4.1 Crop production under semi-arid conditions, as determined by moisture availability

H. van Keulen

4.1.1 Introduction

In the Sections 3.2. and 3.3 a detailed, physiologically based process model of plant growth has been described. An essential prerequisite for application of that model is that the supply of water and nutrients to the crop is not a limiting factor for production. Such a favourable situation is, however, an exception rather than the rule in the various agricultural production systems around the world. Adverse weather conditions, soils low in natural fertility and lack of capital means required for improvements, lead to systems where the low supply of water or plant nutrients to the crop during its growth cycle is the major determinant for its production potential. To simulate the productivity in such situations, it is necessary also to pay attention to the below-ground plant parts and to the processes taking place in the soil that determine the availability of water and nutrients to the roots. In principle, these elements could be added to the comprehensive model indicated above, but that would increase the size of that model substantially, and bring it to a level that is hardly manageable. Moreover, some of the processes that are treated in detail in that model lose much of their relevance when the supply of water or nutrients is the major constraint for production (see Subsection 1.2.2).

Here a model is treated, dealing with simulation of crop production under conditions where moisture is the main limiting factor. The model, named ARID CROP, was developed to simulate growth and water use of fertilized natural pastures in the Mediterranean region. Following the principle of the hierarchical approach, results of BACROS and other detailed models are incorporated in a simplified fashion in the present model. Since it is impossible to treat the complete model within the scope of this contribution, only a number of features will be highlighted. For further information reference is made to detailed descriptions by van Keulen and coworkers (van Keulen et al., 1981; van Keulen, 1975). The meteorological and physiological aspects of the relationship between plant production and water use are discussed in Subsection 4.1.2, followed by an example in which these principles are applied (Subsection 4.1.3). The way in which growth of the vegetation is simulated in ARID CROP is explained in Subsection 4.1.4, emphasizing the differences with descriptions discussed earlier, in Subsections 3.3.3 and 3.3.6. In the Subsections 4.1.5 and 4.1.6, the results obtained with this model are discussed, and possibilities for applying the model in other regions are indicated (Subsections 4.1.7 and 4.1.8).

A FORTRAN version of ARID CROP, programmed by Ungar & van Keulen (1982), is available.

4.1.2 Water use and plant production

Since water is the major production factor considered in the present model, we will first examine the relation between water use by plants and the associated dry matter production. This relation has been subject of extensive experimentation, ever since the work by Briggs & Shantz (1913). De Wit's (1958) analysis of the subject, based on a description of the physical and physiological processes governing transpiration and photosynthesis in plants, indicated that the relation between dry matter production and water use depends on the prevailing level of irradiance during the growing period. The nature of this relation will be considered below.

The rate of water loss from a crop surface (E) (and that from a free water surface as well) is practically proportional to the level of irradiance. The rate of photosynthesis (A) is, however, proportional to irradiance only at low levels, since eventually the rate of CO_2 diffusion towards the active sites becomes the rate limiting factor (Section 3.2). These dependencies and their ratio are shown schematically in Figure 44. The values at very low levels of irradiance are not of practical importance, since under such conditions low temperatures will prevent any crop growth. At intermediate levels, which are characteristic for the larger part of the temperate zone, the ratio E/A remains constant and is independent of the radiation level. At the right-hand side of Figure 44, where conditions are represented that prevail in arid and semi-arid regions situated around the equa-
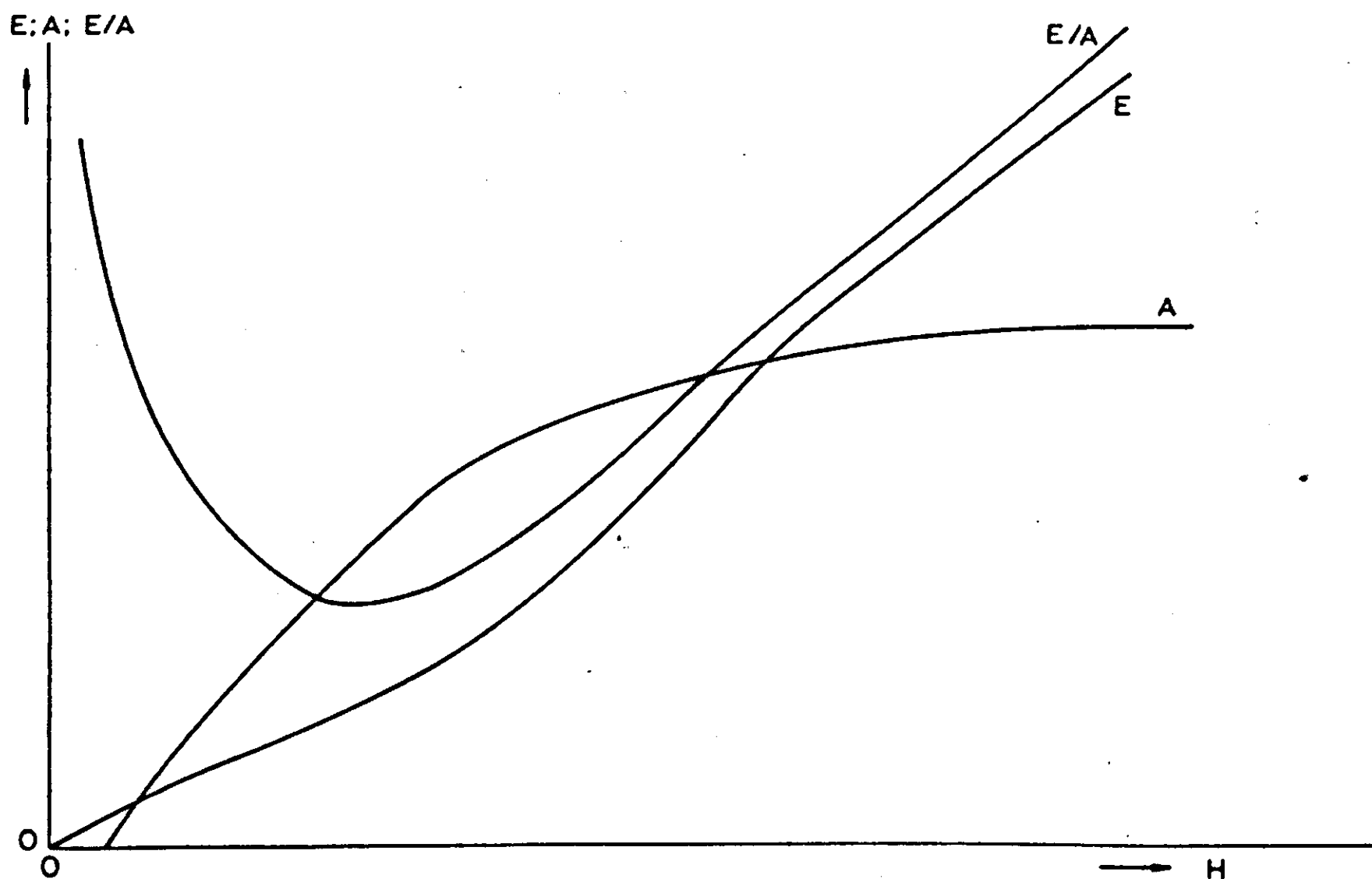

