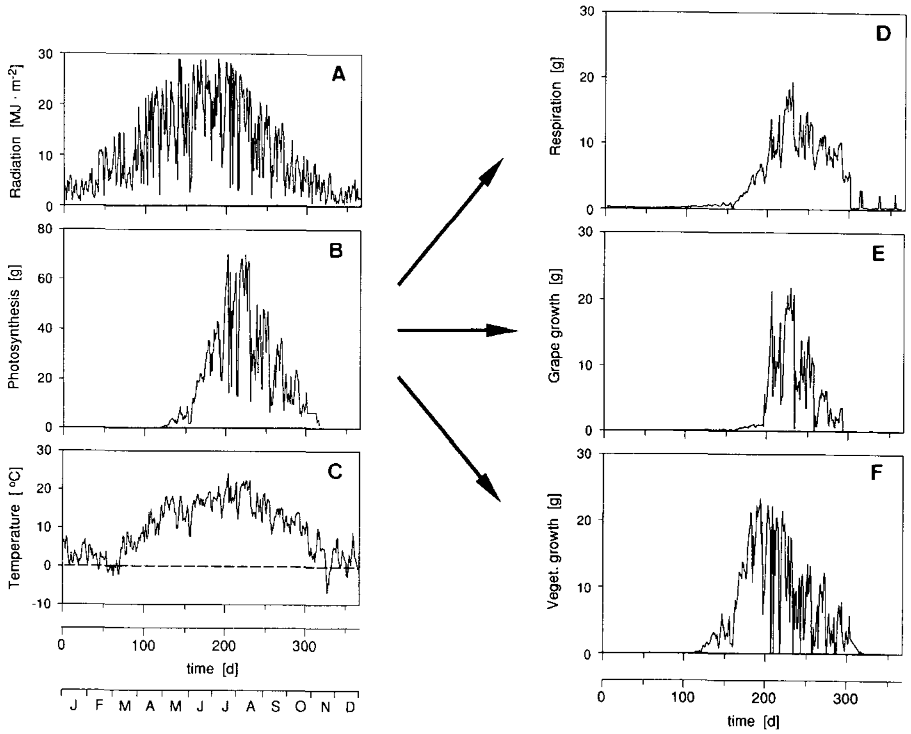

Fig. 5. Photoassimilate production (B) of grapevine on a per-plant basis, given by the climatic factors radiation (A) and temperature (C), and assimilate distribution to the three sinks, maintenance respiration (D), reproductive growth (E) and vegetative growth (F) during the year 1988 at Wädenswil, Switzerland.

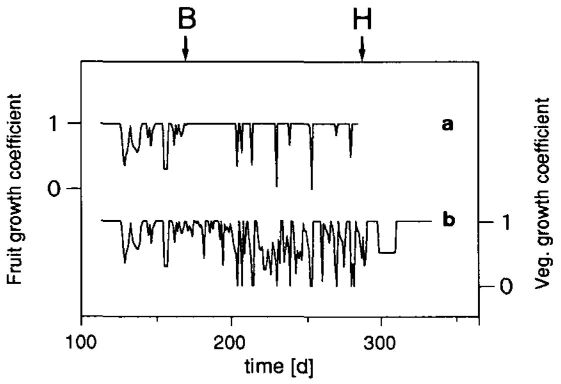

Fig. 6. Course of the dry-matter growth coefficients (Φ_F and Φ_V, see text) for reproductive (a) and vegetative (b) growth during the growing season 1988 at Wädenswil, Switzerland (B, budbreak; H, harvest).

affected by limiting radiation, fruit growth with second priority is occassionally severely impaired, and vegetative growth suffers most from limiting radiation and is characterized by frequent and considerable daily fluctuations. This is confirmed by the behavior of the DM growth coefficients for reproductive and vegetative growth (Fig. 6). Before blooming, they have the same priority and therefore show the same pattern. Thereafter, the vegetative coefficient shows much more fluctuations than the reproductive.

