3.3 Simulation of growth processes and the model BACROS

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3.3.1 Introduction

This section complements the previous section, which dealt with crop photosynthesis and transpiration. The modelling of development in plants is discussed first (Subsection 3.3.2). The simulation of rates of growth (Subsection 3.3.3) and of efficiency of growth processes (Subsection 3.3.4) including growth respiration, are discussed next. Computation of maintenance respiration is the subject of Subsection 3.3.5. Modelling dry-matter partitioning (Subsection 3.3.6) and a discussion of the crop water balance in relation to regulation of partitioning (Subsection 3.3.7) concludes this part of the section.

The comprehensive simulation model BACROS is presented in Subsection 3.3.8 and its use is demonstrated briefly. It contains many of the elements discussed in this and the preceding section. The model, which has been developed in over a decade by a team of scientists, simulates growth and transpiration of field crops in optimal conditions. A detailed description of BACROS has been given by de Wit et al. (1978). The model has been evaluated extensively. Since its publication in 1978, the model found to contain some minor errors, and some new developments have taken place. These developments are published elsewhere (van Laar et al., 1983, see also Subsection 3.3.8), including an up-to-date listing of the model. The publication, which will be updated periodically, is available upon request.

3.3.2 Plant development

Plant development is different from plant growth: 'development' relates to the physiological age of the plant and to its morphological appearance, whereas 'growth' relates to biomass increase in particular. It is often necessary to simulate plant development, as it is a key to the partitioning of assimilates to different organs. Development of plants cannot be expressed simply as ageing, because temperature and other environmental factors can speed up or reduce the rate of development considerably. The approaches given below are highly descriptive, but often function satisfactorily.

The modelling of the development of plants is relatively easy for determinate species, i.e. plants with a terminal florescence. Such plants have a fixed pattern of development: a fairly constant number of leaves is formed before flowering starts and seed filling is initiated. The development stage can conveniently be defined to have the value 1.00 (dimensionless) at flowering and 0.00 at germination. It can be regarded as a state variable, DVS, whose value increases with the

rate of development, DVR. In CSMP one can write:

DVS = INTGRL(0.,DVR)

If it takes 70 days, for example, from germination to flowering, DVR equals 0.0143 d^{-1}.

Exercise 42
DVR may be 0.0143, 0.02 and 0.0286 d^{-1} at 15, 20 and 25 °C, respectively. Explain why a plant at a constant temperature of 20 °C flowers later than one in an environment in which the temperature is 20 °C on average, but fluctuates between 15 and 25 °C.

This description of the development process closely resembles the degree-days concept that is widely used by crop physiologists (cf. Hesketh et al., 1980; Subsection 3.4.7). However, temperature is not the only environmental factor that influences the rate of development. Day length can also strongly modify the rate of development in the vegetative phase. Angus et al. (1981) demonstrate this with an analysis of an extensive set of experiments with wheat; Breman et al. (1979) show the effect of day length on the duration of the vegetative period in some annual grasses in the Sahel. In general, temperature increase speeds up plant development, while long days speed up the development rate in long-day plants, but reduce it in short-day plants. The model of Section 3.1 contains such a description of the development process (Lines 301-307); the numerical data are those for wheat, cultivar UQ189 from Angus et al. (1981). Following their conclusion, the effect of temperature on the rate of development is programmed to change after anthesis. Sensitivity to day length lasts, of course, only up to anthesis. The model BACROS does not contain a simulation of plant development stage.

The relation of DVR to temperature and the effect of day length on DVR are specific for species and variety, and need thus to be established experimentally. This is unfortunate, as in many cases new observations on each new type of plant one is interested in are required. Effects of water stress and of nutrient shortage on the rate of development are usually small.

Day length, for the simulation of photoperiodism, can be computed as in Subsection 3.2.4, or as in SUCROS (Subsection 3.1.2). The photoperiodic reaction is already sensitive to dim light, and the corresponding day length (DLP) must be counted from just before sunrise to just after sunset. This is attained by specifying in the equation for DLP that the effect should be counted for all inclinations of the sun larger than −4 degrees (Line 231).

Exercise 43

a. What change in yield results from the selection of a day length-insensitive wheat cultivar in the conditions specified in SUCROS (Subsection 3.1.2) if the crop is sown on 27 May or on 27 October? Choose the effect of day length on the rate of development to be a constant 0.575.

b. What yield change occurs if a new cultivar is introduced that behaves at any temperature the same as the old cultivar does for a temperature of 1 °C higher?

Though this model of the development process functions well in many cases, other descriptions can be more appropriate for other species. From the review paper of Hodges & Doraiswany (1979), a model can be derived in which the sensitivity for day length is not constant, but small or absent in a juvenile phase and strong thereafter up until flowering. Van der Sar et al. (1983) suggest that drought stress can prolong the juvenile phase. They suggest also that the actual sensitivity to day length may be very short, at least in some grass species. This note makes clear that a general, explanatory model of photoperiodism has not yet been developed in spite of the large amount of physiological knowledge accumulated about this phenomenon.

The development of indeterminate plants can be regarded in the same way (i.e. DVS = 1. at flowering). Growth of vegetative organs will continue parallel with formation of fruits for a period, the duration of which is not genetically programmed, but depends on environmental conditions. Meyer et al. (1979) modelled development of indetermined soybean similar to what is described above, with only an effect of temperature. After flowering, one node with a leaf, a stem segment and a flower is formed per development stage interval of 0.08.

For a continuously vegetative crop, like sugar-beet, there is a problem in defining the development stage, as it does not flower normally. The time-span between formation of leaves in standard conditions, a plastochron, defines then the unit of DVS. This is done, for example, in SUBGOL, a sugar-beet simulator developed by Loomis and collegues (Loomis et al., 1979).

In some cases it is useful to know the distribution of biomass with age or development stage, for instance when the potentials for growth of new organs or for regrowth after cutting are considered. These potentials are much higher in young, meristematic tissue than in old tissue. To make this distinction in the model, total biomass (BM) may be divided, for example into five age classes. The state variables BM1 through BM5 can be defined, where BM1 + BM2 + ... + BM5 = BM. Their growth rates GR1 through GR5 are equal to 0., except for a certain time span: GR1 equals the growth rate GR in the first period and is 0. otherwise, GR2 equals GR in the second period, and so on. BM1 will then be the biomass formed in the first period, BM2 in the second, and so on.

By means of the CSMP INSW function (Table 2, Section 2.2), this can be programmed easily.

Exercise 44
Program this for WLV in the model of Section 3.1 for age classes of 10 days. What are the weights at flowering? What is computed if one uses only one INSW function in each equation?

Instead of having an INSW function responding to TIME, the switch can also be activated and deactivated at certain values of DVS. A potential difficulty is then that the integration step may not quite coincide with the threshold value of DVS for the change to the next biomass class. But this problem is small when relatively short time steps are taken.

A disadvantage of this manner of programming an array of biomass classes is that it requires a large number of state variables (INTeGRaLs). In large models, such arrays may occupy too much computer memory. The 'boxcar train method' may then be a useful alternative. De Wit et al. (1970) developed it to simulate the potential growth capacities of shoots and roots of whole plants; Goudriaan (1973) described the method more extensively. Of a number of 'cars', only the first boxcar is filled. Then, at a certain moment, its content is transferred into the second boxcar, and the filling of the first starts again. At the next shift signal (PUSH = 1.), the content of the second car is transferred into the third, that of the first into the second, and the first is filled again. Programmed in FORTRAN style within a CSMP program, the size of the boxcar train is virtually limitless. Use of fixed time-step integration method RECT is required. Time steps must be many times shorter than the boxcar shift period. Its programming can be done as shown in Table 13.

PUSH can be defined as a function of TIME with the CSMP IMPULS function, or be set equal to 1.0 after each increment DVSI of DVS, as in Table 13, using an INSW function. DVSI is the development stage interval. The distribution of total leaf weight over 25 classes of development at some time after anthesis (DVS = 1.25), simulated in this way with SUCROS, is presented in Figure 30.

Exercise 45
Use the BOXCAR of Table 13 to keep track of the development of leaf weight in SUCROS, and try to obtain the same results as those of Figure 30. Use as an alternative to the assumption that leaves die at a rate of 3% of the weight of dry matter per day after flowering (Lines 112-114), the supposition that leaves function for 1.00 unit of DVS.

