

## 28. Crop simulation and experimental evaluation – a case study

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Once the significance of photosynthesis was understood, a large number of scientists tried to make an estimate of the total amount of dry matter that is produced yearly on our planet. The first to carry out such a calculation was Liebig (1840), who supposed that all the land surface of the earth consisted of one closed green grass surface, producing 5 tons of dry matter per ha each year. On this basis he calculated a total production of  $3 \times 10^{10}$  tons of organic carbon per year. His attempts were later followed by others, who usually found lower amounts, for instance Schroeder (1919*a,b*) who separated the land area into woods, farmlands, steppes and deserts and who arrived at a total amount of  $1.63 \times 10^{10}$  tons of organic carbon per year.

These calculations, however, are not directly related to the process of photosynthesis but are based on practical experience of primary production in different climatic areas around the world.

A different approach is to relate the production of a crop or of vegetation or the total global production to the amount of incoming light energy and to calculate the efficiency with which this energy is used to produce organic material. The low efficiency values found as compared to the photosynthetic efficiency of a single leaf led to speculations as to the possible causes of these differences, the main causes being the wastage of light during the phase when the vegetation is not closed, and the often suboptimal supply of minerals and/or water (Gaastra, 1958).

The next step was then to calculate the potential production rate, i.e. the growth rate of a crop or vegetation in which all the incoming light is intercepted by healthy green plant material and in which water and minerals are supplied in optimal amounts. In 1959 de Wit proposed a model to calculate the photosynthesis rate of a leaf canopy from the photosynthesis–light response curve and the optical properties of individual leaves, the crop architecture and the measured global radiation. Later (de Wit, 1965), this model was refined and the calculations were performed on a computer. This was, however, still a stationary

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model, which did not account for the dynamic behaviour of photosynthesis as a result of changes in weather and crop properties. With the development of high-speed computers and high-level simulation languages, which made it easy to handle dynamic systems, the attention shifted towards non-stationary models, like ELCROS (de Wit, Brouwer & Penning de Vries, 1969). As the knowledge of basic processes increased, this model was further expanded and is at present in a stage, where under a range of circumstances, good agreement is obtained between predicted and observed productivity.

The crux of this approach is that the simulation program contains as much basic data as possible on the photosynthetic capacity of individual leaves, respiration values, leaf position, dry matter distribution patterns between different organs and the factors governing these patterns, as well as the meteorological data. To make these programs not too complicated and to make a check on these programs possible, they are up to now best restricted to a closed crop of a single plant species, in its vegetative state, and supplied optimally with water and minerals. The production actually obtained under these conditions can then serve as an independent control. Once a simulation program works reasonably well it can be used for other purposes. The effect of different plant characteristics, which are thought to influence production, can be studied by varying them one by one and then calculating their effect on dry matter production. Such factors include the light response curve of individual leaves, leaf position, or the dry matter distribution between different plant organs. Furthermore the program can gradually be extended to fit situations in which the water supply or any other environmental factor is limiting production. For instance, after checking against the appropriate field experiments at one place, the program can be used to predict productivity in other arid zones.

Instead of calculating and measuring dry matter production, it is also possible to construct the model in such a way that it calculates the rate of photosynthesis of a crop or a vegetation and then to compare this value with actual photosynthesis measurements under comparable conditions. As photosynthesis measurements can be carried out without destruction of the crop these programs can be used more easily than with measurements of dry matter production to study the effects of variations, in such climatic factors as light intensity, temperature and water availability, or in other features such as crop structure and mineral deficiency.

In this chapter a survey will be given of comparisons of actual and

calculated production of a grass sward grown with optimal supply of water and minerals, and of the measured and calculated photosynthesis rate of such a sward. This survey will illustrate how the experimental results can influence the model, and how the calculations with the model may lead to new investigations into the background of crop production. A short description will also be given of the simulation program and of the apparatus used to measure photosynthesis in the field.

## **Simulation of crop growth**

### *Introduction*

Simulation may be defined as the building of models and the study of their behaviour. A model is a schematic representation of a limited part of reality. The building of a model requires the integration of detailed knowledge into the whole of a working system. Reality is always simplified in a model, partly because our understanding of basic processes is limited, partly because this enables us to handle the model. Hence a model is the reflection of our opinion about how the system works. It also means that the purpose of the simulation is limited. This purpose determines the boundaries of the chosen system, and thus which processes should be part of the model and which processes may be introduced as forcing functions. This determines at the same time which outputs can be used for validation of the model.