DISCUSSION

The presented model (VIMO) is a canopy model representing growth and development of an average plant in a stand. It was developed as a tool to increase understanding of the interactions between different trophic levels, rather than for mere plant-physiology purposes. The development of the plant model is a first step in this process, but at the same time the model is applicable for the assessment of the effect of management practices, such as summer pruning or fertilization, on yield formation and dry-matter production. A sensitivity analysis to determine the effects of different levels of N in the soil on productivity and grape leaf quality is presented elsewhere (Wermelinger and Baumgärtner, 1990). Together with the sensitivity analysis, the model shows its usefulness according to most of the criteria defined by Cale et al. (1983).

In general, the correspondence of the simulation results with the observed field data was good. In this modelling paradigm, the maximum growth rates determined in the field were used as demand parameters that were modified during the season by weather and soil conditions. These interactions produced the growth patterns observed in the field. The most important plant characteristic in the model is maximum leaf growth rate. Sartorius (1969) reports that single cells and not organs were the driving sink for sugars. This suggests the necessity of modelling the age structure of tissues, and supports our concept of N allocation into newly formed tissue zones with a potential demand and a constant N remobilization rate out of ageing tissue. This approach satisfactorily described the development of N concentrations in a biologically reasonable manner. The extracted N may not exit the organ but be reallocated to a newly formed zone in the same organ. In the model, remobilized N is simply added to the common N pool. A similar model was proposed for cassava growth (Gutierrez et al., 1988a) which used age-dependent N extraction rates, i.e. higher remobilization rates from older tissues.

A valuable feature of the present model is that it allows the inclusion of the N submodel by a simple on/off switch. Often, data sets exclude N and under non-limiting N conditions the model can be run as a pure DM model.

However, evaluation of the effects of N supply showed the necessity of including the N submodel under conditions of limited supply (Wermelinger and Baumgärtner, 1990). One of the problems often encountered in models of perennial plants was the lack of reserves at the end of the growing season. In this model, the carbohydrate reserves were depleted by the end of July, where replenishment started and continued until the end of leaf-fall. The level at the end of the year was 20% higher than at the beginning of the year. Roughly one-third would be removed by winter pruning of the shoots. Therefore, the plant would start with an adequate amount of reserves in the following spring. This feature makes the model suitable for multi-seasonal studies. The level of N reserves at the end of the year was 40% higher than the starting level, caused either by excessive N uptake or remobilization from abscised leaves.

The approach of demand-driven photosynthesis is supported by previously developed models (Gutierrez, Baumgärtner and colleagues) successfully using the same concept, and by field observations (Smart, 1974; Koblet, 1985). The proportional reduction of DM demand by the N coefficients is in agreement with the linear relationship between the N content of the plant and relative DM growth rates reported by Hirose (1988). The inclusion of leaf-age-dependent photosynthesis qualifies the model for the analysis of interactions between host plants and herbivores with preferences for certain leaf-age classes.

Similar models on grape growth in California (Gutierrez et al., 1985; Williams et al., 1985) simulated linear growth of leaves and shoots. Since radiation and temperature are not limiting in the Central Valley of California, most of the growth demand was realized in those models and the discrepancies with the field data were attributed to water stress, which was not included in the models. Under the conditions of northern Switzerland, water deficiency rarely poses a problem to vine development. However, the limiting factors may be radiation, temperature and plant nutrition, which are included in the DM and N models.

The shortcomings of the model are its simplistic approach of the dynamics of N in the soil, the poor background information on root development, the insufficiently considered effects of vineyard architecture on light interception, the lack of plant architecture itself, and some estimates of reserve utilization. Most of the improvements require extensive research. A sophisticated soil-N model would require inclusion of soil and plant water dynamics and a desirable extension of the model would be the inclusion of grape sugar content, i.e. wine quality.