Table 13. A BOXCAR function, programmed in CSMP, to distinguish 25 development classes of leaves. GLV is growth rate of leaves, WLV is total weight of live leaves, WLVD that of dead leaves. DVR is rate of development, DVS is development stage.

```
* BOXCAR TRAIN METHOD (SIZE:   26 CARS)
* IN INITIAL:
STORAGE BOX(26)
TABLE BOX(1-26)=26*0.
FIXED I
* I IS USED AS A NUMBER OF A BOXCAR,
* AND IS DECLARED INTEGER IN THIS WAY
* IN DYNAMIC:
BOX1=INTGRL(WLVI,GLV-BOX1/DELT*PUSH)
PROCEDURE WLV,WLVD=BOXCAR(PUSH,BOX1)
     BOX(1)=BOX1
* NEXT 7 LINES ARE ONLY EXECUTED IF PUSH EQUALS 1.
     IF (PUSH.LT.  1.) GO TO 2
     BOXT=0.
     BOX(26)=BOX(26)  +  BOX(25)
     BOX(25)=0.
     DO 1 I=25,2,-1
* NEXT 3 LINES ARE REPEATED FOR DIFFERENT VALUES OF I,
* STARTING WITH 25, AND COUNTING BACKWARDS TO 2
     BOX(I)=BOX(I-1)
     BOX(I-1)=0.
   1 BOXT=BOXT+BOX(I)
   2 CONTINUE
     WLV =BOXT  +  BOX(1)
     WLVD=BOX(26)
ENDPROCEDURE
PUSH=INSW(DVS1-DVSI,0.,1.)
DVS1=INTGRL(0.,DVR-DVSI/DELT*PUSH)
* DIVISION BY DELT TO SUBTRACT DVSI IN ONE TIME STEP.
* SEE ALSO SUBSECTION 2.3.6
PARAMETER DVSI=0.04,  DVR=0.025
METHOD RECT
TIMER DELT=0.2
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Related to this approach to development, but conceptually different, is the simulation of transfer of biomass from one state into the next by means of a time coefficient description. This simulation of 'development' states that each amount of biomass of one class has, at any moment, a certain chance to go into the next class. This may be an expression of a strong external influence on this 'development' or of a considerable heterogeneity within each class. The rate of suberization (named SYR) of roots from the class 'young' (named WYR) to 'old', suberized roots (WOR) with a time coefficient (SUBC) of 5 days is programmed in this way in BACROS, because of its convenience:

SYR = WYR/SUBC
WYR = INTGRL(IWYR,GYR – SYR)
WOR = INTGRL(IWOR,SYR)

(some minor details are omitted, and the rate of growth of young roots, GYR, is not discussed here).

Other examples of this kind of development are presented in Subsection 2.1.8 under the name of first order exponential delay, and some implications of this formulation are discussed there.

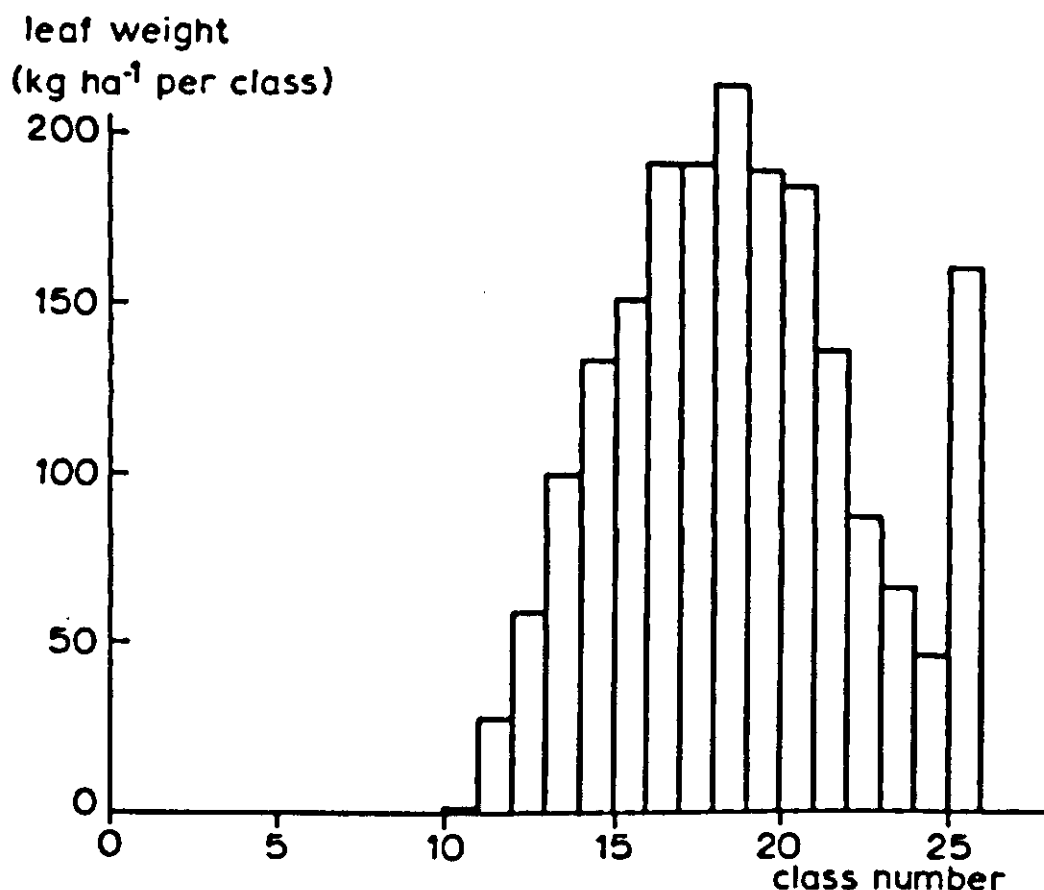If many states of development are to be distinguished instead of only young

Figure 30. Distribution of the total weight of live leaves (WLV) over 25 classes at DVS = 1.25 (TIME = 366.2) for a standard run of SUCROS. Each class represents the leaves formed during one development stage interval. Class 26 represents the total of dead leaves.

and old, the programming with the time coefficient approach looks like the boxcar train approach. However, it remains in principle different. This will become clear if one compares the results of Figure 30 with those of Figure 15, Section 2.1, for the second till nth order exponential delays. By programming development using time coefficients, the dispersion phenomenon can be simulated elegantly (Subsection 2.1.8). This has been programmed by Janssen (1974) to simulate the germination process of winter annuals. Dispersion phenomena, however, are rarely encountered in plant growth models; they are not further discussed here. ˙

3.3.3 Rate of growth

For models in which growth is simulated with time steps of one day or more this subsection is of no interest because all carbohydrates formed during the day are then supposed to be consumed for growth and maintenance within 24 h. Daily growth rate of the total biomass GTW is then sufficiently defined by:

GTW = (GPHOT − MAINT) ∗ CVF

GPHOT and MAINT stand for daily photosynthesis and maintenance respiration, respectively (see Section 2.2). The value of the conversion factor (CVF) is often about 0.7; it is explained below.

If the dynamics of growth during the day are important, one recognizes quickly that GTW is only indirectly a function of GPHOT and MAINT. Growth is a physiological process whose rate depends on internal conditions and environmental factors. 'Growth' is defined as the formation of structural material from

119

reserves. 'Structural material' consists of cell walls, some enzymes and membranes. Once formed, it is never again substrate for growth or maintenance. The total dry biomass of plants consists of structural material plus 'reserves'. Reserves are largely made up of carbohydrates, in particular starch and glucose, though some protein is present as well. However not all starch and soluble sugars are necessarily reserves. In sugar-beet, for example, the stored sucrose is not withdrawn from the beet, even when the leaves are starving. For practical purposes, however, 'reserves' is identical to the soluble sugars plus starch in vegetative organs (cf. Subsection 3.4.7).

The amount of reserves (RES, expressed as glucose, in kg ha^{-1}) can be simulated by:

$$RES = INTGRL(0., GPHOT - MAINT - CGR)$$

in which CGR represents the rate of consumption of reserves in growth processes (this equation is identical to the one in Subsection 2.3.4). The reserve level is the fraction that reserves form of the total plant dry structural weight. An illustration of the fluctuation of the reserve level during the day, as a result of photosynthesis and of growth in particular, can be found in the work of Challa (1976) with cucumber plants (Figure 31).

