8. A Dynamic Model of Plant and Crop Growth

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Introduction

The development of an elementary crop growth simulator (ELCROS),
designed according to the general principles of biological model-building [24]
has been discussed earlier [4, 25], with special attention to the functional
balance between the growth of the shoot and the root.

It is assumed that the individual plant or the whole crop contains a pool
of reserves (RES), largely in the form of carbohydrates. Photosynthesis
(PHR) is the only source of these reserves which are then used for respiration
(RSP), increase in structural root weight (GRW), in structural leaf weight
(GLW) and in structural stem weight (GST). The rates of these changes are
represented by valve symbols in the relational diagram of Figure 8.1.
Photosynthesis and respiration transfer material from and to the environ-
ment, but the growth rates transfer carbohydrates from the reserve pool to
the structural weight of the roots (WRT), leaves (WLV) and stem (WST), i.e.
into organic material that cannot be used as reserves. The levels or contents of
these integrals are represented within rectangles in Figure 8.1, which also
indicates the way in which root growth may depend on environmental
conditions. Soil temperature is determined by direct observation or from the
meteorological part of the programme and the relative growth rate of the
roots (RGRR) is calculated for the particular species concerned. This is not a
growth rate which can be used directly to compute the increase in root
weight, but an auxiliary value necessary for further computations, and as such
is presented in a circle in Figure 8.1. The possible rate of increase in root
weight (PGRW) is now calculated by multiplying the relative growth rate

(RGGR) by the weight of those roots (WRT) which are still young enough to be capable of growth (C). This possible growth rate, again an auxiliary value, is only realized as an actual rate of increase in root weight (GRW) when there are sufficient reserves. In this method of presentation (Figure 8.1), the flow of organic material (kg CH_2O ha^{-1} day^{-1}) is presented by full lines and the flow of information by dotted lines. In view of the daily cycle of environmental conditions, it is assumed that the rates calculated for a particular moment do not change appreciably over a period of about an hour, so that hourly time steps can validly be used in this simulation model.
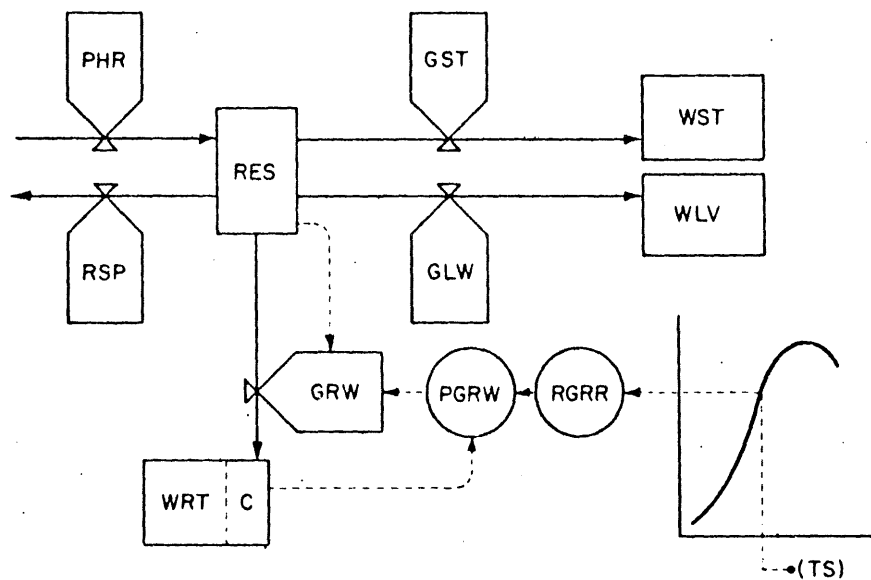

Fig 8.1   The relational diagram of the central part of ELCROS.

Operating versions of this simulation programme (ELCROS) are available in the languages DYNAMO and CSMP/360 [9]. The latter will be used in the present chapter. At the present time a simulation programme of this type must be regarded more as a guide to research than as a final solution, since many ad hoc assumptions regarding the physiological mechanisms underlying plant and crop growth still have to be made. The present chapter will discuss some of the more important of these mechanisms, paying special attention to the rates of photosynthesis, of leaf growth and of respiration. The interrelations between shoot and root growth have been treated elsewhere [4].

Photosynthetic Rate

(i) Physiological Aspects

The photosynthetic rate of a crop depends on the amount of incoming light energy, the area and distribution of leaves in the canopy and the photosynthetic properties of the individual leaves.

The calculation of the photosynthetic rate of the crop at a particular instant is carried out in two stages. Firstly, the light distribution over the

individual leaves of a crop has to be calculated, and secondly, the photosynthetic rate of the crop has to be obtained by integration of the photosynthetic rate of each leaf calculated from its photosynthesis function.
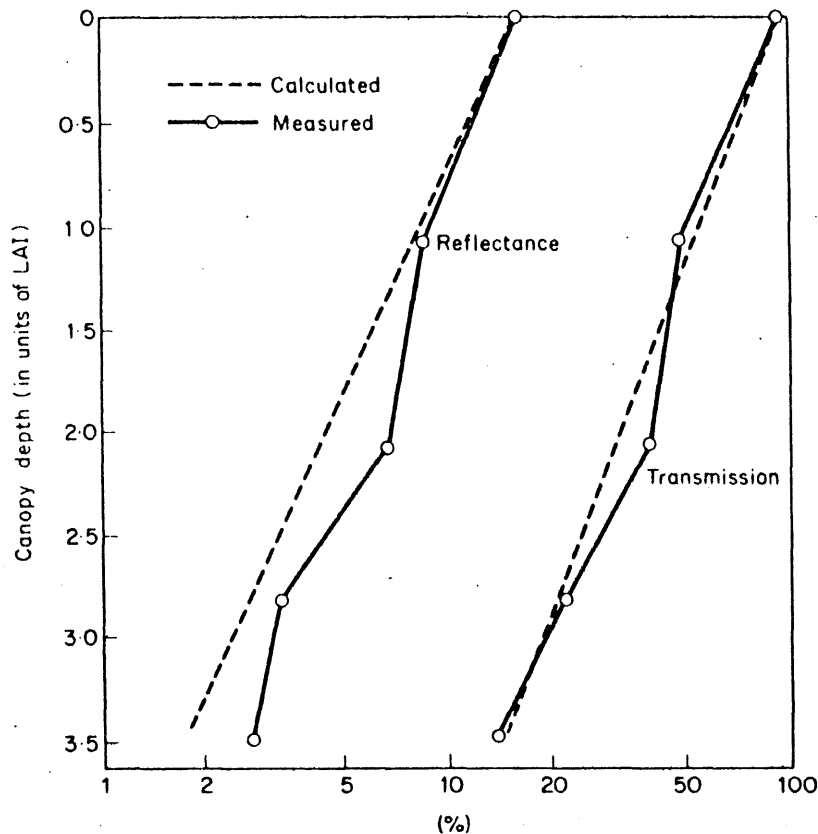
Fig. 8.2   Calculated and measured transmission and reflection in a maize
crop with a leaf area index of 3.5; from Idso and de Wit [8].

The evaluation of the light distribution is a purely geometrical problem, which by now has been largely solved. Figure 8.2, for instance, shows the measured and calculated transmission and reflection rates inside a maize crop, the calculated values being based on measurement of the reflection and transmission coefficients of individual leaves and on the leaf distribution function. Although the architecture of the canopy may vary during the growth of a crop, the influence of variation in leaf arrangement should not be over-emphasized. For instance, the leaf distribution function of a grass canopy varies from very erectophile in short swards in spring to very planophile in long swards in autumn. However, assuming that the photosynthesis function remains the same, this large difference in leaf distribution would lead, under Dutch conditions, to a difference in gross photosynthesis of only 25 — 50 kg CH_2O ha^{-1} day^{-1}, out of a total of about 375 kg ha^{-1} day^{-1} [23].

The influence of the photosynthesis function of the individual leaves is more important, because of its greater variability. If the maximum photo-

synthetic rate of the individual leaves increases by 100%, but the photosynthetic rate at low intensities remains the same, then the photosynthesis of the crop may increase by about 50 per cent [23].

The photosynthetic rate of a leaf will depend to a considerable extent on its age or position along the stem, but such effects cannot as yet be incorporated in the simulation programme, since the distribution of leaves of different ages through the crop canopy is usually not known.

In the present programme (ELCROS), therefore, these effects of ageing are neglected and the instantaneous photosynthesis rate is calculated by the numerical method described by de Wit [23], which assumes that each leaf has a definite life-span, but that the photosynthesis function does not change during the life of the leaf.

In this programme the instantaneous effect of temperature on photosynthesis is taken into account, but no account is taken of any effect of the temperature regime during the formation of leaves on their subsequent rate of photosynthesis.