ACKNOWLEDGEMENTS

Many thanks are due to Dr. D. Rubli for carefully preparing the figures and to Mrs. M. Graf for reviewing the manuscript. The Swiss Meteorological Institute kindly provided the weather data.

REFERENCES

Alexander, D.McE., 1957. Seasonal fluctuations in the nitrogen content of the Sultana vine. Aust. J. Agric. Res., 8: 162–178.

Alleweldt, G., 1977. Wachstum und Reife der Weinbeere. Z. Pflanzenernähr. Bodenkd., 140: 25–34.

Baumgärtner, J. and Gutierrez, A.P., 1989. Simulation techniques applied to crops and pest models. In: Parasitis 88, Proc. Scientific Congress, 25–28 October 1988, Barcelona. Bol. San. Veg., 17: 175–214.

Baumgärtner, J., Genini, M., Graf, B., Gutierrez, A.P. and Zahner P., 1986. Generalizing a population model for simulating 'Golden Delicious' apple tree growth and development. Acta Hortic., 184: 111–122.

Baumgärtner, J., Bieri, M. and Delucchi, V., 1987. Growth and development of immature life stages of *Propylaea 14-punctata* L. and *Coccinella 7-punctata* L. (Col.: Coccinellidae) simulated by the metabolic pool model. Entomophaga, 32: 415–423.

Butler, D.R. and Landsberg, J.J., 1981. Respiration rates of apple trees, estimated by CO_2-efflux measurements. Plant Cell Environ., 4: 153–159.

Cale, W.G., Jr., O'Neill, R.V. and Shugart, H.H., 1983. Development and application of desirable ecological models. Ecol. Modelling, 18: 171–186.

Candolfi-Vasconcelos, M.C. and Koblet, W., 1990. Yield, fruit quality, bud fertility and starch reserves of the wood as a function of leaf removal in *Vitis vinifera*–Evidence of compensation and stress recovering. Vitis, 29: 199–221.

Champagnol, F. (Editor), 1984. Elements de physiologie de la vigne et de viticulture générale. François Champagnol, B.P. 13 Prades-le-Lez, 34980 Saint-Gely-du-Fesc, 351 pp.

Croft, B.A. and Knight, A.L., 1983. Evaluation of the PETE phenology modeling system for integrated pest management of deciduous tree fruit species. Bull. Entomol. Soc. Am. 29: 37–42.

Dent, J.B. and Blackie, M.J. (Editors), 1979. Systems Simulation in Agriculture. Applied Science Publishers Ltd., London, 180 pp.

Field, C. and Mooney, H.A., 1986. The photosynthesis–nitrogen relationship in wild plants. In: T.J. Givnish (Editor), On the Economy of Plant Form and Function. Cambridge University Press, Cambridge, pp. 25–55.

Frazer, B.D. and Gilbert, N., 1976. Coccinellids and aphids: a quantitative study of the impact of adult ladybirds (Coleoptera: Coccinellidae) preying on field populations of pea aphids (Homoptera: Aphididae). J. Entomol. Soc. Br. Columbia, 73: 33–56.

Freeman, B.M. and Smart, R.E., 1976. Research note: a root observation laboratory for studies with grapevines. Am. J. Enol. Vitic., 27: 36–39.

Gutierrez, A.P. and Wang, Y., 1979. Applied population ecology: models for crop production and pest management. In: G.A. Norton and C.S. Holling (Editors), Pest Management. Proc. Int. Conf., 25–29 October 1976. Pergamon, Oxford, pp. 225–280.

Gutierrez, A.P., Baumgärtner, J.U. and Summers, C.G., 1984a. Multitrophic models of predator–prey energetics. Can. Entomol., 116: 923–963.

Gutierrez, A.P., Pizzamiglio, M.A., Dos Santos, W.J., Tennyson, R. and Villacorta, A.M., 1984b. A general distributed delay time varying life table plant population model: cotton (*Gossypium hirsutum* L.) growth and development as an example. Ecol. Modelling, 26: 231–249.