What is of interest is in the first place the growth of the whole plant, rather than growth of individual organs. The rate of plant growth is determined by internal and external factors. Of the internal conditions, the amount of reserves and the maximum capacity to grow are the most important ones; among the external factors temperatures and water stress are most important.
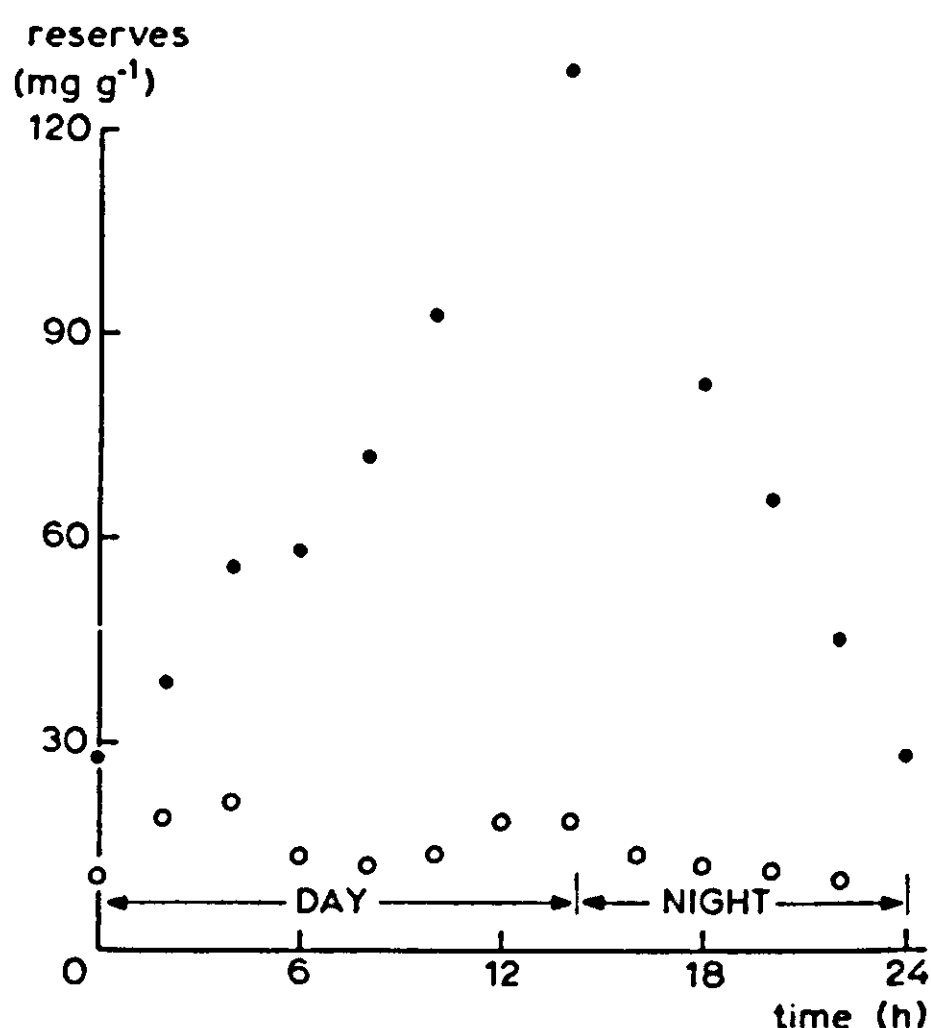

Figure 31. The course of the reserve level during 24 h in cucumber plants (Challa, 1976). Open circles indicate the glucose level, closed circles the level of glucose + starch. Plants were grown in climate chambers.

How the growth rate of wheat plants is related to the reserve level, to temperature and to the water potential is depicted in Figure 32. These results were obtained from laboratory experiments and were more or less similar for rye grass and maize plants (Penning de Vries et al., 1979). Results of Moldau & Sôber (1981), shown in Figure 18 of Section 2.3, show a similar relationship of growth rate and reserve level. In the field, however, such effects are conceivably more smoothed out, as a result of adaptation processes, than in the short duration laboratory study. No observations of that kind are known as yet (Patterson, 1980). However, in the long run, the exact shape of the response curves are not very important, because they are part of a negative feedback loop.

Exercise 46
Of which negative feedback loop are they a part?

And the end result of a simulation over a full day is still that of the one day growth equation. Moreover, the relations may be specific for each species or
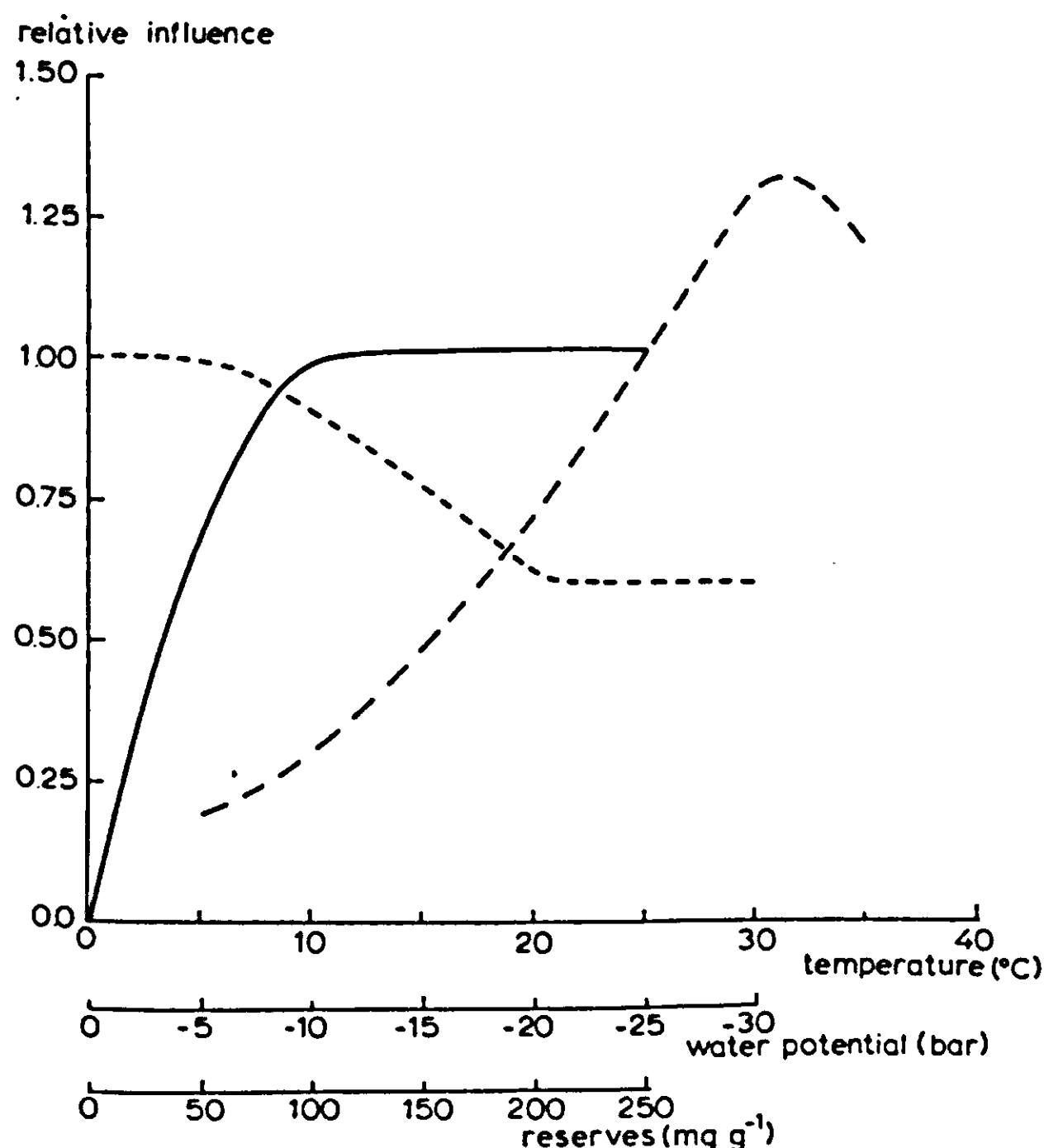

Figure 32. The relative response of the growth rate of young wheat plants to the reserve level (———), temperature (— — —) and water stress (----) (Penning de Vries et al., 1979).

cultivar, so it would be cumbersome to obtain them experimentally. It is thus not worthwhile to spend much effort in improving these relationships.

The cumulative effect of the internal conditions and these external factors is generally simulated by multiplying the relative effects of temperature (ET), water stress (EW) and reserve level (ER) (cf. Loomis et al., 1979):

GTW = BM * RGRS * ET * EW * ER

Exercise 47
As an alternative, the smallest of the individual factors might be chosen. What are the physiological implications of both assumptions? Devise an experiment to distinguish between these possibilities.

The constant before the multiplication factors in the above equation is the relative growth rate in standard conditions for whole plants (RGRS); the current biomass is represented by BM. The constant to be used with the data of Figure 32 is $0.3 \text{ g g}^{-1} \text{ d}^{-1}$. Its value depends on the age of the tissue: young tissues have much higher values than old ones. In fact, the RGRS of the tissue that actually grew in maize plants in the same set of experiments was $1.3 - 1.7 \text{ g g}^{-1} \text{ d}^{-1}$.

The highest values reported of RGRS for whole, autotrophic plants are about $0.5 \text{ g g}^{-1} \text{ d}^{-1}$ (Björkman et al., 1975). RGRS . BM is the maximum plant growth rate at standard temperature. This maximum rate of growth requires special attention in a model when the internal conditions for growth are such that this maximum is attained for some time. In other words, when sink size is limiting the rate of formation of structural dry matter. This occurs often at the level of individual organs during their initiation; it may occur during the filling of the storage organ; and it occurs frequently during regrowth after cutting. This subject is discussed in more detail in Section 3.4, with wheat grain as an example.

The question of whether it is really important to quantify RGRS (and the growth capacity) accurately, depends on feedback: if an intermediate pool of reserves builds up temporarily without modifying the rate of CO_2 assimilation, an improper choise of RGRS will only yield a delayed or advanced reaction of growth to assimilation. However, if the rate of assimilation becomes impaired, for example when the reserve level builds up too high (Moldau & Karolin, 1977), the effect should be clearly considered. But in our opinion plant growth in the vegetative phase and for optimal growth conditions almost never encounters this situation.

BACROS simulates vegetative growth only. It contains a still simpler approach to quantifying the crop growth rate: it is assumed that there is continuously sufficient biomass with the capacity to grow and to consume all reserves in about one day. This is programmed as a relative rate of consumption of reserves of about $1 \text{ kg kg}^{-1} \text{ d}^{-1}$. But this works well only in a fairly smooth

growth situation, where no limitiation due to lack of growing points occurs.

The translocation process of reserves from source to sink need not be discussed here: its rate is well adjusted to the growth rate (although it is possible that some of the responses of growth to environmental factors are in fact responses of the translocation system rather than of the growing cells). Note that this discussion of growth rates does not include hormones or growth substances explicitly. These substances may be transmitters of information about levels of reserves or of potentialities of growth, but need not to be made explicit as such. Hormones seem to be related to development processes and assimilate distribution, possibly by affecting phloem unloading directly, rather than to growth as such (H. Veen, personal communication).

3.3.4 Efficiency of growth processes