Figure 44. The relation between transpiration (E), assimilation (A) and their ratio (E/A) on the one hand and radiation intensity (H) on the other.

torial deserts, the ratio E/A is approximately proportional to the level of irradiance or the free-water evaporation. On the basis of these considerations, de Wit derived the relation:

$$P = M \cdot W \cdot E_0^{-x} \qquad (53)$$

where P is the total dry matter production in kilograms, in most cases referring to above ground material only, W is the total water loss by the plants in kg, E_0 the average daily free water evaporation in kg ha^{-1} d^{-1} and M a proportionality factor, representing water use efficiency. M depends on plant species only, and has as dimension kg ha^{-1} d^{-1}. The value of x appeared to be 1 for conditions characterized by high levels of irradiance, and 0 for those where low levels prevail (Figure 44). This relation described satisfactorily the results of a variety of experiments on water use efficiency carried out in containers as well as under field conditions, some of which are summarized in Table 15.

There is a remarkable difference in the value of M between wheat and alfalfa

Table 15. Summary of measured M values for a number of crops.

Crop	Site	Condi-tion*	M (kg ha^{-1} d^{-1})	Reference
Wheat	Great Plains	C	115	de Wit, 1958
	Turkey	F	106	Janssen, 1972
	Central Great Plains	F	125	Hanks et al., 1969b
	Central Negev	C	102-140	van Keulen, 1975
	Central Israel	C	88	Meyer (unpublished)
Sorghum	Great Plains	C	207	de Wit, 1958
	Great Plains	F	210	Doss et al., 1964
	Central Great Plains	F	140	Hanks et al., 1969b
Alfalfa	Great Plains	C	55	de Wit, 1958
	Central Negev	F	105	Tadmor et al., 1972
	Central Negev	C	108	van Keulen, 1975
	Central Negev	C	53	Meyer (unpublished)
	Wisconsin	F	214	Tanner & Sinclair, 1982
Maize	Great Plains	C	213	Briggs & Shantz, 1913
	Logan	F	215	Stewart et al., 1977
	Fort Collins	F	258	Stewart et al., 1977
	Yuma	F	262	Stewart et al., 1977
	Davis	F	314	Stewart et al., 1977
	Central Israel	F	290	Yanuka et al., 1981

* C = container; F = field experiment.

on the one hand, and sorghum and maize on the other hand. This contrast reflects the different photosynthetic pathways for the species: wheat and alfalfa are C_3 plants, sorghum and maize are C_4 plants. The main carboxylating enzyme in C_4 plants has an affinity to CO_2 that is about twice as great as that of the carboxylating enzyme in C_3 plants. Moreover the photorespiratory process is absent in C_4 plants. As a consequence the light saturated rate of CO_2 assimilation in C_4 plants is about twice as high as that in C_3 plants (Subsection 3.2.2).

Under some conditions, the assimilation process is controlled in such a way that the CO_2 concentration in the intercellular spaces of the leaves is regulated over a wide range of light intensities and external CO_2 concentrations through adaptation of the stomatal opening (Subsection 3.2.6). The level at which the concentration is maintained is about 210 cm^3 m^{-3} for C_3 plants and 120 cm^3 m^{-3} for C_4 plants. The consequence of this difference is that at low levels of irradiance and at normal external CO_2 concentrations of about 330 cm^3 m^{-3}, net CO_2 assimilation is about the same for both plant types but stomatal conductivity and hence the rate of transpiration is about half as great in C_4 plants as in C_3 plants. At high levels of irradiance, the net CO_2 assimilation of C_4 plants is twice that of C_3 plants at comparable values for stomatal conductivity, thus at approximately the same transpiration rate. Assimilation rate and transpiration rate are the main determinants for the M value which is consequently roughly twice as great for C_4 as for C_3 plants, irrespective of the level of irradiance.

Regulation of internal CO_2 concentration does not always occur, however. Some of the differences in the data of Table 15, especially those for alfalfa, can be understood if regulation was present in some cases and in others absent.