Gutierrez, A.P., Williams, D.W. and Kido, H., 1985. A model of grape growth and development: the mathematical structure and biological considerations. Crop Sci., 25: 721–728.

Gutierrez, A.P., Schulthess, F., Wilson, L.T., Villacorta, A.M., Ellis, C.K. and Baumgärtner, J.U., 1987. Energy acquisition and allocation in plants and insects: a hypothesis for the possible role of hormones in insect feeding patterns. Can. Entomol., 119: 109–129.

Gutierrez, A.P., Wermelinger, B., Schulthess, F., Baumgärtner, J.U., Herren, H.R., Ellis, C.K. and Yaninek, J.S., 1988a. Analysis of biological control of cassava pests in Africa: I. Simulation of carbon, nitrogen and water dynamics in cassava. J. Appl. Ecol., 25: 901–920.

Gutierrez, A.P., Neuenschwander, P., Schulthess, F., Herren, H.R., Baumgärtner, J.U., Wermelinger, B., Löhr, B. and Ellis, C.K., 1988b. Analysis of biological control of cassava pests in Africa: II. Cassava mealybug *Phenacoccus manihoti*. J. Appl. Ecol., 25: 921–940.

Gutierrez, A.P., Yaninek, J.S., Wermelinger, B., Herren, H.R. and Ellis, C.K., 1988c. Analysis of biological control of cassava pests in Africa: III. Cassava green mite *Mononychellus tanajoa*. J. Appl. Ecol., 25: 941–950.

Hirose, T., 1988. Modelling the relative growth rate as a function of plant nitrogen concentration. Physiol. Plant., 72: 185–189.

Ho, L.C., Grange, R.I. and Shaw, A.F., 1989. Source/sink regulation. In: D.A. Baker and J.A. Milburn (Editors), Transport of Photoassimilates. Longman, Harlow, Essex, Great Britain, pp. 306–343.

Jackson, J.E. and Palmer, J.W., 1979. A simple model of light transmission and interception by discontinuous canopies. Ann. Bot., 44: 381–383.

Jones, J.W., Hesketh, J.D., Kamprath, E.J. and Bowen, H.D., 1974. Development of a nitrogen balance for cotton growth models: a first approximation. Crop Sci., 14: 541–546.

Koblet, W., 1985. Influence of light and temperature on vine performance in cool climates and applications to vineyard management. In: D.A. Heatherbell, P.B. Lombard, F.W. Bodyfelt and S.F. Price (Editors), Proc. Int. Symp. Cool Climate Viticulture and Enology, Eugene, OR, 25–28 June 1984. Oregon State Univ. Agric. Exp. Stn. Tech. Publ. 7628, pp. 139–157.

Kriedemann, P.E., Kliewer, W.M. and Harris, J.M., 1970. Leaf age and photosynthesis in *Vitis vinifera* L. Vitis, 9: 97–104.

Loomis, R.S. and Williams, W.A., 1963. Maximum crop productivity: an estimate. Crop Sci., 3: 67–72.

Manetsch, T.J., 1976. Time-varying distributed delays and their use in aggregative models of large systems. IEEE Trans. Syst. Man Cybern., SMC-6: 547–553.

Oland, K., 1963. Changes in the content of dry matter and major nutrient elements of apple foliage during senescence and abscission. Physiol. Plant., 16: 682–694.

Penning de Vries, F.W.T. and Van Laar, H.H. (Editors), 1982. Simulation of plant growth and crop production. Simulation Monographs, Pudoc, Wageningen, The Netherlands, 307 pp.

Sartorius, O., 1969. Bildung, Transport, Speicherung und Veratmung der Assimilate des Rebstockes in heutiger Sicht. Wein-Wiss., 24: 428–442.