(ii) Programming Aspects

The numerical calculation of crop photosynthesis from the basic data for each hour of simulation is expensive with regard to computer time. Consequently, calculations are done once and for all and summarized in a two-way table in which leaf area (ALV) and the sine of the angle of the sun are the two variables. Separate tables are used for clear and for overcast skies. The height of the sun at the hourly intervals is calculated from the latitude, the day of the year and the hour of the day according to standard astronomical formulae [23]. The condition of the sky (i.e. clear or overcast) is obtained from the meteorological section of the simulation programme, and the leaf area from the leaf growth section of the programme. The estimates of crop photosynthesis for maize given in Table 8.1 are based on the assumptions that leaf distribution is slightly plagiophile [23], that the scattering coefficient is 0.2, and that the leaf photosynthesis rate is given by

$$(LI/(.365 + LI)) \times 84.5 \text{ kg } CH_2O \text{ ha}^{-1} \text{ h}^{-1}$$

in which LI is the light intensity absorbed in cal cm^{-2} min^{-1}. This function has been calculated for $23°C$, but similar calculations can be made for other temperatures, and in fact the instantaneous effect of temperature for maize may be accounted for quite accurately by the following multiplication factors:

Temp. °C	0	5	10	15	20	25	30	35	40	45
Factor	0	0	0.28	0.54	0.79	1.03	1.08	1.08	0.99	0.45

It is at present assumed in ELCROS that leaf temperature equals air temperature at a standard height i.e. at 10 cm above a soil surface covered with turfgrass, and that root temperature has an amplitude of 0.45 times that

of air temperature and lags two hours behind it. The temperature of the growing point is assumed to be intermediate between soil and air temperature, depending on its position with respect to the soil surface. These assumptions seem reasonable, and can only be improved upon by simulating simultaneously the growth of the crop and the micro-climate.

Table 8.1

Crop photosynthesis rates of maize as dependent on leaf area index (ALV) and the sine of the angle of the sun for clear (C) and overcast (O) skies.

ALV	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	SKY
						SINE						
0	0	0	0	0	0	0	0	0	0	0	0	C
	0	0	0	0	0	0	0	0	0	0	0	O
1	0	7.0	15.5	21.0	25.0	28.2	31.2	34.0	36.0	38.3	40.0	C
	0	1.7	3.2	5.5	7.2	8.5	10.7	12.5	14.0	15.6	16.8	O
2	0	9.0	20.0	28.2	35.0	41.5	47.2	52.1	56.2	60.4	63.7	C
	0	2.0	4.5	7.2	10.0	12.7	15.2	17.9	20.2	22.7	24.5	O
3	0	10.2	21.3	31.0	39.5	47.0	54.5	61.4	66.7	72.6	77.1	C
	0	2.4	5.2	8.5	11.5	14.5	17.5	20.5	23.0	26.1	28.2	O
4	0	10.5	22.0	32.0	42.0	50.0	58.5	65.9	72.5	79.1	84.4	C
	0	2.5	5.7	9.0	12.2	15.5	18.5	21.8	24.7	27.7	29.9	O
5	0	10.8	22.5	32.4	42.2	50.5	59.0	68.2	74.0	82.5	88.3	C
	0	2.5	5.8	9.2	12.4	15.8	18.8	22.3	25.4	28.5	30.7	O
6	0	11.1	22.9	32.7	42.3	51.0	59.5	69.3	75.5	84.3	90.4	C
	0	2.6	5.9	9.4	12.6	16.0	19.2	22.6	25.6	28.8	31.1	O
7	0	11.4	23.3	33.1	42.4	51.5	60.0	69.8	76.5	85.2	91.5	C
	0	2.6	6.0	9.5	12.7	16.1	19.3	22.7	25.7	29.0	31.3	O
8	0	11.5	23.5	33.3	42.5	51.9	60.4	70.1	77.0	85.7	92.0	C
	0	2.6	6.1	9.6	12.8	16.2	19.4	22.8	25.8	29.1	31.4	O
9	0	11.6	23.8	33.4	42.6	52.2	60.8	70.2	77.5	85.9	92.3	C
	0	2.7	6.1	9.6	12.9	16.2	19.5	22.9	25.9	29.1	31.5	O
10	0	11.7	24.0	33.5	42.7	52.5	61.2	70.3	78.0	86.0	92.5	C
	0	2.7	6.2	9.7	13.0	16.3	19.5	22.9	26.0	29.2	31.5	O

Leaf Growth

(i) Physiological Aspects

The rate of growth of the plant or crop has usually been measured in terms of increase in weight, in length and thickness or in area, depending on the aim of the particular experiment.

The present programme (ELCROS) must take several aspects of growth into account. In the first place, it must describe the accumulation of dry matter into the structural tissues, i.e. the dry matter accumulated minus the

directly available reserves, which are kept in a separate pool for distribution to the growing organs. In the second place, the rate of expansion of the leaf surface has to be known to obtain a measure of the size of the photosynthetic system. The primary determinant of growth is therefore the flow of reserves into the structure of the growing plant-parts. The rate of this flow depends on the amount of tissue capable of growth, the relative growth rate of the tissues, and the availability of essential materials for growth.

In the young seedling, all the tissue takes part in growth and, provided that all essential materials are available, growth occurs at the maximum rate for the particular temperature. This maximal rate can be conveniently expressed as the relative growth rate on the basis of total weight (RGR = $(dW/dt)/W$). In older plants, however, part of the tissue is mature and incapable of growth. In spite of this, single plants will grow exponentially when the supply of essential materials for growth increases linearly with the size of the plant.

In this case, the mature material is always a constant (and small) fraction of the total. When, however, deviations from exponential growth occur, as with mutual shading or limiting water supply, the fraction of mature material will vary and may comprise a large part of the total weight. In this case, the relative growth rate, expressed on the basis of total weight, will show variable values, although the relative growth rate of the tissues capable of growth is likely to remain constant, so long as all essential materials are present.

The amount of tissue capable of growth can be estimated from the pattern of leaf growth of the plant or crop. At constant temperature, the consecutive leaves of a maize plant, like most other species [21], appear at a constant rate, and at any one time only the last three visible leaves are increasing in size (Figure 8.3) [6]. From experiments with bean plants, it appears that the leaves next in age, which do not grow in the intact plant, can resume growth when the youngest leaves are removed. This generally-accepted consequence of the removal of sinks [7] probably occurs also in maize, although in this species the complete youngest leaves cannot be removed without damaging the whole plant. The removal of only the visible leaves does not affect the meristem nor the growth of the youngest leaves, since both cell division and cell extension take place within the sheaths of the older leaves [16].

This pattern of leaf growth can be illustrated by considering a maize plant with ten visible leaves, numbered from 1 (the oldest) to 10 (the youngest). Leaves 10, 9 and 8 are growing at about the same rate [6] and are assumed to be fully capable of growth. Leaves 1 to 5 will not grow any more even if the shoot apex is completely destroyed, although their axillary buds can develop into new tillers. The intermediate leaves, 7 and 6, can resume growth to a certain extent only. The fraction of tissue fully capable of growth thus decreases with the age of the plant, and this effect has to be introduced into the simulation programme.

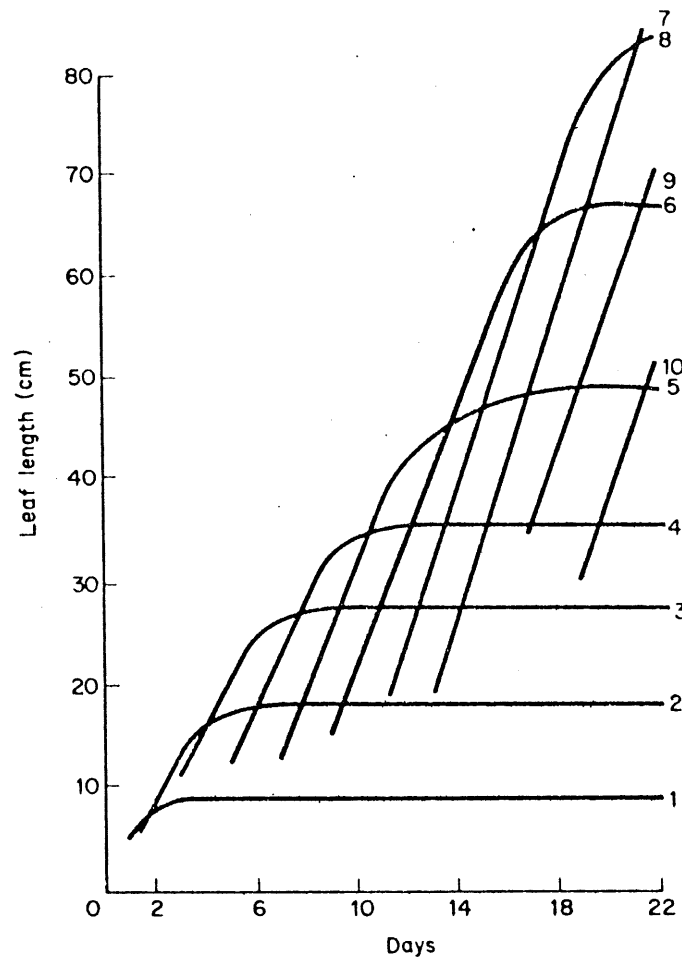A maize plant growing at a temperature of 20°C may take 2.3 days