Detailed information on physical, physiological and chemical properties of plants can be collected under controlled conditions and then used to simulate the field situation. When such information is not available reasonable estimates may be used. The relative importance of such estimated parameters can be tested by 'sensitivity analysis', i.e. running the program with different values (or relations) and comparing the output.

Another possibility is to describe the relevant physiological processes on basis of biochemical knowledge and to incorporate this into the model. This introduces, however, a large amount of detail. Moreover the relaxation time – that is the time to recover from small changes – of the extreme processes in the model may differ by a factor of 10000. In that case it may be only possible to execute the model in time increments of 1/10000 or less of the total time span. Computer time and budget will then become the limiting factors. It is virtually impossible to build multi-level models in which the relaxation times of the extremes may differ up to a factor of  $10^7$ .

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In the crop production model, an hierarchical approach is used, that is, more basic processes are incorporated via the outcome of separate models. Such models, for example, those for respiration (Penning de Vries, Chapter 20) and for microclimate (Goudriaan & Waggoner, 1972) comprise only part of the system and describe the relevant processes in more detail.

To check on the validity of our opinion, a model should be tested properly. This means on the one hand, that the same data are not used in both the construction and the evaluation of the model. On the other hand agreement should not be reached by adjusting the parameters and functions. That would lead to a most dangerous method of curve-fitting. The proper procedure, in cases where discrepancies between simulation and experiment exist, is to examine the relevant processes and to improve their description.

If good agreement exists between simulated and measured values, the model may be used to predict productivity under different environmental conditions, i.e. to extrapolate knowledge to other areas.

Simulation, if combined with experimentation, is a useful tool in testing the validity of our opinion, in pointing out weak areas in our knowledge and so designing new experiments, and in the extrapolation of our knowledge.

### *The crop growth model*

The present model has many inputs, consisting of physical, physiological and chemical plant properties, as well as macrometeorological data from standard weather stations. These data are summarized in Table 28.1. The model calculates the increase in dry weight and the transpiration of a plant or a canopy.

A relational diagram of the model is shown in Fig. 28.1. The rectangles represent quantities, the valves represent rates, while the circles represent intermediate variables.

The growth of the canopy, defined as the increase in dry weight of the structural material, is dependent on the amount of reserves present in the crop, whereby the influence of the temperature and the water status of the crop can be taken into account. A functional balance, governed by the water status (Brouwer & de Wit, 1969), determines the division of the newly formed material between shoot and root.

The amount of reserves, consisting of soluble carbohydrates, is calculated from the rate of photosynthesis of the crop and the respiration

Table 28.1. *Input data for the model*

Meteorological		Physiological		Physical		Chemical	
Variable	Units	Variable	Units	Variable	Units	Variable	
Total global radiation	$\text{J m}^{-2} \text{d}^{-1}$			Leaf area index	-	Composition of material	
Dew point	$^{\circ}\text{C}$			Leaf angle distribution	-		
Maximum temp.	$^{\circ}\text{C}$			Average width of the leaves	m		
Minimum temp.	$^{\circ}\text{C}$			Scattering coefficient of leaves	-		
Wind speed	$\text{m s}^{-1}$						
				Root conductivity ( $\text{kg H}_2\text{O m}^{-2} \text{d}^{-1} (\text{bar m}^{-1})^{-1}$ )			

PAR—photosynthetically active radiation.