The M value is a useful parameter to describe the relation between production and water use, integrated over a reasonable period of time. It is especially suitable to compare different locations, different growing periods or different species. However, its application in the prediction of the growth pattern is much more limited. For regions with high levels of irradiance, to which most of the arid zone belongs, this is clear already from its numerical value: this value represents in fact the maximum attainable growth rate in situations where transpiration is equal to the free-water evaporation. Of course, the growth pattern of crops is such that the potential growth rate in mass of dry matter is low in the beginning of the growth period with incomplete light interception, whereas it increases to values of 200 (for C_3 plants) to 350 (for C_4 plants) kg ha^{-1} d^{-1} when complete cover is reached. The latter values could never be realized by using M values as tabulated in Table 15. Moreover, there are considerable fluctuations in M values when they are calculated over short periods of time, as is illustrated in Figure 45. These fluctuations are caused by different influences of the vapour pressure deficit of the air on crop transpiration and free-water evaporation. For a crop canopy the transpiring surface — the leaf area — may be a multiple of the surface area. Each of the leaf layers reacts practically independently to the vapour pressure deficit in the atmosphere and the transpiration increases virtually proportionally with increasing leaf area index. Thus, when the vapour pres-
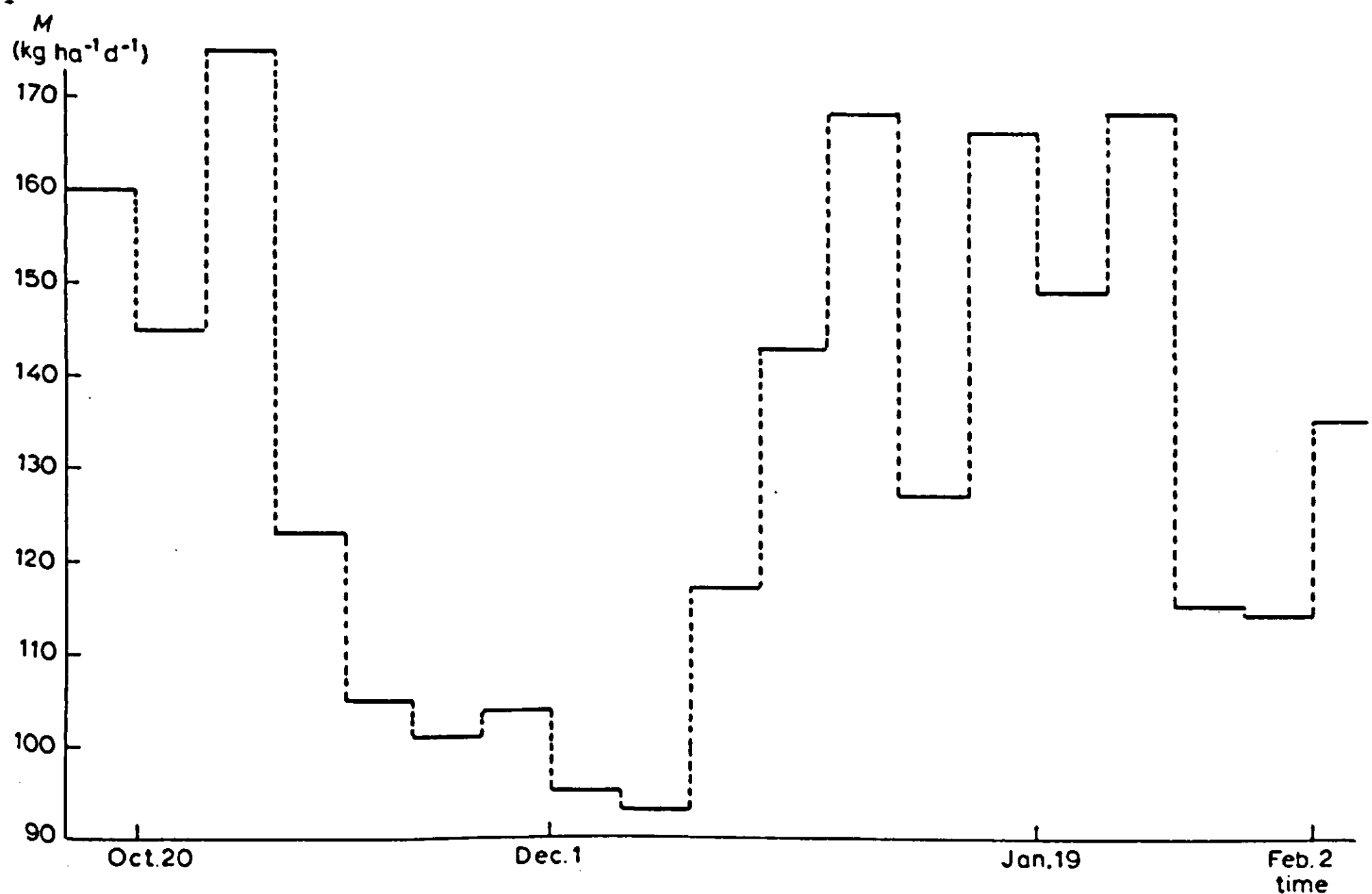
Figure 45. The variation in the calculated proportionality factor M for weekly periods in Avdat (Israel) 1972/1973.

sure deficit increases, crop transpiration increases relatively more than free-water evaporation, consequently the ratio W/E will increase, leading to lower values for M.

To avoid these difficulties the actual value of the transpiration coefficient ((W/P) from Equation 53) may be calculated in a simulation model for each individual time interval. The transpiration coefficient of the crop at a certain moment is equal to the ratio of potential crop transpiration rate, and potential dry matter production rate, both of which are obtained independently from the meteorological data of the current day.

4.1.3 Application in the simple crop growth model

The water use efficiency concept, worked out in Subsection 4.1.2 can be applied in a simplified way to obtain an indication of the water requirement of a crop growing at its potential rate in a high irradiation environment.

When for a C_3 plant an average M value of 125 kg ha^{-1} d^{-1} is assumed (Table 15), the ratio between dry matter production and transpiration can be estimated when E_0, the average rate of free-water evaporation (or the evaporation from an evaporation pan) is known. As an example a value of 4 mm d^{-1} is

taken, which is equivalent to 40 000 kg ha^{-1} d^{-1} of water. The production of 1 kg of dry matter is then coupled with a transpiration loss of (Equation 53) 40 000/125 = 320 kg of water, thus giving a transpiration coefficient of 320.

In the model presented in Section 3.1 the rate of increase in dry matter (GTW) is simulated. Multiplying that with the transpiration coefficient (TRPCF) yields the crop water requirement WREQ (kg ha^{-1} d^{-1}), which can be integrated to obtain total water requirement (TWREQ):

```
PARAM   TRPCF  = 320.
WREQ   = GTW*TRPCF
TWREQ  = INTGRL (0., WREQ)
```

To illustrate the influence of water shortage on crop production in an example, a very simple soil water balance can be added to the model (the next section treats this subject extensively). The amount of water available in the profile may be tracked in an integral (SWAT), initialized with pre-emergence soil water storage (ISWAT), and with effective rainfall (RAIN) and transpiration (TRANS) as rate variables. The rate of transpiration equals the actual growth rate (AGTW) times the transpiration coefficient. AGTW equals GTW when sufficient water is available, but becomes lower when moisture shortage occurs:

```
AGTW = GTW*RED
RED   = AFGEN (REDTB, SWAT/SWATM)
FUNCTION REDTB = (0., 0.), (0.04, 0.), (0.06,1.), (1.,1.)
PARAM SWATM = 150.E4
```

The degree of reduction in growth (RED) is related to the relative content of available water in the soil, which equals the actual amount in the soil (SWAT) divided by its maximum value (SWATM). Both quantities have the units kg ha^{-1}.

```
SWAT  = INTGRL (ISWAT, RAIN − TRANS)
INCON ISWAT = 150.E4
TRANS = AGTW*TRPCF
```

For simplicity, soil evaporation is neglected in this model. In this very schematized way some indications may be obtained about total water requirement for crops growing under different conditions, as well as about the necessity for supplemental irrigation.

Exercise 55

Add this water balance to the model SUCROS (Table 9, Section 3.1); replace GTW by AGTW in the Lines 107 and 108. Assume a rainfall of 15 mm each 14th day. Reduce the integration interval to 1 d.

Because of the considerable discontinuity introduced by the sudden rainfall expressed on a daily basis, simulation must proceed with time steps of 1 d (Section 2.3). Usually this will not cause any inconvenience. However, if the supply of water is as regular as in Exercise 55, as for an irrigation scheme, one might want to use time steps of 7 d to reduce computer costs. Particularly with the integration method RECT, a high rate of transpiration at the beginning of a time step may be extrapolated for too long, which leads to a negative soil water content and other nonsensical results. A way around such a problem is to compare SWAT plus the RAIN during a period with a duration of DELT with the amount of water potentially transpired in the period (WREQ * DELT), and to set the actual amount of water transpired equal to the lowest of these. The actual rate of transpiration in kg ha^{-1} d^{-1} is then equal to

TRANS = AMIN1(WREQ * DELT, SWAT + RAIN * DELT)/DELT

The potential growth in such a period is not computed from the relative soil water content, which changes too much in this period, but directly from the amount of water transpired:

AGTW = GTW * (TRANS * DELT)/(WREQ * DELT)

Exercise 56
Make these changes in the program of Exercise 55. Assume a soil with initially 50 mm water in the profile, irrigation of 25 mm every 14 days and DELT = 7.