Fig. 8.3   The increase in length of successive leaves of the maize plant with time; only three leaves are growing at the same time. From Grobbelaar [6].

between the initiation of two successive leaves, so that, following the above assumptions, it is only the tissue which has been produced in the last 4 x 2.3 i.e. 9.2 days which is still fully capable of growth. Within this period the plant weight increases at least ten-fold, which means that only 10 per cent of the total weight consists of mature tissue. Hence no large errors are introduced into the first estimate of the relative growth rate by using total plant weight as a basis for calculation, provided that the plants have been growing exponentially with a constant supply of such essential materials for growth as carbohydrates, water and minerals. In the present version of the simulation programme (ELCROS) the mineral supply is assumed to be optimal throughout for all plant parts. However, although water is assumed to be optimally available to the roots, local water stress may occur in the transpiring parts, due to resistance in the plant. The extent of this water stress can be estimated by comparing the amount and activity of the roots which are present with the amount and activity of those required to maintain full turgidity of the leaves, taking into account the transpiration rate [4].
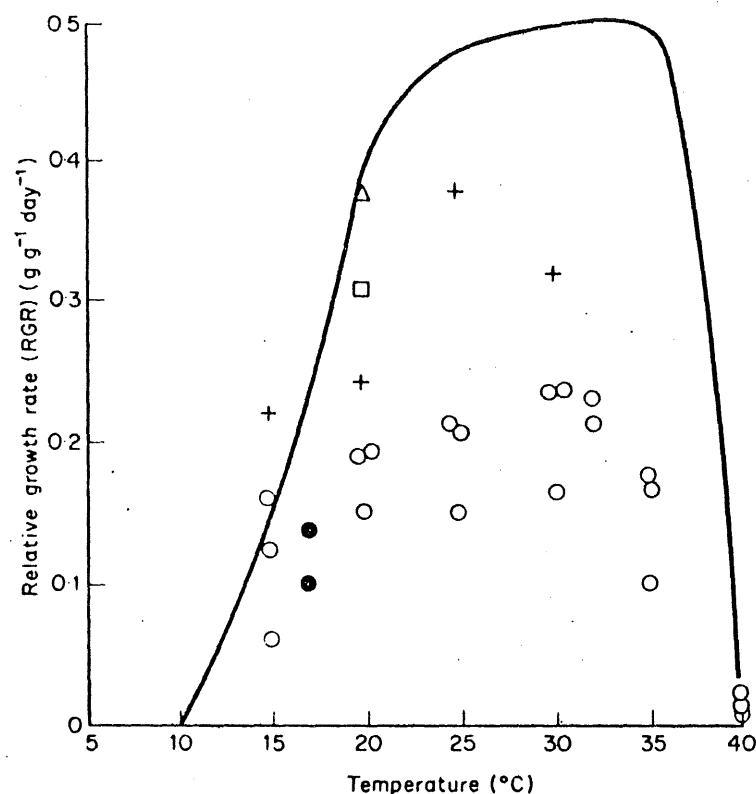
Fig. 8.4   *Relative growth rates of maize tops and roots under various conditions (see text), and the estimated relation between temperature and the relative growth rate of young tissue, when well supplied with carbohydrates and at full turgidity.*

The effect of temperature on relative growth rates, derived from various experiments, is given in Figure 8.4, and it can be seen that there is considerable variation in relative growth rate over the range 15 to 30 °C. This variation is due to various other limitations to growth. The open circles (o) indicate the relative growth of the roots of plants which were kept with their shoots at a temperature of 20 °C. As Figure 8.5 shows, between 20° and 30 °C, the carbohydrate content of these plants was low, and growth was therefore limited by lack of reserves. The relative growth rate of whole plants, growing at various temperatures under comparable conditions is probably also subject to this limitation, although water stress in the above ground parts of the plants may also be operating.

To overcome these limitations, plants were transferred from a nutrient solution with nitrogen to one without nitrogen. Shoot growth was now inhibited by shortage of nitrogen, resulting in an increased carbohydrate content and an enhanced growth rate of the roots [3]. The relative growth rate of the roots calculated for a five-day period after transfer is shown as an open square (□) in Figure 8.4. Prolonged growth without N gives plants with a relatively well-developed root system and a high carbohydrate content, the growth of the leaves being limited only by the N supply. Supplying N

removes this limitation almost immediately, so that for a time leaf growth proceeds uninhibited by the lack of carbohydrates, or minerals, or even by water stress, since the large water-absorbing area of the roots compared with the smaller transpiring surface of the shoots, decreases the resistance to transfer of water. The relative growth rate of the shoots under such conditions is plotted as a triangle (△) in Figure 8.4 [3]. Even this high value may not, however, represent the maximum possible, since as a result of the previous check in shoot growth, the plant contains a relatively high percentage of older tissue.
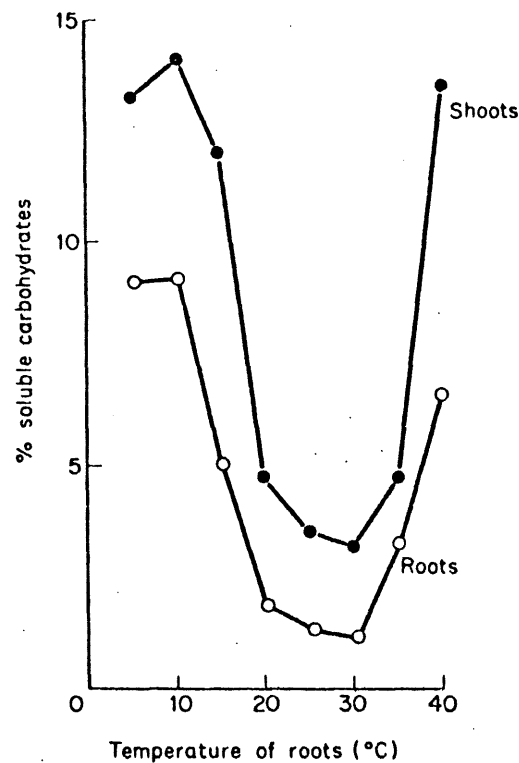

Fig. 8.5   The influence of root temperature on the carbohydrate content of maize, at a shoot temperature of 20°C; from Grobbelaar [6].

An indication of the maximum growth rates possible may be obtained from the values for young seedlings, still dependent on the materials in the seeds, which are shown as crosses (+) in Figure 8.4. Even in this case, however, there is still some doubt whether all essential materials for growth were optimally available, since Kny [12] showed that removing either the roots or the shoots from seedlings resulted in a faster growth of the remaining part, and Brown and Rickless [5] observed relative growth rates of 2.4 day^{-1} for the root tips of cucumber grown in vitro. Hence, even the highest values found in the present experiments may not indicate the maximum possible relative growth rates of young tissue grown without any limitations due to lack of reserves, water stress or shortage of minerals. Bearing in mind that maize cannot grow at temperatures below 11 °C, that under favourable

conditions the optimum temperature for growth appears to be at least 35 °C, and that the maximum possible growth rates were probably rarely achieved, the response of relative growth rate to temperature used in the present simulation programme (ELCROS) is given by the curve drawn in Figure 8.4. The use of this curve provides satisfactory comparisons of simulated and actual growth rates, but may need modification when more information is available on the maximum growth rates possible under non-limiting conditions.

(ii) Programming aspects

Even using the above physiological information in the simulation programme, it is still necessary to make *ad hoc* assumptions regarding some details of the operations, and one great advantage of attempting to construct such a programme is that it reveals quite clearly many of the important gaps in our knowledge.

Since the capacity of leaves for growth depends on their age, it is necessary to keep track of the age distribution of the leaf material in terms of its stage of development. This stage of development can be quantitatively characterized as follows.

Silking of maize in the field occurs at practically the same date, irrespective of the density of planting, which indicates that the rate of leaf initiation is independent of the size of the individual plant. Since, at constant temperature and daylength, the rate of leaf initiation is also independent of the number of leaves already formed, it is possible to specify a rate of development of maize which depends only on the external variables, daylength and temperature. Taking the stage of development (DVS) at seedling emergence as zero and that at the appearance of the male flower as one, the rate of development (DVR) may be expressed in units of day^{-1}.