The six chemical components to be distinguished in plants are: carbohydrates (structural), proteins, lipids (including oils and fats), lignin, organic acids and minerals. Other types of molecules are rarely important quantitatively. Different biochemical pathways are employed for conversion of reserves into each of these components, and differences in efficiencies (on a weight basis) are its result. These efficiencies are characterized as 'conversion efficiencies'. Their values for these five organic fractions are presented in the equation below in an inverse way, which shows how much glucose is required for synthesis of one gram of the components. These values were determined in a series of theoretical analyses, and account for changes in atomic composition and for energy requirement in biosynthesis. The cost of transportation of molecules is relatively low, and was included in the conversion equation. The value of the conversion factor for growth of biomass, weighted according to its composition, can be computed in a simple way from the fraction of carbohydrates, proteins, fats, lignin, organic acids and minerals (FC, FP, FF, FL, FO, FM, respectively) in the current dry matter increase:

$$CVF = 1./(FC*1.242 + FP*1.704 + FF*3.106 + FL*2.174 \ldots$$
$$+ FO*0.929 + FM*0.050)$$
$$CPF = FC*0.170 + FP*0.462 + FF*1.720 + FL*0.659 \ldots$$
$$- FO*0.011 + FM*0.073$$

CVF is expressed as the ratio of structural biomass formed over glucose consumed (kg kg^{-1}). CPF stands for the carbon dioxide production factor and is the ratio of CO_2 evolved per amount of component formed (kg kg^{-1}) and can be used to calculate the growth respiration. There are good reasons to suppose that those equations and constants apply to all species at all non-extreme temperatures (Penning de Vries et al., 1974).

In SUCROS it is assumed that leaves, stems and roots of annual crop species, growing in optimal conditions, have a more or less typical biochemical composition, which leads to a more or less typical value for CVF for each of these

organs independent of species (Line 238, Table 9, Section 3.1). The storage organs of different crops are too variable in their composition to generalize on the efficiency of their formation. Values for 23 important crop species are reported by Penning de Vries et al. (1982).

A slightly different procedure to calculate the efficiency of growth is followed in BACROS: growth of individual biochemical fractions and the corresponding starch consumptions are computed; the computation of a CVF value for biomass as a whole has been skipped. The values in the above equations are also not completely identical to those in the BACROS program (see de Wit et al., 1978), because of simplifications introduced here. Moreover, reserves in BACROS are expressed as starch; for conversion of glucose into starch equivalents multiply them by 0.900.

Exercise 48
Structural dry matter consists of carbohydrate, protein, fat, lignin, organic acid and minerals. Of those components, 1 g of dry leaves may contain 520 mg, 250 mg, 50 mg, 50 mg, 50 mg and 80 mg respectively, 1 g of dry stems may contain 620 mg, 100 mg, 20 mg, 200 mg, 20 mg and 40 mg respectively, while 1 g of dry roots may contain 560 mg, 100 mg, 20 mg, 200 mg, 20 mg and 100 mg respectively; 1 g of dry wheat grain contains 760 mg, 120 mg, 20 mg, 60 mg, 20 mg and 20 mg, respectively. Calculate the corresponding CVF and CPF values. Show that the sum of the fractions always equals 1000 mg g^{-1}.

In somewhat approximate simulations of growth of vegetative biomass, the value of CVF of 0.7 will often do fairly well. If a higher degree of precision is required, not only is the computation of CVF to be repeated more often, but also the chemical composition of the biomass increment must be specified. Such information can be given directly, as in SUCROS, or computed in the simulation program from observed field data. The latter route is taken in BACROS. A prediction of what biochemical composition will be in a given species and under certain conditions has not yet been tried.

A feature recently added to BACROS is that of legume crops. The most obvious change is the cost of nitrogen (N) fixation in root nodules, which replaces the cost of nitrate reduction, a process that usually occurs in leaves. According to Minchin et al. (1981) the lowest cost of fixation, expressed as a C/N ratio, is 2 g g^{-1}, but values of 6 - 15 g g^{-1} have been established for field plants. Apparently the fixation cost varies with species, and possibly with growth conditions. Faba bean *(Vivia faba)* tends to be a very efficient N fixer, and hence the cost in this model has been set to the minimum value (see Subsection 3.3.8). Another change is that amino-acid synthesis in legumes occurs in roots, whereas most of the synthesis in non-leguminous crops under optimal conditions occurs in leaves. These aspects change some of the equations in the program a little. The option to use

BACROS to simulate a leguminous or non-leguminous crop type is effectuated by setting a parameter LEG to a value of 1. or -1., respectively, which changes all necessary constants in equations accordingly with an INSW function.