4.1.4   Crop growth in the simulation model ARID CROP

In this subsection a brief overview will be given of the growth part of the comprehensive model ARID CROP. The soil section is treated in more detail in Section 4.2.

At the onset of the growing season seeds start to germinate after the first rains. Germination is assumed to be completed when the seeds, present in the upper 10 cm of the profile, are in a moist environment long enough to accumulate a heat sum of 150 degree-days (temperature above 0 °C). When the top soil compartments dry out before that moment, the seedlings die and a new wave of germination starts after rewetting only. When the required heat sum is accumulated, above ground and below ground dry matter is initialized with a predetermined initial biomass.

After initialization, the growth rate of the canopy, that is the rate of increase in dry weight of structural plant material, is obtained from the actual rate of transpiration and the value of the transpiration coefficient (Subsection 4.1.2). The latter is calculated as the ratio between the potential growth rate of the

canopy and the potential rate of transpiration ('potential' is defined here with respect to the actual state of the vegetation, but disregarding effects of water shortage). The potential growth rate follows from the rate of gross CO_2 assimilation, calculated from the leaf area index, the level of irradiance and the photosynthesis light-response curve of individual leaves (Subsection 3.2.4). Respiratory losses include maintenance respiration as a function of total amount of material present and temperature, and growth respiration, expressed as a weight conversion efficiency (Subsection 3.3.4). The potential rate of transpiration of the canopy is determined by the evaporative demand of the atmosphere (Subsection 3.2.5) and the leaf area index of the vegetation. The value of the transpiration coefficient is assumed to be independent of phenological stage of the canopy or moisture conditions in the soil. The latter assumption is an oversimplification, but one that has only a small effect on the ultimate dry matter production, since the amount of water transpired during drought periods is small. The actual rate of transpiration follows from the potential rate taking into account the interactive effects of rooting depth and soil moisture status.

During continuous testing of the model, using an increasing number of available data sets, it became clear that prolonged water stress influences some of the basic plant properties. The relative transpiration deficit (RTRDEF) is therefore included as a measure of the degree of moisture stress that the plant experiences. It is defined as the difference between potential (PTRAN) and actual (ATRAN) transpiration, as a fraction of the former:

RTRDEF = (PTRAN − ATRAN)/PTRAN

Its value divided by a time coefficient (in this case 10 days) is integrated to yield the cumulative relative transpiration deficit (CTRDEF). The assumption that a mild water stress will not have any lasting effect on plant performance, has resulted in a formulation that accumulates the relative transpiration deficit only when it exceeds the, rather arbitrarily chosen, value of 0.4:

CTRDEF = INTGRL (0., RARDEF − RDRDEF)
RARDEF = INSW (RTRDEF − 0.4, 0., RTRDEF/10.)*(1. − CTRDEF)

The value of the cumulative transpiration deficit is constrained between 0. and 1. by multiplying its rate of accumulation by 1. minus its own value.

Exercise 57
What other formulation could have been chosen to limit the range of CTRDEF? What are the implications for the hypothesis on which these formulations are based?

When after a drought moisture becomes available again, the effect of the previous period of water shortage gradually disappears. This is described by an exponential extinction of the cumulative transpiration deficit (RDRDEF) at a relative rate of 0.1 d^{-1}, when the value of the relative transpiration deficit is below 0.4.

RDRDEF = INSW (RTRDEF − 0.4, CTRDEF/10., 0.)

Qualitatively this approximation provides a satisfactory description of the processes involved.

The light-use efficiency at low levels of irradiance and the CO_2 diffusion limited maximum value at light saturation of the photosynthesis light-response curve for individual leaves are both defined as state variables in ARID CROP. Both are initialized with the value valid for leaves grown under optimum conditions. There are indications that the CO_2 assimilation capacity of leaves, subjected to a prolonged period of water stress is impaired. This is taken into account by assuming that both the initial efficiency and the maximum level of CO_2 assimilation decrease when the cumulative relative transpiration deficit (CTRDEF) exceeds 0.5. The relative rate of decline of both state variables increases linearly from $0.$ when CTRDEF is below or equal to 0.5 to a maximum value of 0.05 d^{-1} when the latter reaches 1. When the cause of the stress is removed, i.e. when the relative transpiration deficit drops below 0.4, the photosynthetic capacity recovers at a rate proportional to the relative growth rate of the vegetation. Sufficiently prolonged favourable conditions may lead to complete restoration of the photosynthetic capacity of all remaining leaves. Such behaviour seems reasonable considering the fact that the newly formed leaves will have the maximum photosynthetic capacity and that in the surviving old leaves, impaired enzymes and membranes may be rebuilt.

The total amount of structural plant material produced each day is partitioned between roots, leaf blades, non-leaf vegetative material (stems and leaf sheaths) and seeds. As explained in Subsection 3.4.2, the physiological principles governing the morphogenetic characteristics of plants are only partially understood and it is difficult therefore to include morphogenesis in models at this stage. However for the type of models discussed here it is of prime importance to take the distribution pattern into account because it determines the division between below ground and above ground material, the latter being amenable to validation. Moreover the dry matter produced is in most cases exploited by grazing. To take that into account, the possibility of selective removal of certain plant organs (leaves) must be present.