The relation between this rate of development and temperature for one Dutch variety of maize and one of oats, determined under controlled conditions at fourteen hours daylength, is shown in Figure 8.6(a). The temperature of the growing point (TG) can be computed from data in the meteorological section of the programme, and using the language CSMP as mentioned earlier, the rate of development for each moment may be calculated from:

$$DVR = AFGEN (DVRTB,TG)$$

FUNCTION DVRTB = (-5.,0.), (10.,0.), (15.,0.011), (20.,0.025), . . .
                          (30.,0.04), (35.,0.04), (40.,0.004), (60.,0.004)

The curve of Figure 8.6(a) for maize is here characterized by the pair of values of the function DVRTB, the first number of each pair being the value of the independent variable TG and the second number being the rate of development (DVR). The AFGEN function states that the value of the rate of

development is obtained by interpolation in DVRTB with TG as the independent variable. The stage of development (DVS) is now obtained by

$$DVS = INTGRL (0, DVR)$$

a CSMP function that indicates that the initial value of DVS at seedling emergence is zero, the rate of change is DVR and that DVS is obtained by integration.
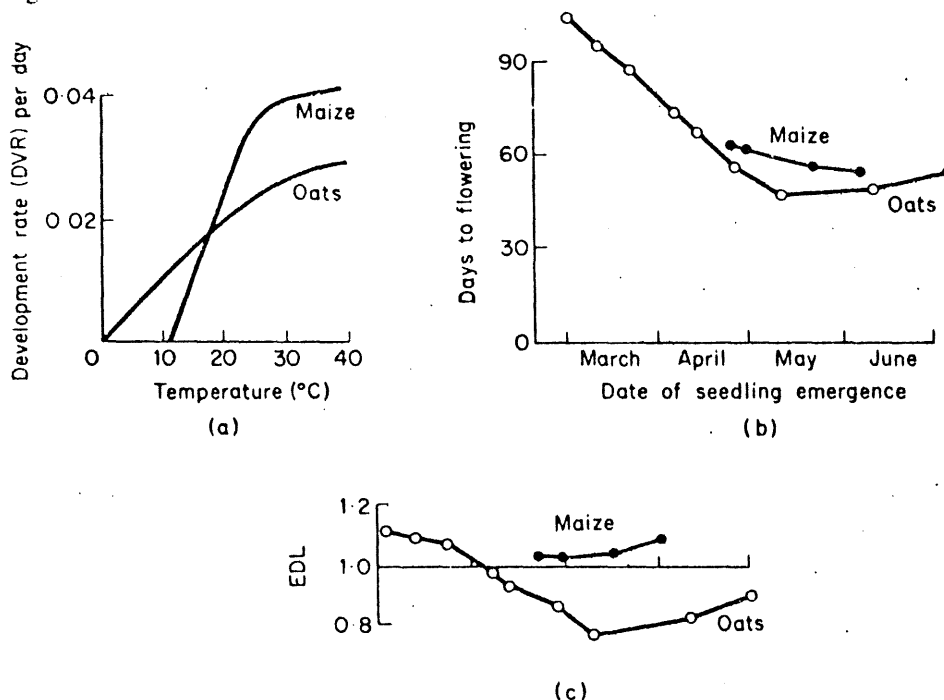

Fig. 8.6   **(a)**   *The relation between temperature and development rate (DVR) of a maize and oat variety at a daylength of 14 hours.*

          (b)   *The relation between date of seedling emergence and time from emergence to flowering in the field in the Netherlands.*

          (b)   *The classical concepts of optimum and ceiling leaf area index on the assumption that respiration is proportional to total dry matter.*

The actual number of days from seedling emergence to flowering of maize and oats sown at successive intervals in the field is shown in Figure 8.6(b), while Figure 8.6(c) gives the ratio of the actual and the computed vegetative period. For maize, this ratio is very close to one, indicating that under Dutch field conditions maize behaves as a day-neutral plant. However, in oats the ratio is larger than one before the half of April and smaller then one thereafter, indicating that the oat plant is sensitive to daylength under Dutch conditions. A simulation of the influence of daylength will, however, have to be based on a thorough study of the relevant literature.

To determine the age distribution of the leaf material in terms of the stage of development at its time of formation, a function which may be called

a 'box-car train' is introduced into the programme, as shown in Figure 8.7.
The rate of growth is integrated in the first box-car of the train, and each
time the stage of development is increased by a factor 0.04, the content of
the last box-car is discarded and that of the others is transferred to the car
with the next highest number. Hence, just before a transfer, the 1st, 2nd and
3rd and 31st box-cars contain the leaf material that is $0 - 0.04$, $0.04 - 0.08$,
$0.08 - 0.12, \ldots 1.2 - 1.24$ units old in terms of stage of development. When
the plant has reached the stage of 0.4, only the first ten box-cars of the train
contain leaf material. In the CSMP version of ELCROS this operation which
gives the weight of the leaves (WLVB) may be referred to as

$$WLVB = TRAIN\ (31,GLW,DVS,0.04)$$

The symbol WLVB refers to the weight of the leaves in the box-car-train, 31
denotes the number of box-cars in the train, GLW denotes the increase in leaf
weight and the symbols DVS and 0.04 state that the contents are transferred
each time that the stage of development is advanced by 0.04 unit.

The total weight of the leaves (WLV) may now be obtained from the
expression

$$WLV = SUM1\ (31,WLVB)$$

a function which indicates that the contents of the thirty-one box-cars in the
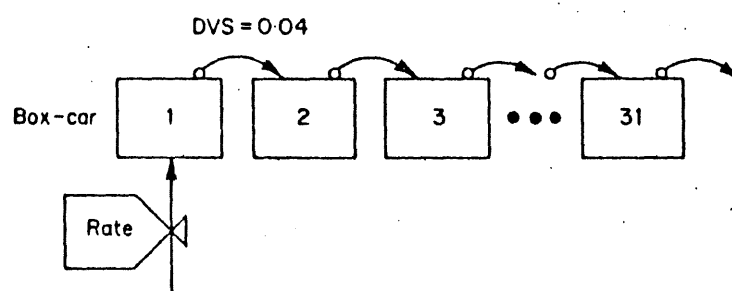train WLVB are summed.

Fig. 8.7   *Diagram of a 'box-car-train' to determine the age distribution of
growing material.*

On the basis of the number of leaves that are capable of growth at a
particular time, it may be assumed that the capacity for growth of the
contents of the thirty-one box-cars of the train WLVB may be expressed as
follows, showing the effect of maturity (EMA).

$$EMA\ (1\text{-}31) = 5 \times 1.,0.88,0.67,0.43,23 \times 0.02$$

This means that the contents of the first five box-cars are fully capable of

growth, that the contents of the last twenty-three box-cars have retained only a rudimentary capacity for growth (by means of dormant axillary buds), and that the ability to grow decreases linearly from the fifth to the ninth box-car. Hence, the weight of the leaves that are capable of growth (WLVC) may be obtained from

$$WLVC = SUM2 \ (31,WLVB,EMA)$$

a function which means that WLVC is the sum of the thirty-one products of the content of each box-car of the train WLVB and its EMA-value.

To calculate the amount of growth of the leaves, the relative growth rate of the leaves (RGRL) must first be calculated from the air temperature (TA) around the plants as

$$RGRL = AFGEN(RGRTB,TA)$$

$$FUNCTION \ RGRTB = (-5.,0.), (10.,0.), (15.,0.17), (20.,0.25), \ldots$$
$$(25.,0.56), (40.,0.22), (45.,0.08)$$

in which the RGRTB function is similar to the curve in Figure 8.4.

The maximum possible growth of the leaves (PGLV) i.e. when there are no limitations of water stress or carbohydrate shortage, is now given by

$$PGLV = WLVC \ x \ RGRL$$

In considering the influence of the reserve percentage (RPR), it is assumed that at a reserve percentage of 0, growth is zero, and at a value of 4 per cent, growth is at its maximum rate; in other words, the growth constraint of the leaves due to lack of reserves (GCLR) is

$$GCLR = LIMIT \ (0.,1.,RPR/4.)$$

This function makes GCLR equal to 0 or 1, when RPR is smaller than 0 or larger than 4 respectively, and otherwise takes the value of RPR/4.

It follows from Figure 8.1 that the total reserves in the plant are given by the integral

$$RES = INTGRL \ (0.,PHS - RSP - GLW - GRW - GST).$$

and that the reserve percentage equals RPR = RES/TWT, in which TWT is the total weight of the plant or crop.