There is a large variation in the rate of growth of individual plant organs in time. Their biochemical composition changes also: less protein and more carbohydrates are usually formed when the organ gets older. This makes the growth respiration change. The intensity of the maintenance processes is also not constant (see below). Each of these aspects contributes to a continuous drift in the rates of respiration of the organs and of the whole plant. Not only is this a complex phenomenon to register, it is also tricky to simulate correctly because of the complexity of the process. It is therefore wise to include a carbon (C) balance in a comprehensive model, and to check continuously its completeness. The amount of C in plants can be found in two ways: from the total net CO_2 assimilation of the whole crop during the whole growing season (in kg ha^{-1}) after multiplying it by 12/44 to obtain the weight of the C; and as the sum of the fraction C in each of the biochemical components grown, plus the change in the amount of reserves in the plant. The C content of structural carbohydrates is on average 0.4504 g g^{-1}, 0.4444 for reserves, 0.5556 for proteins, 0.7733 for fats and oils, 0.6899 for lignin, 0.3746 for organic acids and 0.0 for minerals. Both ways of computing the C content should give identical results. Rounding-off errors of up to 1% can be permitted, but larger differences must result from incorrect changes in the program or improper data of the biochemical composition. In BACROS the simulation is then halted by a FINISH condition.

Exercise 49
Is a C balance in equilibrium proof of a correct simulation, or only proof of consistency of the assumptions about growth and CO_2 exchange? Add a C balance to SUCROS and program two types of error to illustrate your answer.

3.3.5 Maintenance respiration processes

Maintenance processes in plants consist of resynthesis of degraded proteins (protein turnover) and maintenance of ion gradients across cell membranes. Both processes require a constant supply of energy, delivered by the maintenance respiration process: the mitochondrial combustion of glucose. The efficiency of energy production of this process is about as high as is biochemically possible, but the intensity of the process is still insufficiently quantified. As a result the quality of simulation of maintenance respiration is less than that of growth respiration. Effects of environment on the intensity of the process are also not well established. Temperature, the most important factor, usually stimulates the maintenance processes by a factor of 2.0 per 10 °C temperature increase, and this Q_{10} of 2.0 is commonly used. However, both lower and higher

Q_{10} values have been reported (cf. Subsection 3.4.7). A light water stress does probably not affect the intensity of maintenance processes.

The description of the effect (TEFF) of the actual temperature (ATEMP) on maintenance respiration with a Q_{10} concept can be programmed easily with the Q_{10} value (Q10) and the reference temperature (RTEMP) as follows:

TEFF = Q10* *((ATEMP – RTEMP)/10.)
PARAMETER Q10 = 2., RTEMP = 25.

Note that in this equation it is not expressed that the range of validity is only 10-20 °C.

For the calculation of the rate of maintenance respiration of a crop at standard temperature, three different procedures can be followed (indicating that its modelling is still in a preliminary phase; see Subsection 1.3.2). The simplest is to state that maintenance requires daily 0.015 g reserves (glucose) per gram biomass. It is used for example in the model of Section 2.2. This is roughly correct at the temperature to which the crop is adapted and grows very well, which may be 20-25 °C for temperate crops, and 30-35 °C for tropical crops (McCree, 1974). It is slightly more sophisticated to indicate that the processes are related to protein content, in part, and hence to base its calculation on protein content of the tissue. This was done, for example in ELCROS (de Wit et al., 1970) a predecessor of BACROS. This requires, however, additional information: the protein content of the crop. The information can also be given indirectly, by stating that leaves, the organ with the highest protein content, have the highest rate of maintenance respiration: about $0.03 \text{ g g}^{-1} \text{ d}^{-1}$ for field grown plants; stems have much lower rates – about half of that of leaves – and roots lower still. Storage organs may be high or low in protein, but most of their protein is inactive, so that their maintenance requirement is low (cf. Penning de Vries et al., 1982). The assumption that the rate of maintenance respiration of organs differs, but is more or less specific per type of organ at the reference temperature, was the basis for the formulation in SUCROS (Section 3.1):

MAINTS = WLV*0.03 + WST*0.015 + WRT*0.01 + WSO*0.01

The third approach to the quantification of maintenance processes was followed in BACROS: it is computed from protein and mineral content and in addition from the average metabolic activity of the crop. This is based on the observation (Penning de Vries, 1975) that more active tissues have higher rates of maintenance respiration than less active ones. Its explanation is that probably more enzymes are turned over and maintained at high than at low activity. Leaves, which are more biochemically active than stems or roots, have the highest rates of maintenance respiration per unit of tissue. The rate of CO_2 production related to maintenance respiration is 44/30 times the rate of glucose consumption.

Exercise 50
Add an INTGRL of glucose consumed for maintenance to SUCROS, and test the sensitivity of the model to the coefficients used for different values for various organs, and for the Q_{10} value.

3.3.6 Assimilate distribution