Schaller, K., Löhnertz, O., Geiben, R. and Breit, N., 1989. N-Stoffwechsel von Reben. 1. Mitteilung: N- und Arginindynamik im Holzkörper der Sorte Müller-Thurgau im Verlaufe einer Vegetationsperiode. Wein-Wiss., 44: 91–101.

Schaub, L.P. and Baumgärtner, J.U., 1989. Significance of mortality and temperature on the phenology of *Orthotylus marginalis* (Heteroptera: Miridae). Mitt. Schweiz. Entomol. Ges., 62: 235–245.

Severini, M., Ricci, M. and Baumgärtner, J., 1990a. Distributed delay model of apricot tree bud-break phenology: parameters estimation based on field data. Acta Hortic., 276: 175–182.

Severini, M., Baumgärtner, J. and Ricci, M., 1990b. Theory and practice of parameter estimation of distributed delay models for insect and plant phenologies. In: R. Guzzi, A. Navarra and J. Skukla (Editors), Meteorology and Environmental Sciences. World Scientific Publishing Co., Singapore (in press).

Smart, R.E., 1974. Photosynthesis by grapevine canopies. J. Appl. Ecol., 11: 997–1006.

Stadelmann, F.X., 1988. N in der Landwirtschaft: Kreislauf, Probleme, Verluste, Synthese, Schlussfolgerungen. Report Eidgenöss. Forschungsanstalt Agrikulturchemie Umwelthygiene, CH-Liebefeld-Bern, Conf. 27. Oct. 1988, 51 pp.

Taylor, B.K. and May, L.H., 1967. The nitrogen nutrition of the peach tree. II. Storage and mobilization of nitrogen in young trees. Aust. J. Biol. Sci., 20: 389–411.

Taylor, B.K. and Van den Ende, B., 1969. The nitrogen nutrition of the peach tree. IV. Storage and mobilization of nitrogen in mature trees. Aust. J. Agric. Res., 20: 869–881.

Vansickle, J., 1977. Attrition in distributed delay models. IEEE Trans. Syst. Man Cybern., SMC-7: 635–638.

Wermelinger, B. and Baumgärtner, J., 1990. Application of a demographic crop growth model: an explorative study on the influence of nitrogen on grapevine performance. Acta Hortic., 276: 113–121.

Wermelinger, B. and Koblet, W., 1990. Seasonal growth and nitrogen distribution in grapevine leaves, shoots and grapes. Vitis, 29: 15–26.

Wermelinger, B., Oertli, J.J. and Delucchi, V., 1985. Effect of host plant nitrogen fertilization on the biology of the two-spotted spider mite, *Tetranychus urticae*. Entomol. Exp. Appl., 38: 23–28.

Williams, D.W., Williams, L.E., Barnett, W.W., Kelley, K.M. and McKenry, M.V., 1985. Validation of a model for the growth and development of the Thompson Seedless grapevine. I. Vegetative growth and fruit yield. Am. J. Enol. Vitic., 36: 275–282.

Williams, L.E. and Smith, R.J., 1985. Net CO_2 assimilation rate and nitrogen content of grape leaves subsequent to fruit harvest. J. Am. Soc. Hortic. Sci., 110: 846–850.

Winkler, A.J., Cook, J.A., Kliewer, W.M. and Lider, L.A. (Editors), 1974. General Viticulture. University of California Press, Berkeley, CA, 710 pp.

Yang, Y.S., Hori, Y. and Ogata, R., 1980. Studies on retranslocation of accumulated assimilates in 'Delaware' grapevines. II. Retranslocation of assimilates accumulated during the previous growing season. Tohoku J. Agric. Res., 31: 109–119.

Zahner, Ph. and Baumgärtner, J., 1988. Analyse des interactions plante-tétranyques-phytoseiides. I. Modèles de population pour la dynamique de *Panonychus ulmi* et *Tetranychus urticae* en vergers de pommiers. Acta Oecol./Oecol. Appl., 9: 311–331.