A similar growth constraint due to lack of turgidity can be calculated from the relative amount of roots. If it is now assumed that growth is limited by the smallest of these constraints, then the actual growth rate in terms of leaf weight (GLW) is

$$GLW = PGLW \ x \ AMIN1 \ (GCLR,GCLT)$$

Finally, it is important to consider the rate of increase of leaf area. A simple assumption is that the increase in leaf area is proportional to the increase in leaf weight, so that leaf area may be found from leaf weight, using

a factor of about 750 kg ha^{-1} (7.5 mg cm^{-2}).

However, the specific leaf area (i.e. the amount of leaf surface per unit leaf weight) is greatly influenced by environment conditions. The influence of water and soil nutrients can be neglected in the present treatment, since the main purpose of the ELCROS programme is to stimulate the growth of the crop under optimal conditions of water and nutrient supply. The supply of carbohydrates to the growing leaves, however, has a large influence on their morphology. For instance, if it takes thirty days for seedling emergence to flowering and fifteen leaves are formed within this period, there is only a two days supply of carbohydrates available for each leaf. At a plant density of 100,000 plants ha^{-1} and a carbohydrate production of 200 kg ha^{-1} day^{-1}, this amounts to an average 4 g of carbohydrates per leaf. If, however, the plant density is doubled the carbohydrate supply per leaf is reduced to 2 g, and if the plant density is halved the supply is increased to 8 g. A leaf of 8 g is not only longer and wider, but also thicker than a leaf of 2 g, an effect which is catered for in the ELCROS programme by including the specific leaf weight (WARL) which varies from 500 kg ha^{-1} (5 mg cm^{-2}) for an average growth rate of 1 g per leaf per day or lower, to 1000 kg ha^{-1} (10 mg cm^{-2}) for an average growth rate of 4 g per leaf per day or higher. Maize plants, for instance, usually possess comparatively thin leaves when they are young or densely planted, or grown at low light intensities in growth rooms, and comparatively thick leaves when widely spaced in the field.

At any particular moment, therefore, the growth of the leaf area (GLA) may be calculated as

$$GLA = WARL \times GLW$$

which in turn is integrated in a 'box-car-train' to give the area of the leaves (ALVB),

$$ALVB = TRAIN (31,GLA,DVS,0.04)$$

Although the main factors which influence specific leaf weight can be qualitatively introduced in this way, the whole question of leaf morphology provides a good example of an area where the critical physiological basis for the simulation programme is still lacking.

Respiration

(i) Physiological Aspects
It is often assumed that the respiration rate of a crop at any particular temperature is proportional to the amount of leaf tissue. This assumption leads to the well-known graph (Figure 8.8(a)) which indicates the optimum area of the leaves (ALV) at which net photosynthesis is at its maximum, and the ceiling leaf area, at which photosynthesis is fully counterbalanced by respiration. The use of this assumption in the simulation programme leads to inconsistent results. If respiration per unit plant material is assumed to be

low, then the programme predicts yield levels similar to those observed in the field, but also predicts respiration rates under controlled conditions which are far smaller than those obtained by experiment. If it is assumed that respiration per unit plant material is higher, the predicted respiration rates under controlled conditions agree with the observed values, but the predicted ceiling yields in the field are far too small.
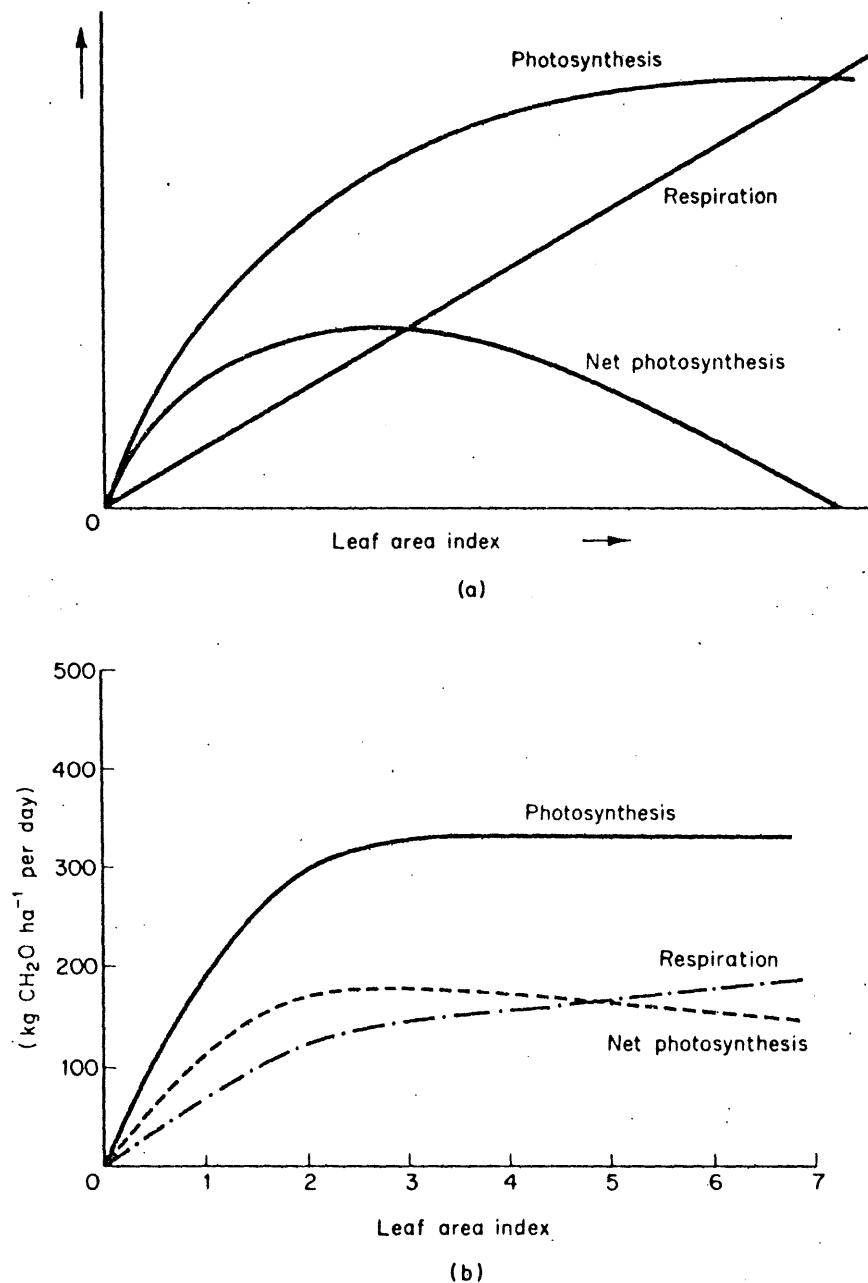

(a)

Leaf area index

(b)

Fig. 8.8   (a) The classical concepts of optimum and ceiling leaf area index on the assumption that respiration is proportional to total dry matter.

(b) Photosynthesis, respiration, and net photosynthesis in relation to leaf area index, as measured in Trifolium repens at 20°C; from McCree and Troughton [15].

Recently, McCree and Troughton [15] have shown conclusively that respiration rates of crops are not proportional to the weight of the vegetative material (or to the area of the leaves), but are in fact related to the photosynthesis rate of the crop surface (Figure 8.8(b)). The incorporation of this information into explanatory models of crop growth requires more detailed physiological and biochemical knowledge of the relevant growth processes.

There is abundant evidence that in plants respiration is regulated to meet changing metabolic demands through an intimate coupling of respiration to phosporylation [1]. Many processes in the cell, like synthesis, growth and solute transfer, need energy which is obtained from the conversion of adenosine triphosphate (ATP) to adenosine diphosphate (ADP) and inorganic phosphate (IP). The APD and IP are required for glycolysis, and this process would be brought to a standstill if all available ADP were converted into ATP, as indicated by experiments with uncoupling agents such as dinitrophenol. These substances destroy the coupling between oxidation and phosphoryla- tion of ADP, but ATP breakdown is unaffected and the result is an increased supply of ADP.

In actively growing tissue, the drain of respiratory intermediates and the consumption of ATP is high, so that the respiration rate in these tissues is likely to be greater than in older tissue in which ATP turnover is lower, whereas the stimulation by DNP is likely to be smaller in the younger tissues. In fact, in carrot slices the actual respiration decreased from 100 per cent of the uncoupled rate in young material to about 30 per cent in older, whereas the rate of respiration in the uncoupled state (+ DNP) remained the same [1]. This suggests that the amount of enzymatic material did not change with age, and that respiration was in fact geared to the needs of the plant.

In a recent paper Beevers [2] has distinguished between (i) growth respiration, associated with synthetic events, (ii) maintenance respiration, associated with protein turn-over in older cells and with repair and maintenance of inherently unstable cell-structures and (iii) idling respiration, concerned with hydrolyses of ATP in which there is no useful outcome to the plant.

In the ELCROS programme, the coefficient of growth respiration is expressed as the weight lost during the synthesis of one unit of weight of structural material, and may be estimated in various ways.