The usual way to describe the distribution of current assimilates over plant organs, often called dry-matter distribution, is by employing a certain key. This key changes with the development stage of the plants. Figure 33 presents typical keys of the distribution of dry matter over the principal organs of wheat, potato and soybean plants (van Heemst, personal communication). These keys are characteristic for each crop, and its course with DVS may even be different for cultivars of one species. The effects of environmental conditions on the pattern of assimilate distribution are often fairly small at the level of potential productivity. (For lower levels of production, see Section 4.1 and 5.3).

About the internal control of distribution of assimilates in plants, still little is known. This implies that data about dry-matter distribution are to be collected experimentally, and also that all simulation models are fairly weak in their application to conditions where morphology may be expected to be different than in the area where the data were obtained.

However, in addition to the static description of dry-matter distribution, some inroads into its dynamic simulation have been, or are being, developed. Among them are the simulation of grain production in wheat crops as a function of C and N reserves and of current CO_2 assimilation and N uptake, as is presented in the Subsections 3.4.5 and 3.4.7, and in the simulation of tiller dynamics and grain initiation (Subsection 3.4.10). Another inroad is the analysis by Horie et al. (1979) of leaf size and leaf number in developing plants in an attempt to characterize morphology with a minimum of parameters.

One assimilate distribution mechanism that merits special attention is the interaction between shoot growth and root growth. According to the functional balance concept of Brouwer (Brouwer & de Wit, 1968), the shoot needs a certain amount of roots to provide it with water, while the roots cannot do without assimilates from the shoot. As a consequence, growth of the shoot becomes reduced when there are too few roots for a sufficiently high water uptake (as a result of root damage, an increased transpirational load or a drier root environment). Roots, closer to the source of water, supposedly suffer less. As a result of a decrease in shoot growth and in utilization of reserves, the reserve level builds up, and root growth becomes stimulated to a higher level. This continues until the equilibrium is restored. Due to this balance, most of the growth of roots occurs during the day and most of the growth of shoots during the night.

The functional balance in ELCROS (de Wit et al., 1970) was simulated by different responses of shoots and roots to water stress and reserve level. SUBGOL (Loomis et al., 1979) does likewise. The current version of BACROS simulates it by considering the water status only, stating that a low relative water content of the crop stimulates root growth but reduces shoot growth, and vice versa.

In spite of the existence of the functional balance, many models, including SUCROS, simulate crop growth using a predetermined distribution of biomass between shoot and root (excluding tubers and beets), as shown in Figure 33. The reason for following this procedure, rather than the dynamic concept, is that it is simpler and also often satisfactory at the highest production level if one is not
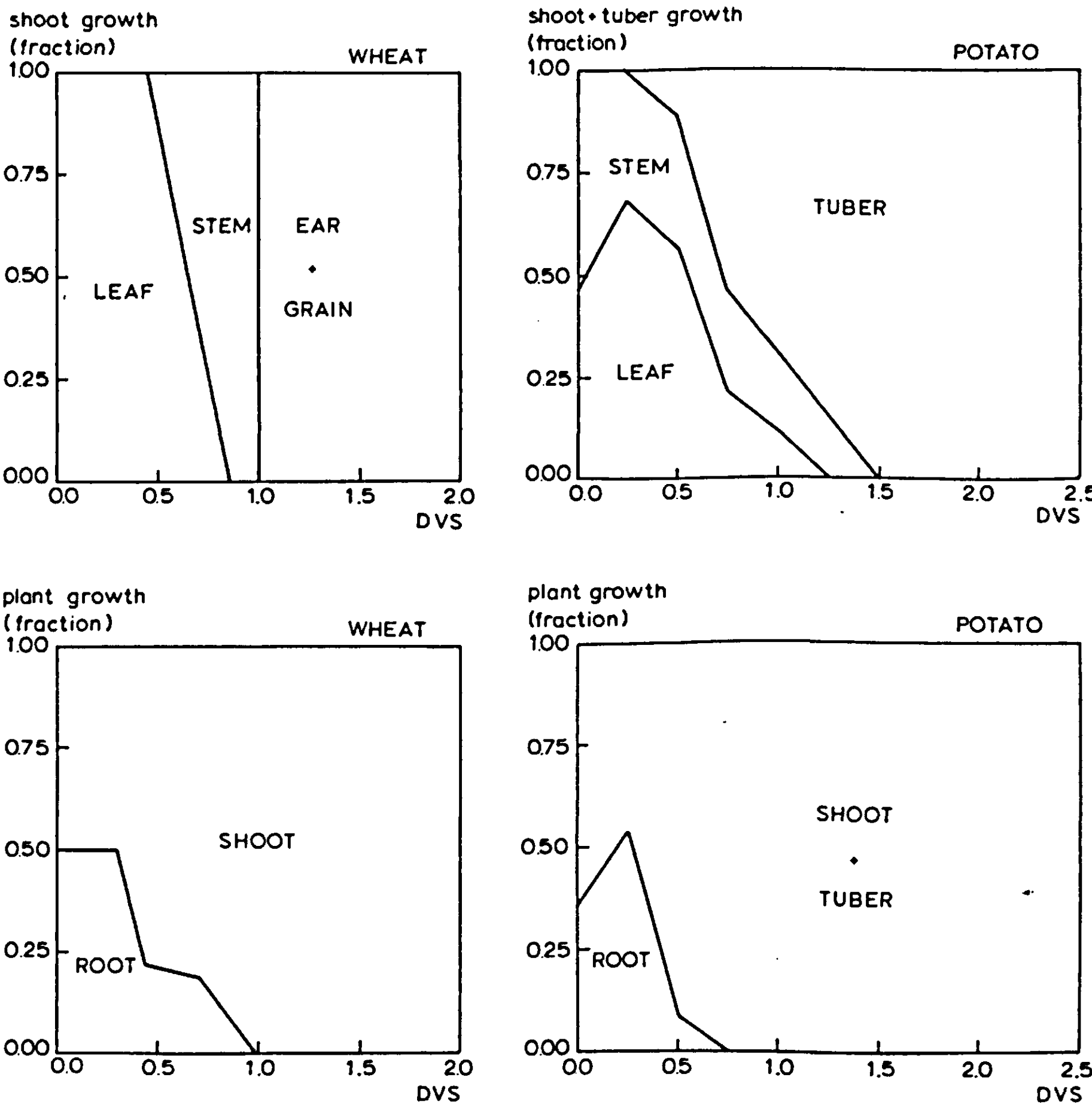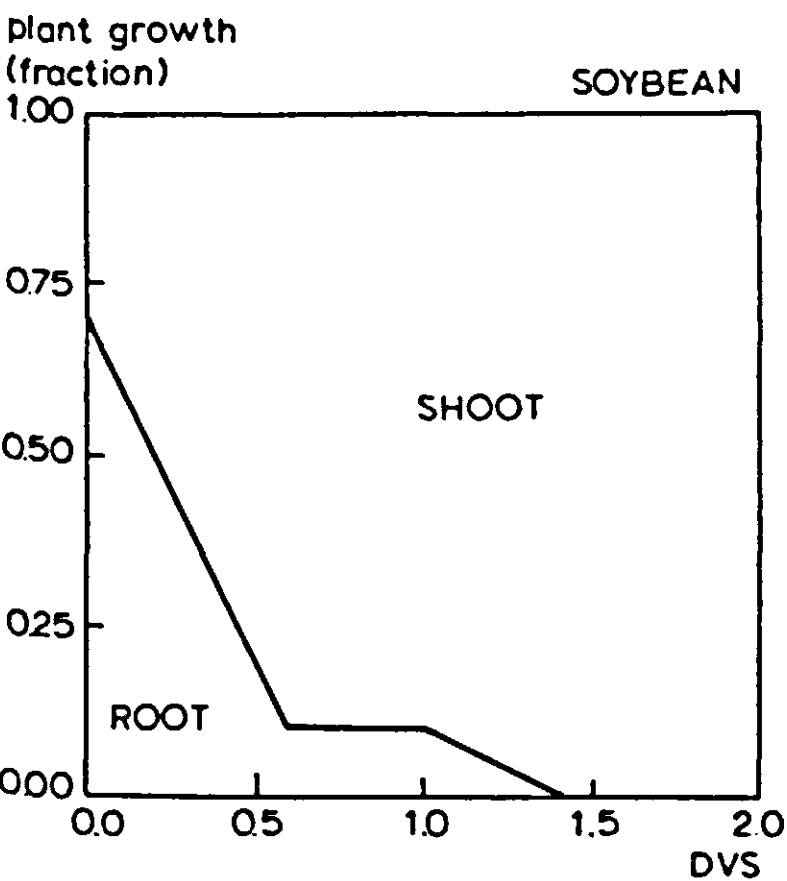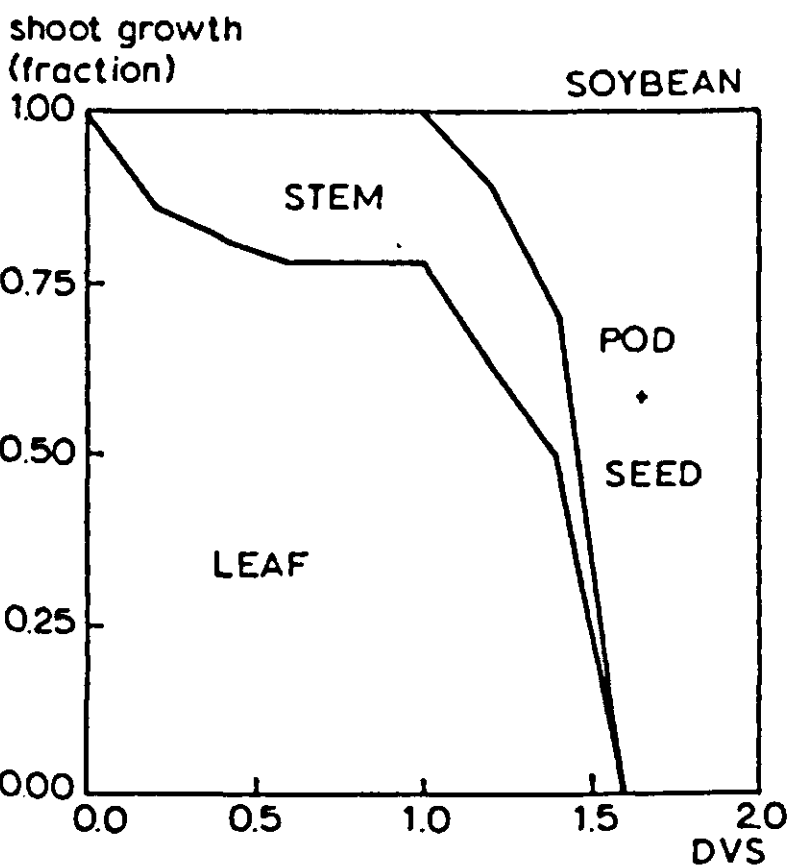

Figure 33. The partitioning of dry matter increments over shoot and root (lower graphs) and among shoot organs (upper graphs) during development of three crop species: wheat (a), potato (b) and soybean (c) (van Heemst, personal communication). The fractions are presented in a cumulative fashion.

interested in the daily course of processes. At the level of production where water or nutrients are limiting growth, the shoot-root distribution pattern changes towards roots. This change can also be programmed fairly easily in this way (Subsection 4.1.4 and 5.3.2) by increasing the fraction going towards roots to an extent that is related to the degree of water shortage.

3.3.7 Crop water balance

To simulate the dynamics of shoot growth during a day in the field at the highest level of production, the degree of water shortage in the crop has to be

tracked. A water balance of the canopy must thus be included in the model. The balance can be simple, as the conductivity for water in the tissues is high and important differences in potential between plant parts usually do not develop at this level of production. The only resistance to water entering the plant is the root resistance, the only one to water leaving the plant the stomatal resistance plus air-layer resistance. Moreover, the availability of soil water is supposed to be continuously optimal (by definition). Another reason for simulating the crop water balance is the computation of transpiration. This might be useful in itself, for example to establish the water requirement of the crop for irrigation purposes and provide another possibility to evaluate model behaviour.