The partitioning of dry matter between shoot and root is governed by a phenology-dependent distribution factor (Subsection 3.3.6) and is furthermore influenced by the moisture status of the vegetation. The functional balance between shoot and root (Subsections 3.3.6 and 3.4.3) implies that moisture stress in the plant leads to sub-optimal growth rates for the above-ground plant parts, which results in increased growth of the roots and hence in a shift in the shoot/root
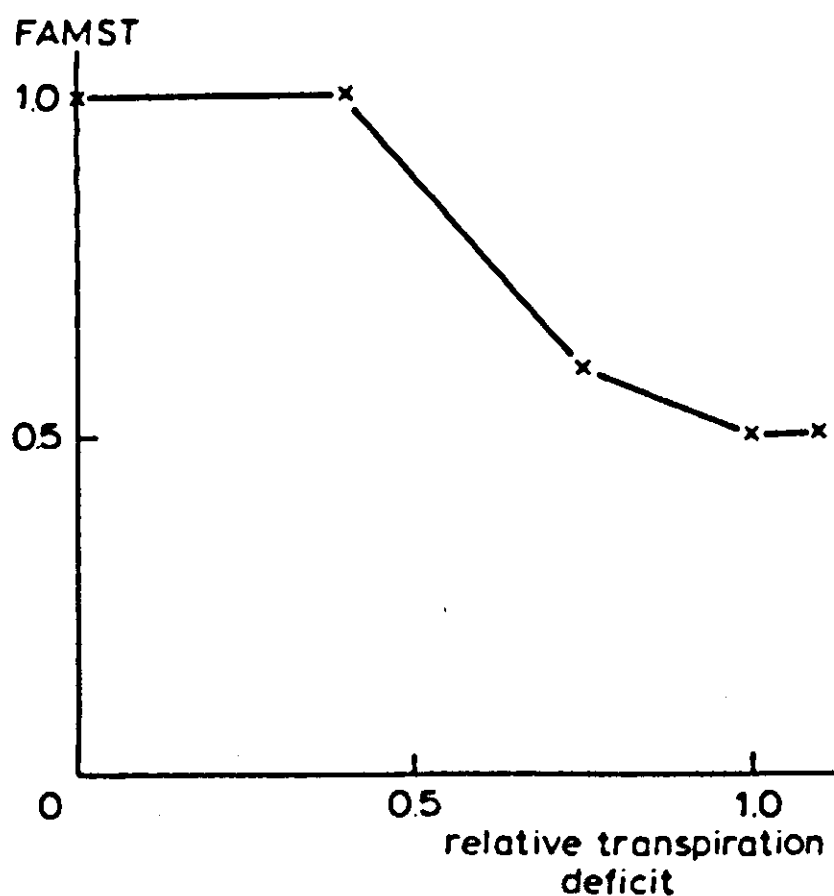
Figure 46. The relation between the reduction factor for shoot growth (FAMST) and the relative transpiration deficit.

ratio. The function presently applied in the model to restrict the share of the shoot in favour of the root in relation to the value of the relative transpiration deficit, is presented in Figure 46.

The material available for growth of the above-ground plant parts is partitioned into seeds, leaves and non-leaf material. Growth of the seeds starts at flowering and a constant fraction of the available dry matter is henceforth allocated to the seeds. (Both the development stage at flowering and the fraction allotted to the seeds are estimates based on field observations, which is a simplification especially when applied to a mixed sward. The differences in development pattern between species are often considerable, e.g. legumes and many other dicotyledons with indeterminate flowering as compared to grasses with determinate flowering.) The material remaining after the seeds have had their share is divided between leaf blades and other structures. The applied distribution factor is again a function of the development stage of the vegetation. The general shape is such that progressively less of the available dry matter is invested in the formation of new leaves (cf. Figure 33 of Section 3.3). The actual values used in ARID CROP are at the moment subject of renewed investigations.

Once plant tissue has been formed, it can lose its viability and die. In the model, two causes of death are considered. Upon completion of the plant's life cycle its vegetative structures stop functioning and dry up, either because of physiologically determined processes or due to translocation of vital elements from these structures to the developing seeds. Dying because of senescence also occurs at earlier stages of plant development, since the leaves have a limited lifespan and the first leaves will disappear at an early stage. This phenomenon could be taken into account if the developing leaves were kept in age classes. Where that is not the case, as in the present model, application of a relative death rate to the actual leaf mass present at any moment will overestimate senescence in the early stages. It has been assumed therefore that until the onset of

seed-fill leaf death from senescence is negligible. From then on, leaves die at a relative rate of 0.005 d^{-1} initially, a value that increases to a maximum of 0.1 d^{-1}, attained at maturity (cf. Subsection 3.1.2). These values describe fairly realistically the situation in the field, where towards maturity the vegetation dries up in about a fortnight, even when soil moisture is still available.

A second cause of death, especially important in the present context, is insufficient moisture in the soil. In the present formulation of the model, death under the influence of moisture stress is governed by the combined effect of the moisture status in the soil and the evaporative demand of the atmosphere. Especially during periods, characterized by high temperatures and low humidity (referred to in Israel as 'chamsin') the vegetation visibly deteriorates, even when soil moisture is well above wilting point. Evidently a situation develops, where even complete closure of the stomata does not prevent dehydration of plant tissue and subsequent death. It is assumed now that the rate of dying due to water shortage is proportional to the difference between the actual daily transpiration rate and the potential water loss through cuticular transpiration. The time coefficient for dying is set at 5 days, reflecting the considerable buffering capacity of the plant and the heterogeneity of the soil. The relative death rate is applied to both the leaf blades and to the non-leaf material, of which, in reality, the leaf sheaths will be much sooner affected than the stem proper. The result of this description is that appreciable death of leaves only takes place when the soil has dried out till permanent wilting point, except in situations where actual transpiration rates fall far short of the evaporative demand.

4.1.5 Evaluation of ARID CROP

Since the proof of the pudding is in the eating, the degree to which the model represents reality must be judged by comparison of its behaviour against that of the real world system. For this purpose it is of prime importance to have at one's disposal a number of data sets collected completely independently from the development of the model. In practice, however, the situation is often such that data collection and model development proceed in parallel, done by the same person or group. That fact introduces the danger of strong interactions between data collection and model development, and consequently the use of the model as a sophisticated curve-fitting method (cf. Subsection 1.3.6). Such behaviour is especially obvious when only one data set is available. In our situation we have at least the advantage that a relatively large number of years, each one with its own specific environmental conditions, is available to test the model. These data sets were collected in the northern Negev desert of Israel, a semi-arid environment with an average annual rainfall of 250 mm. The vegetation consists of a mixture of annual species, typical of abandoned crop land (van Keulen, 1975).

The results of two reasonably representative years are presented here in Figures 47 and 48, a more complete validation has been described by van Keulen et

al. (1981). The 1972/1973 growing season was a 'wet' year with high rainfall, favourably distributed over the growing season, whereas 1975/1976 was a year of prolonged drought, sufficiently severe to create stress conditions for the vegetation.

The measured and simulated growth curves for 1972/1973 (Figure 47a) are in excellent agreement for most of the growing season, except for a burst of growth towards the end of the growing period. The simulated and measured values of soil moisture in the rooting zone (Figure 47b) are also in close agreement.

In Figure 48a the measured and simulated course of dry matter production is given for the 1975/1976 growing season. Also for this season, the results of the model are in close agreement with the measured values. The present description of the influence of moisture stress on growth and development seems to be satisfactory, but needs further confirmation. Data on the moisture balance are given in Figure 48b. Only small changes occur over the growing season and there is a tendency for the simulated values to be lower than the measured ones, but the deviations are within the error bound set by the accuracy of the moisture sampling technique used.