Firstly, at 25 °C the relative growth rate of young tissue, well supplied with essential materials for growth, may account to about 0.5 day^{-1}, whereas the relative respiration rate of such tissue is about 0.25 day^{-1}. In the absence of maintenance and idling respiration this would indicate a growth respiration coefficient of about 0.5, a value within the range reported for animal growth [11, 17].

Alternatively, the efficiency of synthesis of structural materials, on a weight basis can be calculated from the biochemical pathways of synthesis. Assuming that all the products of photosynthesis are channelled through

glucose and that N is supplied as NO_3, it can be calculated that the formation of 1 g each of proteins, fats, polymers of sugars and the uptake of 1 g of minerals requires about 2.35, 2.94, 1.15 and 0.1 g of glucose, respectively. Hence, for the formation of 1 g of tissue, consisting of 25 per cent protein, 6 per cent fat, 59 per cent polymers of sugars and 10 per cent of minerals, about 1.45 g of glucose is necessary. From these calculations, it follows that the weight of the CO_2 produced is about 0.5 times the weight of plant tissue formed, which agrees with the value of 0.33 reported by McCree [14], for the ratio between respiration and net photosynthesis. Since there is no indication that biochemical pathways depend on temperature, it is assumed that the growth respiration coefficient is independent of temperature, an assumption which seems to be confirmed in recent experiments with maize seedlings.
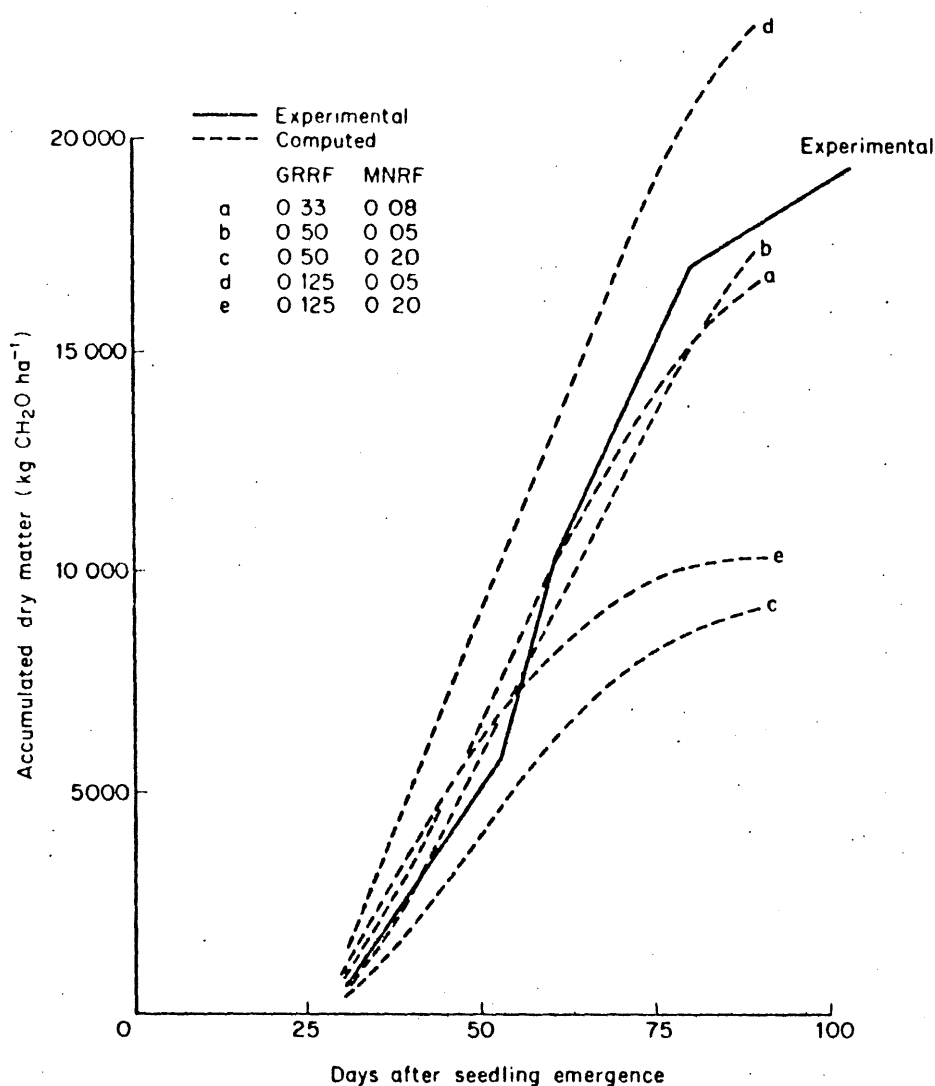

Fig. 8.9   Actual and simulated growth of maize in Ames (Iowa) in 1963; experimental data from Shibles [20]; respiration factors from McCree [14].

At present, it is difficuly to separate maintenance and idling respiration, but it can be tentatively assumed that both are proportional to the amount of enzymatic material. According to Price [18], this uncoupled respiration rate, in the presence of optimal substrate, oxygen and uncouplers, amounts to 200-300 $\mu 1O_2$ h^{-1} mg^{-1} protein-N at 25 °C. The value corresponds to a relative uncoupled respiration rate of 0.28 kg CH_2O (kg dry matter)$^{-1}$ day^{-1} for tissue with 4 per cent protein-N. From the values given by Price [18] a Q_{10} of 2.2 can be assumed for the uncoupled respiration rate over a wide temperature range.

Earlier observations [10, 13, 19] have suggested that the respiration rate of mature leaves, expressed as a fraction of the uncoupled respiration rate, is about 0.25, but the data of McCree [14] suggest a value of about 0.08.

Clearly the maintenance respiration coefficient is still not well defined, but an idea of its acceptable order of magnitude can be obtained from the comparison of actual growth curves for maize with simulated curves based on a range of growth and maintenance respiration coefficients (Figure 8.9). The use of a maintenance respiration coefficient of 0.25 in the programme predicts ceiling yields which are less than half the values actually observed, but the lower coefficients for the growth and maintenance respiration (GRRF and MNRF) calculated by McCree [14] result in predicted yields of the right order of magnitude.

(ii) Programming Aspects

The programming of the respiration rate of a crop is now straightforward. The respiration rate associated with the growth of the various organs (RSPAWG) is taken as:

$$RSPAWG = GRRF \times (GLW + GRW + GST)$$

in which the growth respiration factor (GRRF) is taken as 0.33 and GLW, GRW and GST are the growth rates of leaf weight, root weight and stem weight, respectively. (The simulated results of Figure 8.10, 8.11, 8.12 and 8.13 were obtained using earlier estimates of 0.2 and 0.125 for GRRF and MNRF respectively).

Assuming that the relation between temperature and the uncoupled relative respiration rate of an organ with 1 per cent organic N is given by

FUNCTION URRTB = (-50.,0.0061), (0.,0.0093), (5.,0.014), . . .
                         (10.,0.021), (15.,0.031), (20.,0.047), (25.,0.070), . . .
                         (30.,0.104), (35.,0.15.,), (50.,0.14)

where the first value between brackets is the temperature, then the uncoupled relative respiration in the air (URRA) and in the soil (URRS) is obtained from

$$URRA = AFGEN (URRTB, TA)$$

$$URRS = ARGEN (URRTA, TS)$$

where TA and TS are the air and soil temperature respectively.

From observation it is assumed that in a well-fertilized maize plant, the nitrogen content of the leaves (NLV), of the roots (NRT) and of the stem (NST) decrease for successive 'box-cars' of their train according to

NLV (1-31) = 10 x 4 . . . , 5 x 3.9, 3 x 3.8, 2 x 3.7, 3.6, . . .
              3.5, 3.4, 3.3, 3.2, 3.1, 2.9, 2.8, 2.7, 2.6

NST (1-31) = as for leaves
NRT (1-31) = 1% lower than for leaves.

Thus, the uncoupled respiration rate of the whole crop is

URRC = URRA(SUM2(31,WLVB,NLV) + SUM2(31,WSTB,NST)) . . .
          + URRS (SUM2(31,WRTB,NRT))

The respiration associated with maintenance is then ·

RSPAWM = MNRF x URRC

in which the maintenance respiration factor (MNRF) is taken as 0.08.

Comparison of Simulated and Observed Results

An example of the operation of the present simulator programme (ELCROS) some simulated results will be discussed and compared with actual experiment observations.

As mentioned earlier, ELCROS operates using a time step of one hour, i.e. every hour all rates of changes are re-calculated and integrated. Hence in the course of one day, all calculations are performed twenty-four times.