The water balance consists basically of the rate of transpiration, discussed in Subsection 3.2.5, the rate of water uptake by the root system and a buffering volume of water in the plants. As the relative water content (grams water per gram fresh weight over grams water per gram fresh weight of fully saturated tissue) decreases and the water potential in the plant becomes more negative, stomata start to close and transpiration becomes reduced; a higher water potential difference across the roots, on the other hand, increases water uptake. It is not very important to know the absolute position of the relations between the relative water content and the degree of stomatal closure and between the relative water content and the water potential, again because of negative feedback (cf. Exercise 46). This also makes modelling of the water balance relatively simple. An example of a simple water balance can be found in the model PHOTON (de Wit et al., 1978), a special form of BACROS that is described below.

However, a time-step size problem may arise (see also Subsections 1.4.4 and 2.3.5): the margin in water content of a fully watered crop and a wilted one is often in the order of $1000 \, l \, ha^{-1}$. The plant regulates turgidity by modifying its stomatal resistance on a much finer level. The rate of transpiration of a closed canopy can reach $0.5 \, mm \, h^{-1}$, or $5000 \, l \, ha^{-1} \, h^{-1}$. Hence, a 1 h time step will be too large, and probably cause an unrealistic oscillation in the simulation of the plant water content. The 1 h time step, on the other hand, may be very suitable for the simulation of the C balance processes. There are three solutions to this problem: make more computations of these C balance processes than necessary, make the water balance calculations as often as required and the others less frequently, or make all computations less frequently and adapt the program. The first solution is the easiest. But it is the most expensive, and it also gives the false impression of a higher degree of precision in time of the C balance simulation then is actually the case. The second requires some skillful programming, using the so-called bypass method (Goudriaan, 1977), and is not advised for novices. The third is used in BACROS: it simulates the canopy water content only once per hour, and assumes that transpiration and water uptake are continuously equal, although their values may be different each time step. This is another way of saying that the conditions for the water balance change slowly during the day. This method does not provide a fully dynamic simulation of the water balance, but a realistic simulation of equilibrium situations. By using an implicit

loop (see Subsection 2.3.4), the equilibrium water content at each hour is found. (A disadvantage of the CSMP IMPLicit loop is that its equations need to be grouped, reducing the readability of the program. Therefore, a self-constructing implicit loop has been programmed in BACROS by means of two sortable procedures called BSCIL and ESCIL. A dummy variable SELECT was defined exclusively to optimize the result of the sorting procedure.)

Water uptake can be simulated using an equivalent to Ohm's law, with the water potential difference between plants and soil as driving force, and root conductivity as the only limitation to it. The conductivity of the root system in BACROS is modelled in a rudimentary way by distinguishing two categories of roots (Subsection 3.3.2) with different conductivities: old ones, suberized, are three times less permeable than young ones. Young roots become old roots with a time coefficient of 5 d. These values are not critical, and received little attention in evaluation studies.

3.3.8 Results of the models BACROS and PHOTON

Elements of the model BACROS have been presented in this section and in Section 3.2. There are many more elements, particularly in details and in crop micro-meteorology. For those elements and arguments about their background, see de Wit et al. (1978) and van Laar et al. (1983). The model BACROS simulates plant growth during a growing season with time steps of 1 h. The principal data to be specified for its use are given in Table 14.

To evaluate its behaviour, field experiments with periodic harvests have been performed. They provide useful background data for evaluations, but yield few suggestions of explanations if differences are encountered. Moreover, a day by day comparison is practically impossible, given the unavoidable sampling errors, and field heterogeneity. Crucial aspects of the gas exchange processes could therefore not be evaluated profoundly. To overcome this handicap, two things were done. The first and simplest step was to develop the model PHOTON, that is identical to BACROS except that it uses much smaller time steps (in the order of a few minutes, as determined by the integration method RKS) and requires therefore a somewhat different elaboration of some processes, such as the water balance. To avoid excessive computation costs, it is only used for periods of a few days. The second step was to start to measure continuously crop gas exchange processes (CO_2 and H_2O) in a crop enclosure in the field using mobile equipment (Louwerse & Eikhoudt, 1975). Evaluation runs of the models BACROS and PHOTON have been published (de Wit et al., 1978).

Another example of such a two-level evaluation is provided here to give an impression of the 'state of the art' of modelling at the level of potential crop production. A Faba bean experiment was followed throughout the 1979 season with periodic harvests to establish overall crop growth rates. The Faba beans grew very well in conditions that must have approached closely optimal growth conditions (Subsection 1.2.1). Nodulation of roots was excellent. A few times

Table 14. List of input variables that must be specified to use the model BACROS. Variables of Category 1 must be given in all cases; those of Category 2 must be given for simulation of specific experiments; those of Category 3 can be specified for maximum accuracy. If a variable is not specified, a default value is used.