The results presented here indicate that the model performs reasonably well in two growing seasons with strongly contrasting environmental conditions.
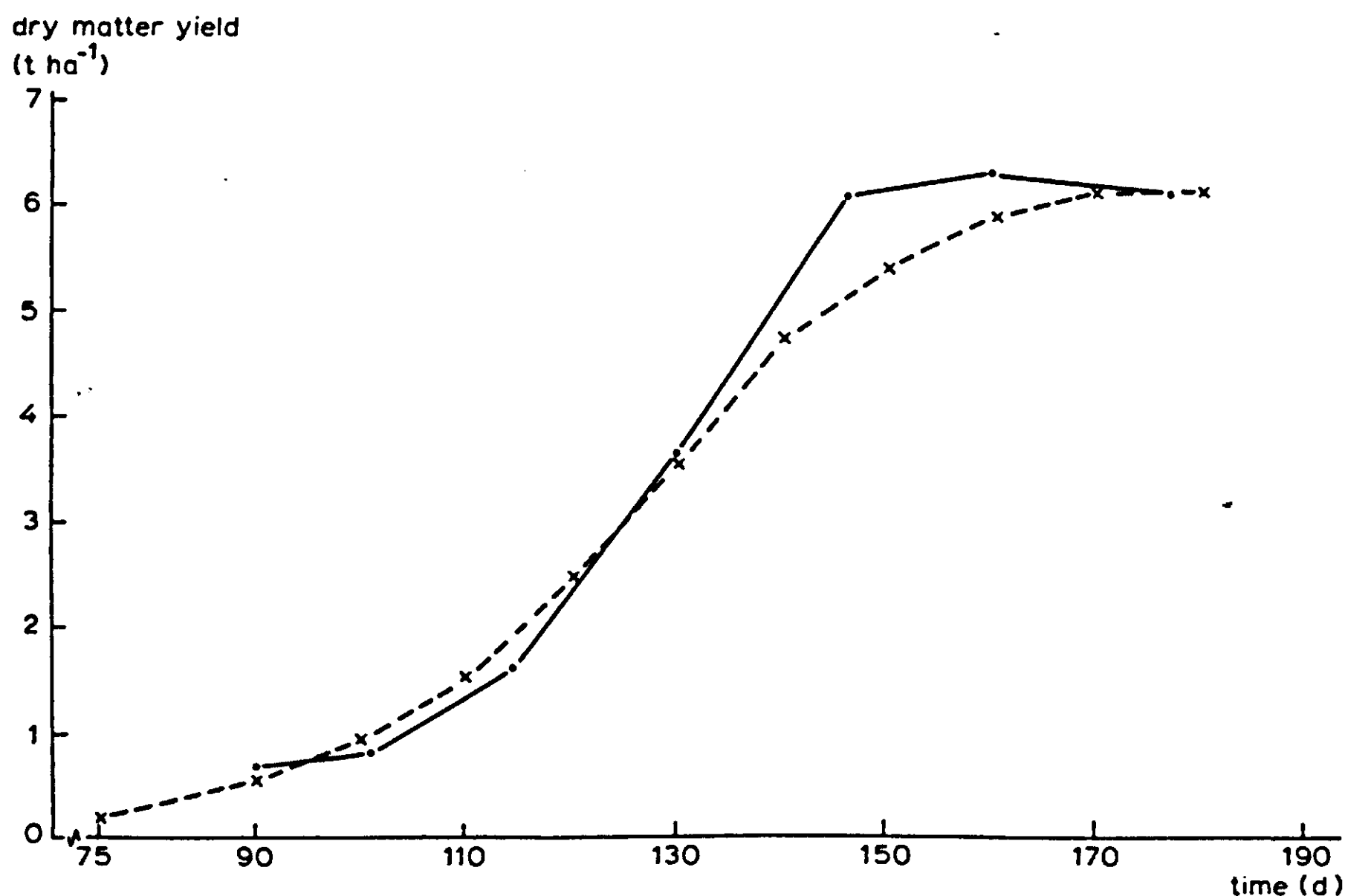