The simulated results for the growth of maize for a period of twenty-four hours, during its nineteenth day after emergence are presented in Figure 8.10. At midnight, the reserve percentage is decreasing, accompanied by decreased growth rates. At the onset of light, the reserve percentage increases again, followed by increased growth rates first of the leaves, then of the roots. At the beginning of the dark period, there is a rather sudden increase in the growth of the leaves; this is a result of the decrease in transpiration, accompanied by an increase of turgidity. The growth rate soon drops again due to the decrease of the reserve level.

The respiration is coupled to the growth rate and therefore lags behind the photosynthesis rate. The small increase in photosynthesis and transpiration during the day reflects the increase in leaf surface, the leaf area index being slightly greater than 1. The relative growth rates of the shoot and root during the day are 0.16 and $0.10 \, g \, g^{-1} \, day^{-1}$ respectively. The shoot-root ratio is also increasing somewhat because of increased mutual shading. These relative growth rates are comparable with the actual values observed in maize under the same conditions (Figure 8.4), indicating that net

photosynthesis, rather than the capacity to grow, governs the rate of growth. Figure 8.11, which compares actual and simulated data for the growth of maize, shows that the present programme simulates the influence of temperature on the rate of growth and development resonably well, although the rate of development of the plants used in this particular experiment deviated from that introduced into the programme earlier.
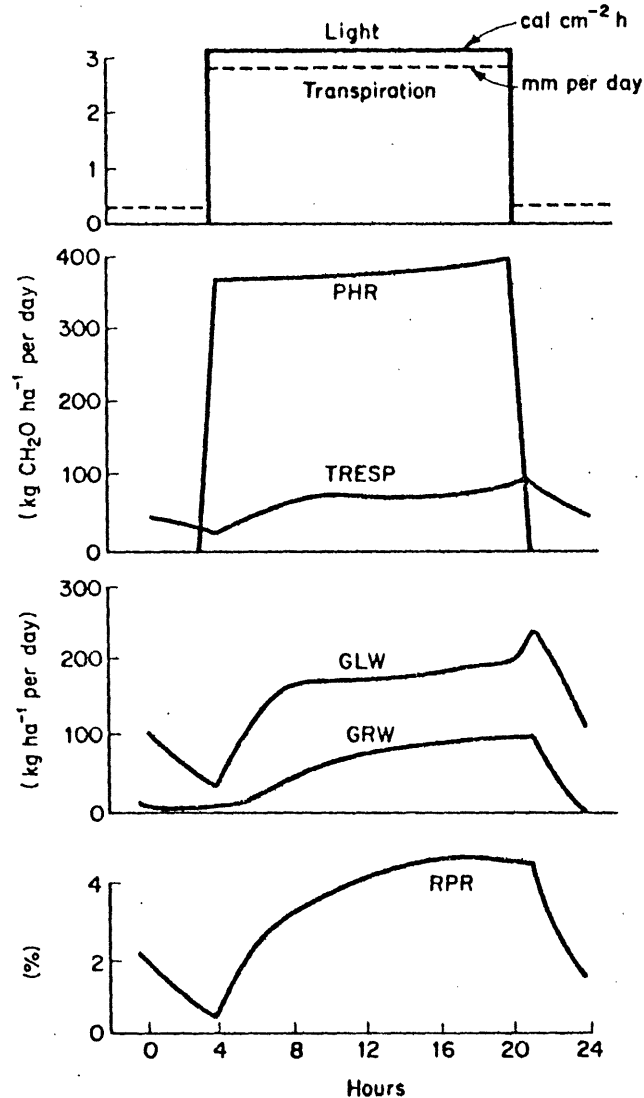

Fig. 8.10   The simulated photosynthesis (PHR), respiration (TRESP), transpiration (TRANSP), growth of leaves (GLW) and of roots (GRW), and reserve percentage (RPR) of maize under controlled conditions during a 24 hour period. (29 January, 1969; air temperature $20\,^{\circ}C$, soil temperature $20\,^{\circ}C$, relative humidity 65%, daily photosynthesis 272 kg ha^{-1}, daily respiration 55 kg ha^{-1}, total weight 1146 kg ha^{-1}, leaf area 1.3 ha ha^{-1}.)
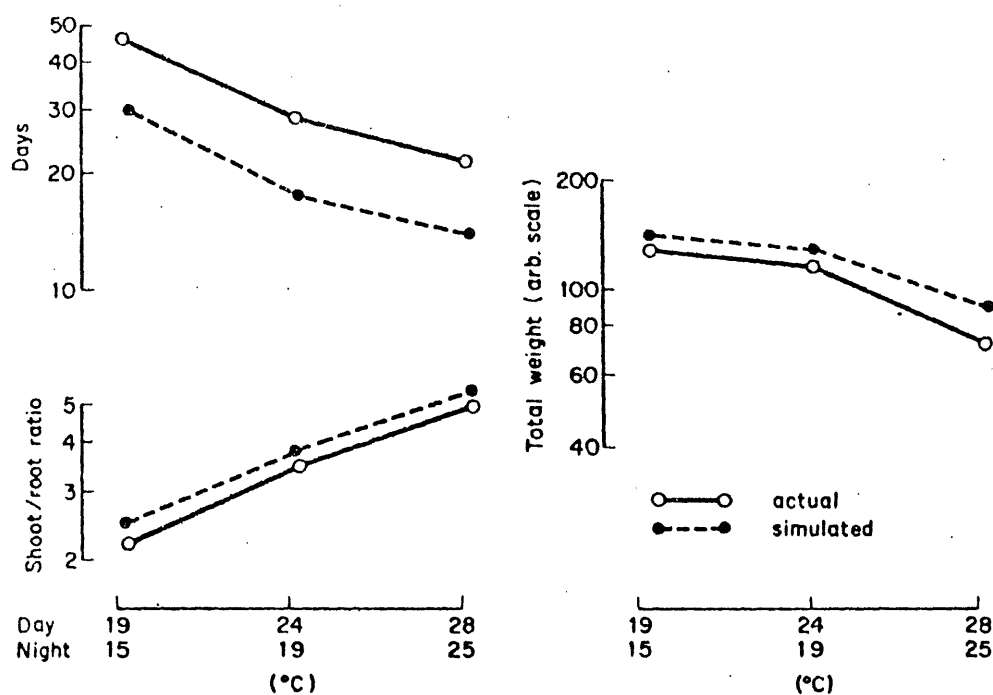
Fig. 8.11   Simulated and actual growth of maize up to the 11th leaf stage
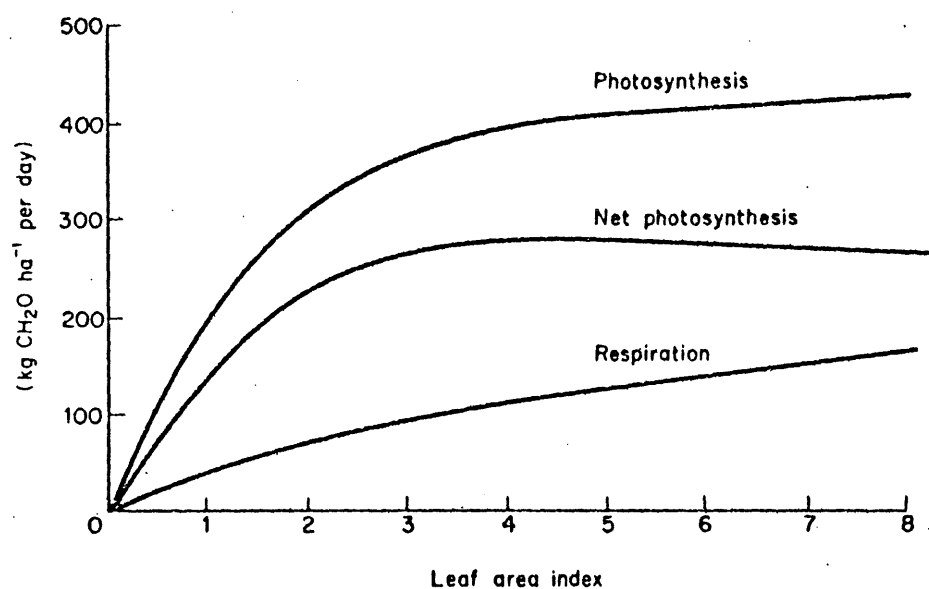(DVS = 0.6).

Fig. 8.12   Simulated photosynthesis, respiration, and net photosynthesis in
maize in relation to leaf area index, at a temperature of 20 °C.

The simulated relation between the leaf area index and the daily
photosynthesis, respiration, and net photosynthesis under controlled con-
ditions is presented in Figure 8.12. These results are very similar to those
obtained from actual experiments (Figure 8.8). This similarity is a result of

the assumption that respiration is partly coupled to the growth rate, but a similar agreement is obtained when it is assumed that respiration depends on the reserve level, rather than being directly coupled to growth. These two possibilities may, perhaps, be distinguished by studying the behaviour of plants during short periods of water stress, which are accompanied by decreased growth rates and increased reserve levels.