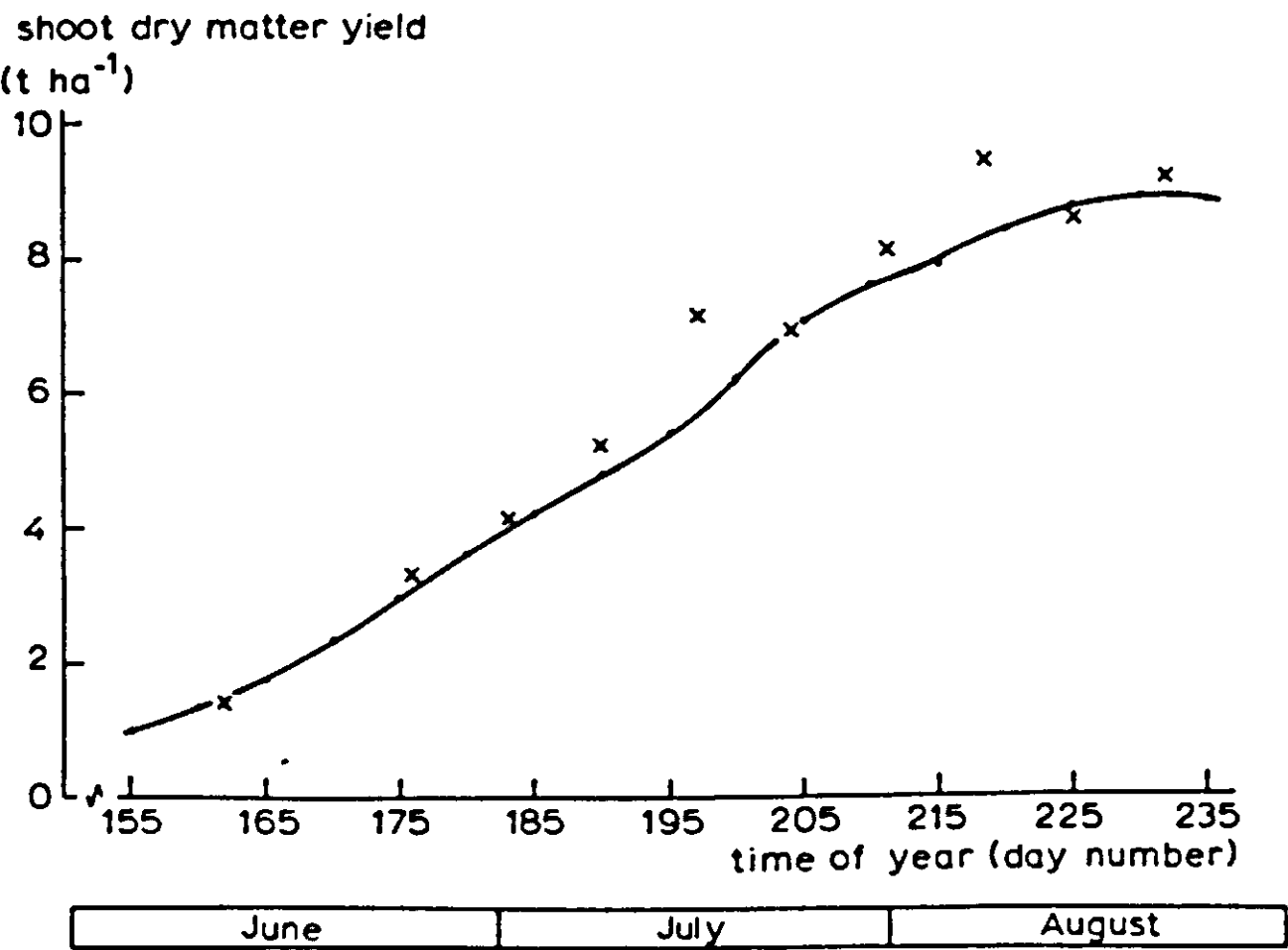| Category	Data on crop	Weather data	Other
1	C_3 or C_4 maximum rate of leaf photosynthesis leguminous or non-leguminous crop stomatal regulation effective or not	daily total global radiation daily maximum and minimum temperature and humidity	latitude start and duration of the vegetative growth period
2	width of leaves leaf area development in a similar experiment	windspeed	
3	temperature effect on photosynthesis plant height development development of biochemical composition of biomass	constants in long-wave radiation equation	

Figure 34. The measured (x) and simulated (—) above-ground biomass of a Faba bean crop in Wageningen, 1979.
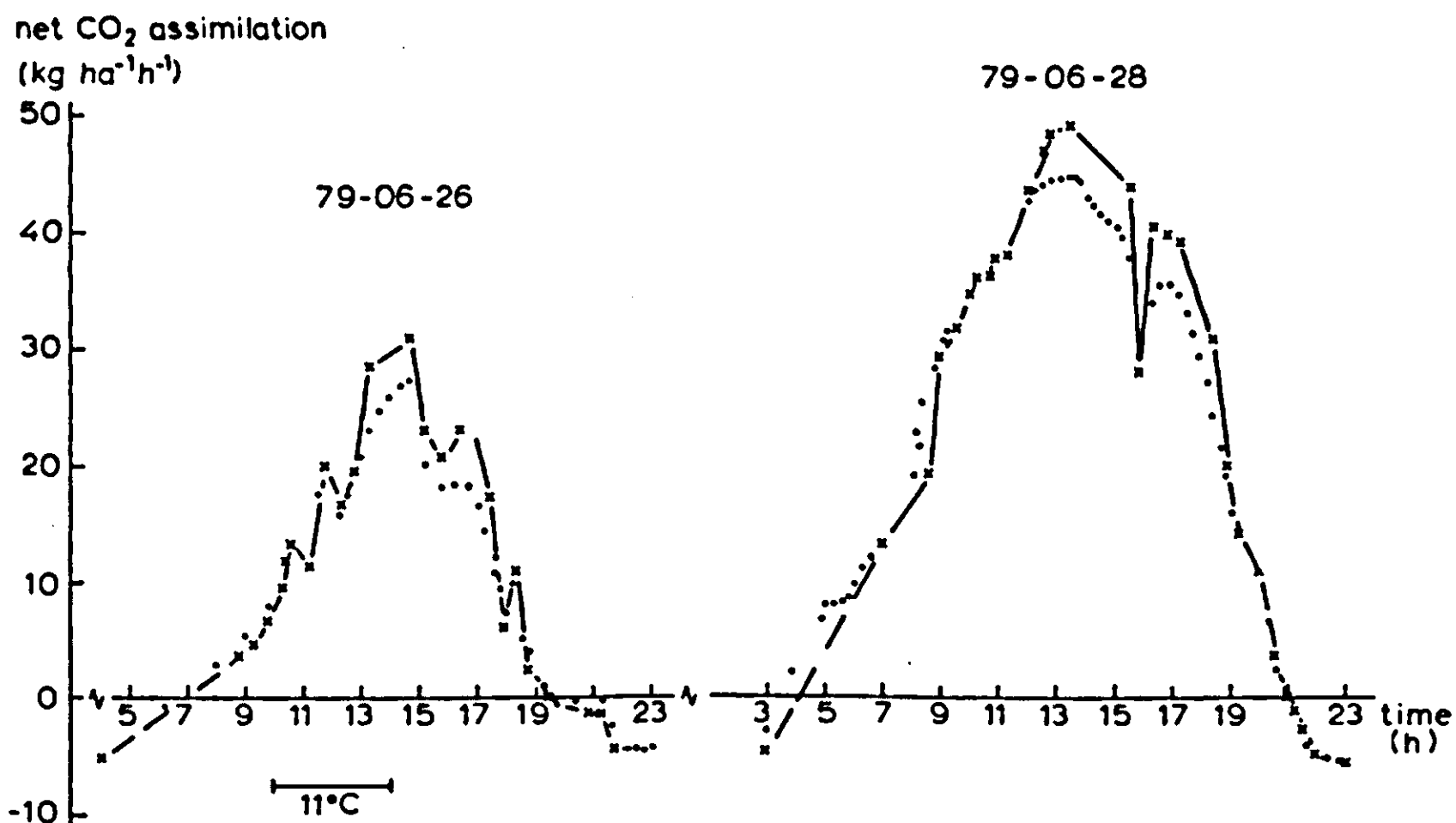
132

Figure 35. The measured (x) and simulated (•) rates of net CO_2 exchange of the Faba bean crop on 26 and 28 June 1979; temperature was set at 20 °C, except for an induced 9 °C temperature drop. Both days had plenty of bright sunlight. Daily total global irradiation was 0.9 10^7 J m^{-2} on the first day, and 2.4 10^7 J m^{-2} on the second.

during the season, the mobile equipment was used on the same field to measure gas exchange. Simulation was done with a program identical to that of van Laar et al. (1983), with account being taken for the fact that the crop was grown under a plastic cover (that reduced light intensity by 20%, and net long wave radiation by 100%). Unfortunately a direct measurement of the maximum rate of leaf photosynthesis of these field-grown Faba beans was not available, so that an estimated value had to be used. Results of this experiment and its simulation are provided in Figures 34, 35, 36a and 36b.

Figure 34 shows the evolution of the total above-ground biomass of the crop; leaves, stems and pods are not distinguished. Agreement between observed and simulated growth rates is good, although there are a few deviations and the simulation tends to underestimate the real growth rate slightly. Additional measurements with the mobile equipment in June and simulation of the same situation (initializing PHOTON with values simulated with BACROS for those days), confirmed that the model describes this fast-growing, almost completely vegetative, canopy reasonably well on a day to day and an hour to hour basis. Also the simulated rate of transpiration agreed very well with observed values. The reduction of the gas exchange rate that resulted from an induced 9 °C temperature drop was also simulated properly (Figure 35).

Later in the season, in August, the simulated growth rate exceeds the observed growth rate. But the behaviour of PHOTON was qualitatively still appropriate, as Figures 36a and 36b show: the simulated directions of change of net CO_2 assimilation and of transpiration as a result of an experimentally in-

net CO_2 assimilation
$(kg\ ha^{-1}h^{-1})$
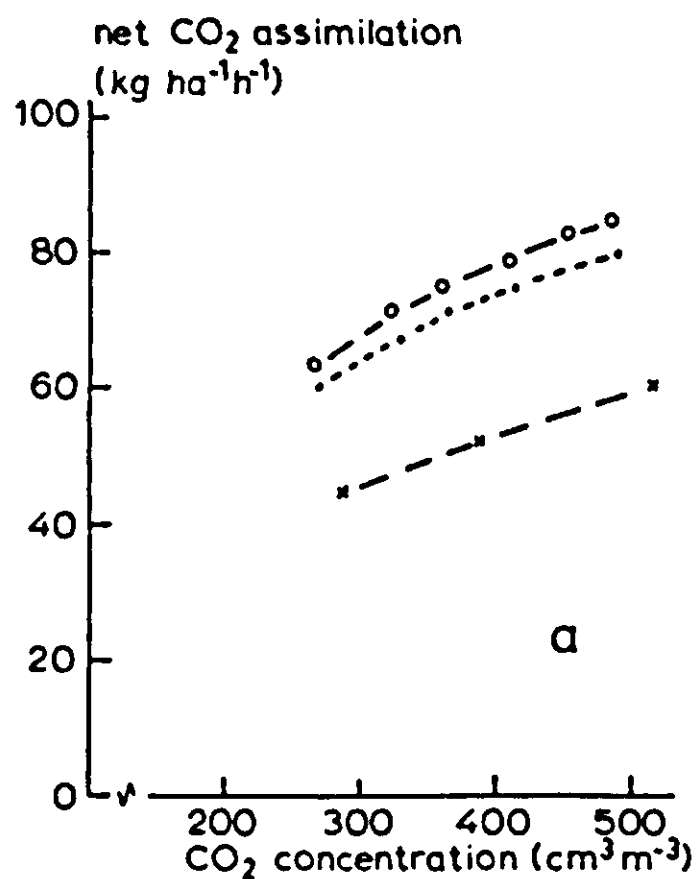

a

CO₂ concentration $(cm^3 m^{-3})$

Figure 36a. The measured (x) and simulated (• : with regulating stomata; o : non-regulating stomata) response of the net CO_2 assimilation rate to the ambient CO_2 level at a constant light intensity $(330\ J\ m^{-2}s^{-1}$ artificial light) and temperature $(20\ °C)$ on 2 August 1979.

duced increase of the ambient CO_2 level are similar to what has been measured. This indicates that stomata in the field plot plants, with old leaves by that time, were still regulating their stomatal conductance (Subsection 3.2.6). If not, the response curves would have had quite a different shape.

It is not surprising that differences develop between the simulated and the observed growth rate in a crop approaching maturity. By that time the redistribution of proteins and possibly of carbohydrates from vegetative parts towards pods is intensive. Those processes require quite some energy, but are not yet included in BACROS. In addition, senescence of leaves may have started, as a result of which leaf photosynthesis may decrease, which is another phenomenon that is not yet included. (We will come back to this in the Subsections 3.4.5 and 3.4.7). In fact, those two processes should decrease the growth rate even further
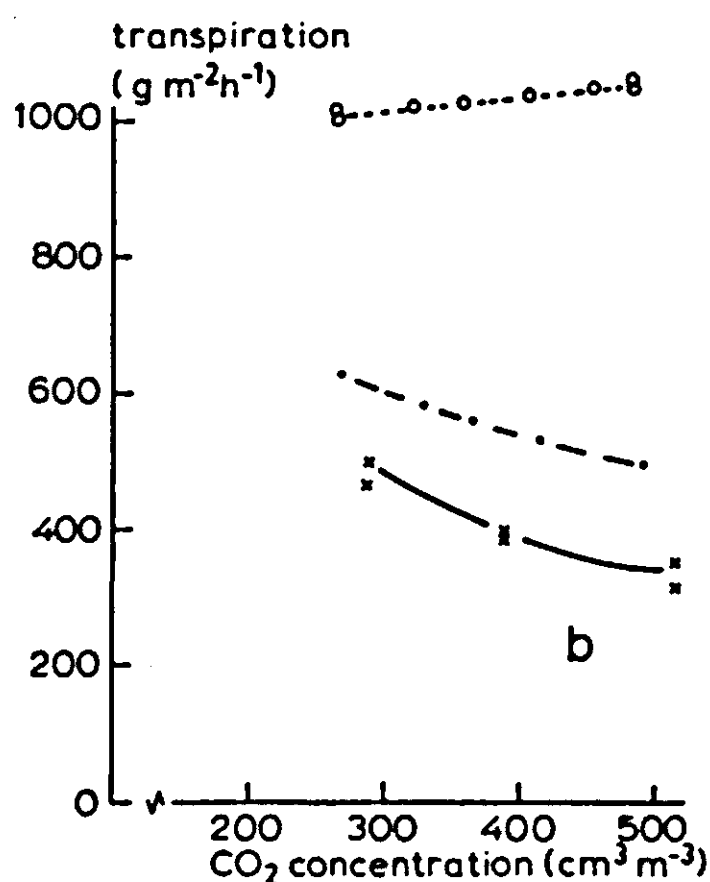
transpiration
$(g\ m^{-2}h^{-1})$

b

CO₂ concentration $(cm^3 m^{-3})$

Figure 36b. The measured (x) and simulated (• :with regulating stomata; o : non-regulating stomata) response of the canopy transpiration rate in the experiment of Figure 36a.

134

than what is observed in Figure 34. The fact that the growth rate is still simulated fairly well may even be caused by a compensating underestimation of the rate of photosynthesis. Although further analysis of experimental and literature data is still required, it seems that at least one oversimplification leads to an underestimation of canopy photosynthesis: the CO_2 assimilation submodel in BACROS (Subsection 3.2.4) is based on the assumption of an instantaneous adaptation of the rate of leaf CO_2 assimilation to the incident light intensity. This may not be quite correct (Sager & Giger, 1980), and it could cause an underestimation by 20-30% of the rate of CO_2 assimilation of a canopy with fluttering leaves in bright, direct light; at lower light levels the underestimation would be less. The simulated maximum rate of canopy CO_2 assimilation in Figure 35 stays below the measured rate, which is an argument that supports this hypothesis.