Figure 47a. Comparison between measured (•) and simulated (x) dry matter accumulation of natural pasture in Migda (Israel) 1972/1973.
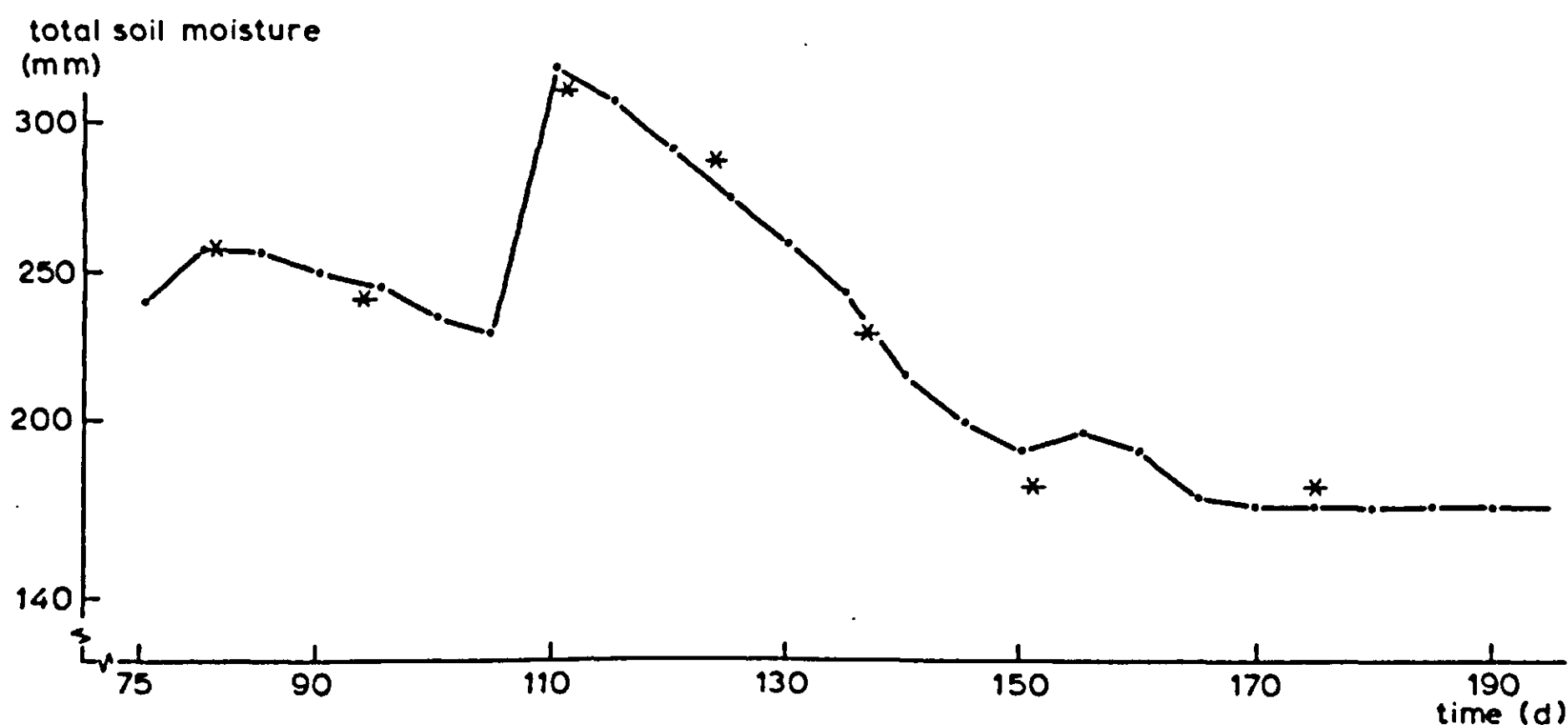
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Figure 47b. Comparison between measured (*) and simulated (•) total soil moisture under natural pasture in Migda (Israel) 1972/1973.
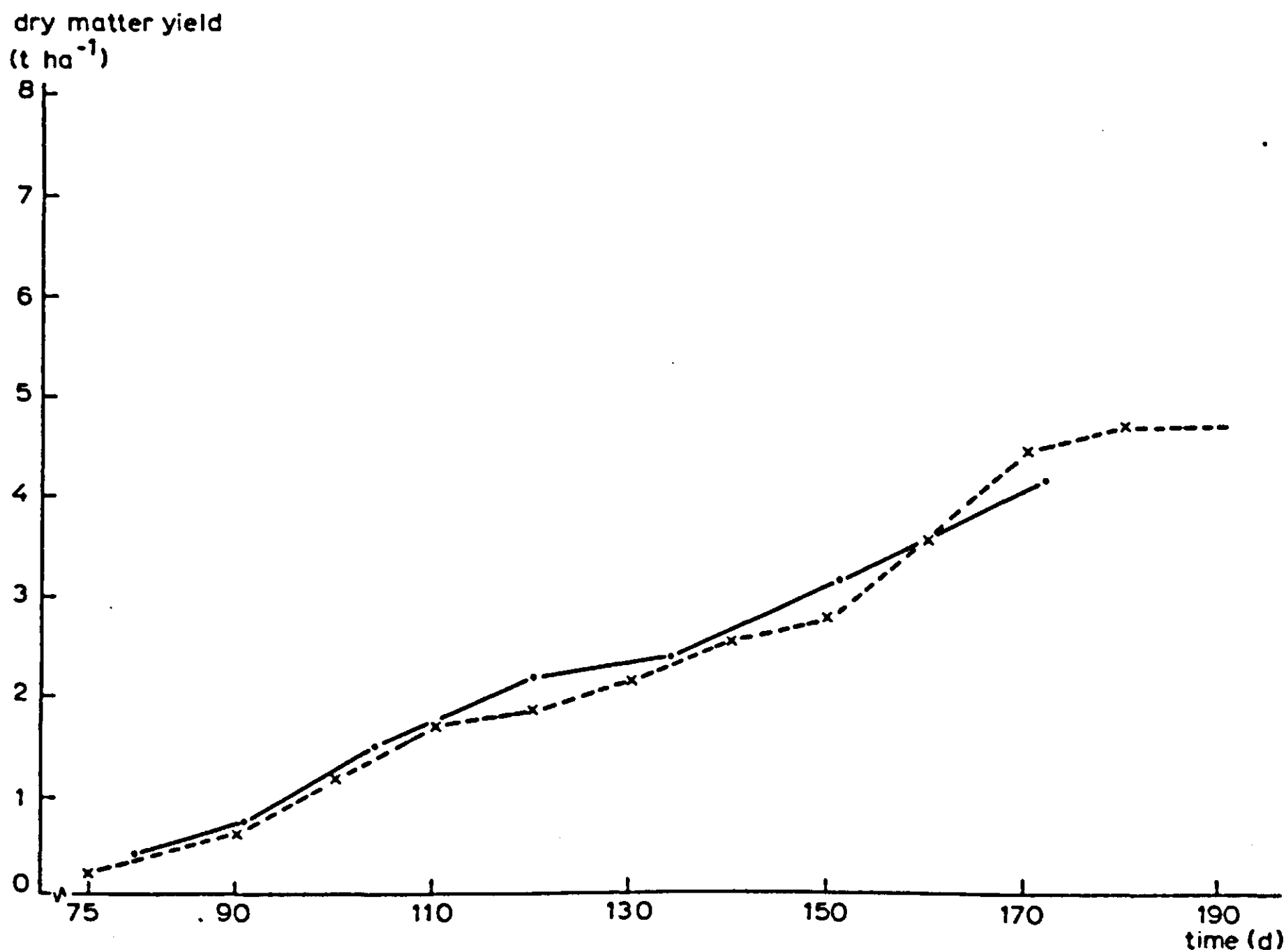

Figure 48a. Comparison between measured (•) and simulated (x) dry matter accumulation of natural pasture in Migda (Israel) 1975/1976.
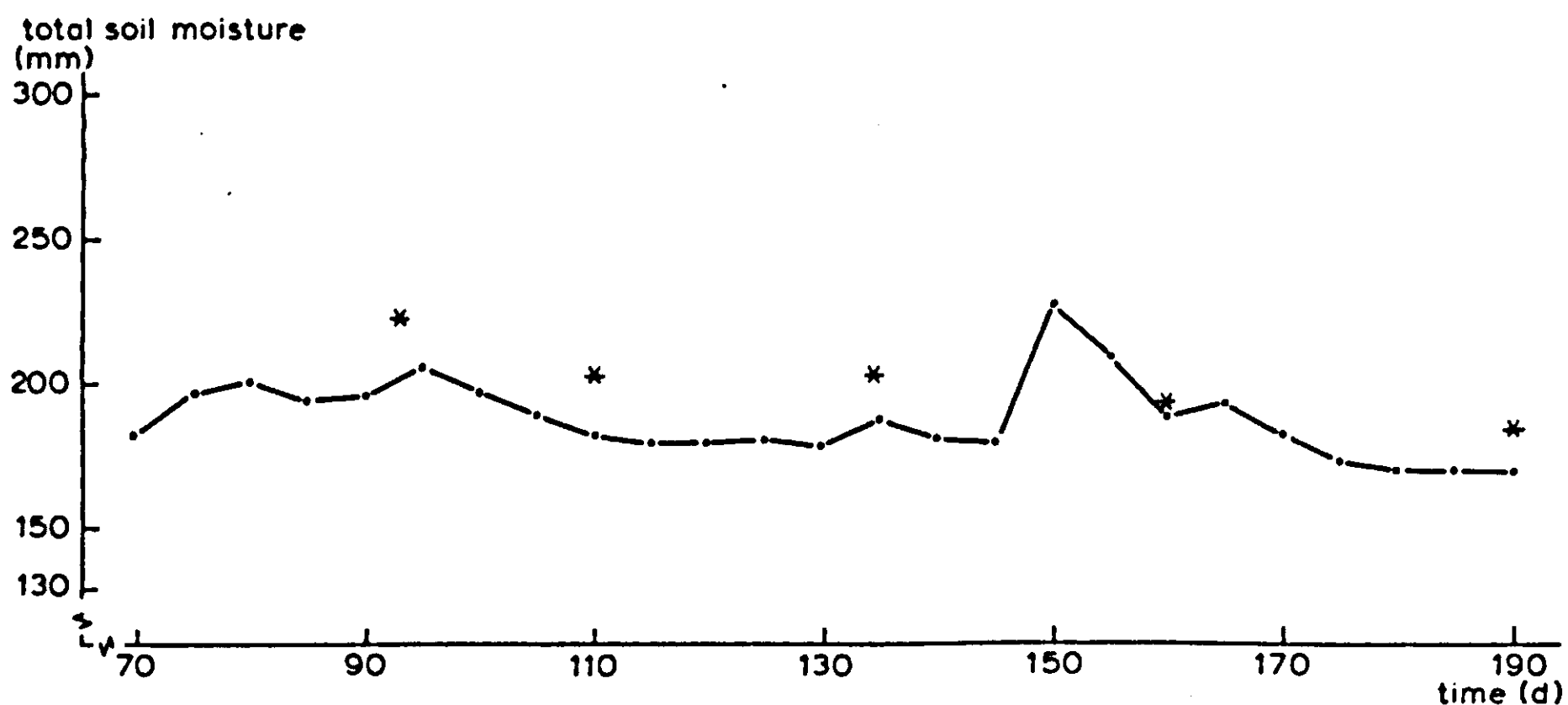
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Figure 48b. Comparison between measured (*) and simulated (•) total soil moisture under natural pasture in Migda (Israel) 1975/1976.