Such a similarity between simulated and observed values could never be obtained from the assumption that respiration is mainly controlled by the amount of plant material present.
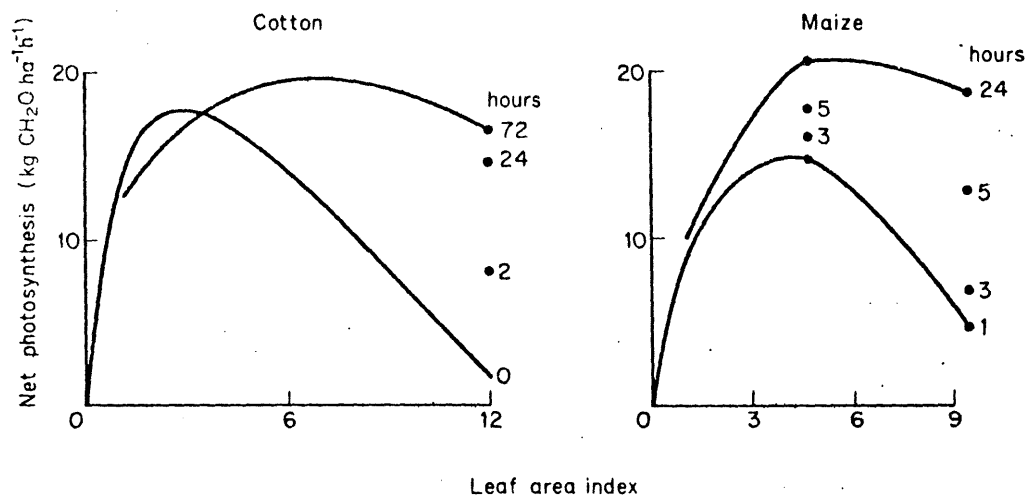

Fig. 8.13   The net photosynthesis of cotton (actual experiment) from Ludwig, Saeki, and Evans [13], and maize (simulated experiment) at various times after increasing the leaf area index by placing single grown plants close together.

Figure 8.13 compares the results of an actual and simulated experiment in which plants grown at a wide spacing were suddenly transferred to high densities with a leaf area index of about 10. The actual experiment using cotton revelas that the net photosynthesis at high densities falls to zero directly after transfer, but that within twenty-four hours the situation is modified, so that net photosynthesis no longer depends on the leaf area index within the dense range. This is because of a decrease in respiration during the twenty-four hour period. The simulated experiment using maize reveals the same behaviour. Further analyses of the simulated data showed that mutual shading due to crowding reduced the photosynthesis per unit leaf area, resulting in a decreased reserve percentage, which was in its turn accompanied by a decreasing growth rate and a decreasing respiration rate. Because the speed of adjustment in the actual and simulated experiment is about the same, it seems likely that a similar mechanism is operating in the actual and in the simulated plants.
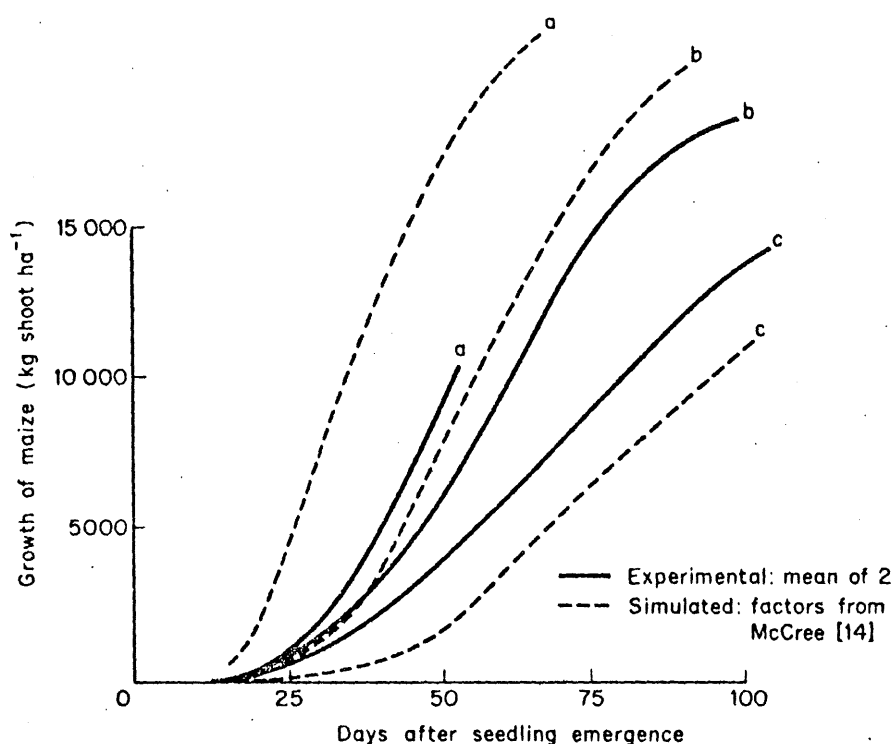
Fig. 8.14   Actual and simulated growth of maize under field conditions, (a)
            in California, (b) in Iowa, and (c) in the Netherlands; from
            Williams, Loomis, and Lepley [22], Shibles [20] and unpub-
            lished.

The actual and simulated growth rates of maize in California, Iowa and
the Netherlands are presented in Figure 8.14 The simulated curves were
obtained by using the latitude, seedling emergence data and weather data for
the locations and years concerned. None of the other parameters were
adjusted to obtain better agreement. Closed crop surfaces are reached at
yields of 1500 kg ha^{-1} and the slope of the curves thereafter is termed the
crop growth rate. At each of the three locations, the actual and simulated
crop growth rate is roughly the same, although the differences between
locations are considerable. This shows that the present version of ELCROS
gives reasonable predictions for this particular characteristic.

The simulated crop in California is much earlier in reaching its grand
period of growth than the actual crop, whereas the reverse is the case in the
Netherlands. However, the average temperature in California during the early
stages of growth was around 25 °C and in the Netherlands about 10° lower.
The effect of these large temperature differences on the relative growth rate
and the photosynthesis rate may well account for the differences between
simulated and actual performance in California and the Netherlands. It is not
clear, however, why, in the actual experiments, the periods from seedling
emergence until the closed canopy of 1500 kg ha^{-1} was reached are so similar
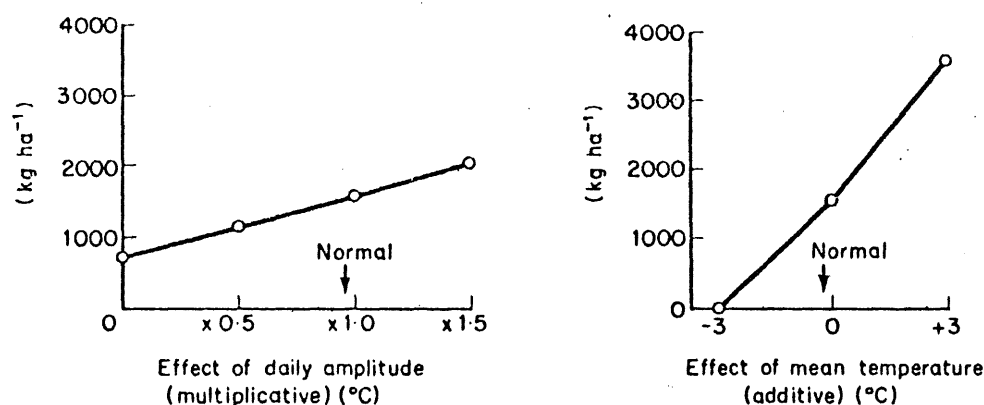in both locations.

Fig. 8.15   *Simulated influence of the daily amplitude and the mean of air
and soil temperature on the total weight of maize in 1938 in the
Netherlands (at the date when a weight of 1500 kg ha^{-1} is reached
under normal conditions).*

Since relatively small temperature changes within the range of 15° to
25 °C can have large effects on the growth of maize, it may well be that the
large discrepancy in early growth between actual and simulated experiments
are due to systematic differences between the actual micro-climate and the
simulated micro-climate. The influence of changes in the daily amplitude and
in the average daily temperature on the early growth of maize was therefore
simulated for Dutch conditions (Figure 8.15). It appears that a difference in
average temperature of only 1 °C could account for the difference obtained
between the actual and simulated growth curves. Relatively large errors in
temperature amplitude, on the other hand, do not appear to have much
effect. Apart from this influence of temperature, it may be questioned
whether, under dry conditions, as in California, the water supply during the
early stages of growth has always been sufficient.

Hence, the accurate simulation of the early growth of maize depends to a
large extent on the accurate prediction of the average temperature and
moisture status at the surface of the soil.

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