4.1.6 Major problem areas in the model

Although the performance of the model is often realistic when compared to real-world behaviour, a number of weak points are known to exist. Most of these points are related to plant physiological questions. Some of them are briefly discussed here:

— The amount of dry matter present at the completion of the germination stage depends on the number of seedlings of the various species that can establish themselves. That number not only depends on the conditions during the germination process, such as the length of the wet period, temperature, etc., but is codetermined by the composition and the quality of the seed stock present in the soil. It is, at the moment, virtually impossible to determine the quantity of seeds present and it is even less clear how their viability should be appraised. The process of germination itself is complex, and although our insight into the various parameters influencing it is increasing, it is not yet possible to include that knowledge in a model as the one presented here. Prediction of the initial biomass therefore remains a major difficulty that needs attention. The best alternative at the moment is to measure biomass early in the growing season and adjust the initial value accordingly.

— The influence of prolonged moisture shortage on assimilation, partitioning of dry matter and dying of the tissue in ARID CROP is based on intelligent guesses. Much more experimental work is needed, both to determine these relations under controlled conditions and to collect data in the field that can serve for validation of the model results.

— Although the influence of moisture shortage on production is fairly well described, its effect on plant survival is largely unknown. What happens in the transition zone between the end of a positive carbon balance and the complete

disappearance of the vegetation has not been investigated in enough detail.

– Crop morphogenesis is by no means understood and the functions now governing the distribution of dry matter among the various plant organs are speculative. More research into quantitative aspects of leaf formation and the effects of environmental factors on the process are needed.

– Phenological development of the vegetation is also incompletely understood. In most cases the present description, in which the development rate is governed by temperature, satisfactorily predicts the behaviour of the canopy. However, in a subsequent season, where germination was very late – towards the end of December – temperature only proved to be inadequate to predict development. Apparently day length also plays a role then (cf. Subsection 3.3.2), as in many species found in the Sahelian region. Due to lack of observations these effects are still difficult to quantify.

– A point which needs attention is the fate of the root system under conditions where above ground material dies of water shortage. It seems reasonable to assume that the plants will hang on to the roots as long as possible, when water becomes scarce. However, when whole tops die, so will their roots. Since this process is not taken into account in the model, a situation may develop where, under severe stress, virtually all the above ground material is dead, yet a substantial root system is maintained.

4.1.7 Application of the model ARID CROP in a summer rainfall region

The model ARID CROP, developed for the conditions prevailing in the northern Negev desert, was subsequently applied in the Sahel (Penning de Vries & Djiteye, 1982). Apart from the introduction of the appropriate parameter values and driving variables for climate and soil conditions, a few modifications of the model were necessary to obtain a realistic behaviour. For changes in the soil water balance, see Subsection 4.2.3.

Description of the germination process along the lines applied for the winter annuals in the Northern Negev was not applicable to the conditions in the Sahel, where it rains in the summer. Therefore the start of the growing season is empirically defined as the moment that a certain amount of biomass is present in the field.

A summary submodel in ARID CROP accounts for the reduction of canopy transpiration as a result of stomatal closure of leaves at low light levels down in the canopy. This summary model in the form of a set of tables in ARID CROP is computed with BACROS (Subsection 3.3.8) for the appropriate conditions (van Keulen, 1975). It turned out that these values are much more invariable in the warm Sahel area than in the cool Mediterranean region of the Negev, and they could be replaced by the constant of 0.7 for the whole growing season.

Small changes are also introduced with respect to the quantification of the respiratory processes described by van Keulen (1975): the conversion efficiency is changed to 0.70, whereas a maintenance respiration requirement of 0.015 kg

$kg^{-1} d^{-1}$ is applied, since the high levels of irradiance permit a greater contribution directly from assimilatory processes.

The Sahelian species are in general quite sensitive to day length. Phenological development is therefore governed by both temperature and day length (see also Subsection 3.3.2). Semi-empirical formulations, based on extensive experimentation (de Ridder, 1979) are introduced in the model.

Some of the results obtained for the Sahelian region are presented in Section 4.2.

4.1.8 Concluding remarks

The results presented in this paper and elsewhere (van Keulen et al., 1981) show that ARID CROP performs well in relatively wet years, but most problems arise in the relatively dry growing seasons, thus the model does not quite live up to its name. This points to the fact that the survival and recovery response of annual plants subjected to moisture stress for a prolonged period cannot be explained without reference to the effects of that stress on morphological development, photosynthetic performance and phenology of the species involved. That in itself is, however, in a way a major justification for the development of the model, since it clearly points to the limits of the concepts underlying the model, in explaining the behaviour of arid production systems.

The model in its general outline seems applicable for different ecological conditions, provided that water is the major production determining factor. However, certain adaptations, related to specific plant properties, either physiological or phenological may be necessary. Lack of sufficient understanding of some of the basic principles, which leads to the application of partly descriptive rather than explanatory formulations, is the major reason for this requirement.