RWC—relative water content

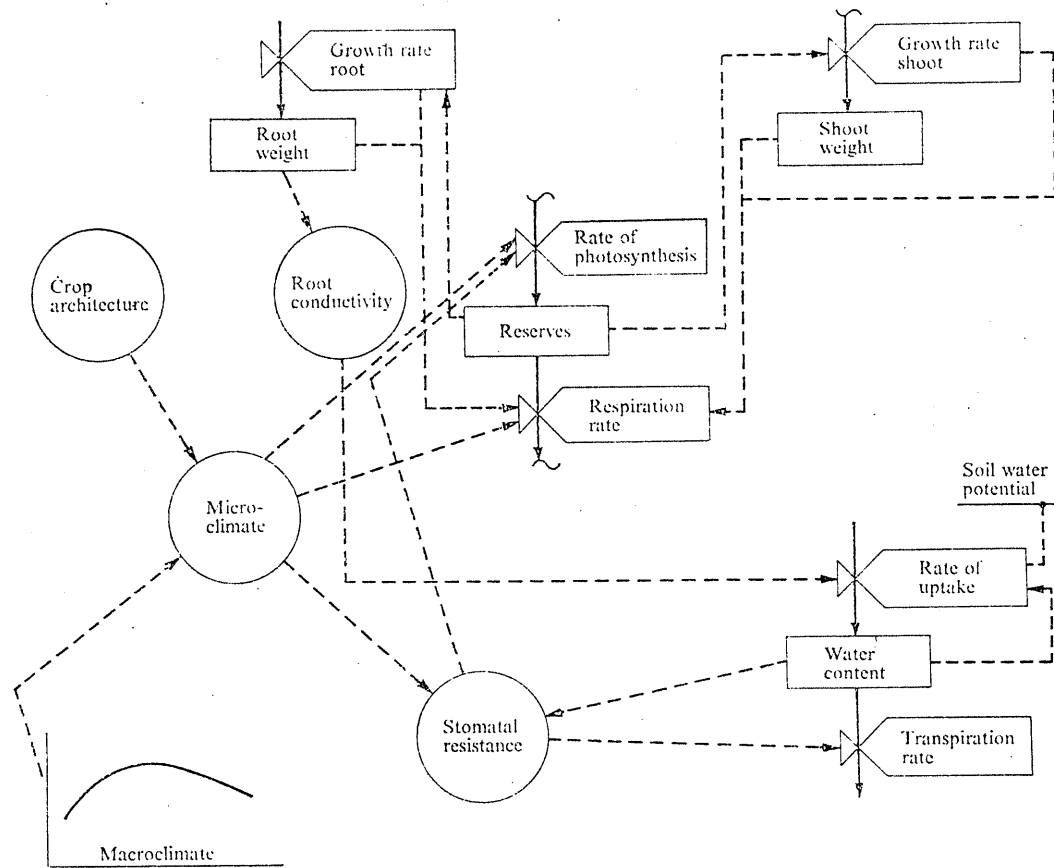


Fig. 28.1. Relational diagram of the simulation model.

rate. The respiration is the total of maintenance respiration, which is a function of the amount of material present, and respiration associated with growth, which depends on both the growth rate and the chemical composition of the structural material that is formed. Allowance is made for the influence of crop temperature on both respiratory processes.

Crop photosynthesis is calculated by adding the photosynthetic rates of a number of leaf layers, each with a certain leaf area, into which the total leaf area of the crop is divided. The photosynthetic rate of each layer is derived from the photosynthesis–light response curve of individual leaves and is dependent on the light intensity, the concentrations of  $\text{CO}_2$  and the resistance for diffusion of  $\text{CO}_2$  from the atmosphere towards the active sites.

The intensity of the visible light in each layer is calculated from the measured global radiation, taking into account reflection and assuming an exponential extinction with depth in the canopy. Allowance is made to distinguish between direct and diffuse light and between sunlit and shadowed leaves. The extinction and reflection coefficients are calculated from the leaf angle distribution of the crop, the scattering coefficients of the leaves, and the direction of the incident light.

The concentration of  $\text{CO}_2$  is assumed to be constant throughout the canopy. The resistance for diffusion of  $\text{CO}_2$  includes (i) a turbulent resistance above the canopy, dependent on the windspeed and the stability of the atmosphere; (ii) a resistance of the laminar layer around the leaves, which is a function of wind velocity and of the size of the leaves; (iii) a stomatal resistance and (iv) an internal resistance (mesophyll resistance). The stomatal resistance is governed by either the incident light intensity or the water status of the crop. (At present the working hypothesis is adopted that the stomatal resistance depends on the concentration of  $\text{CO}_2$  in the stomatal cavity rather than on incident light intensity.) The internal resistance is a function of the leaf age and the temperature, and allowance can therefore be made for adaptation of the plant to different temperature regimes.

The water status of the plants is assumed to be constant throughout the canopy and is determined by the balance between transpiration and the water uptake from the soil. Transpiration is found by adding the transpiration rates of the various leaf layers. These rates are calculated from the absorbed radiation in each layer, the stomatal resistance, the resistance of the laminar layer, the turbulent resistance above the canopy and the humidity of the ambient air. The latter is again assumed

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to be constant throughout the canopy. This calculation also computes the temperature in the leaf layer from the heat balance. These temperatures are used in the photosynthesis calculation and can also be averaged to give the average crop temperature that influences growth and respiration.

Water uptake from the soil is determined by the conductivity of the root system and the difference in water potential between plant and soil,

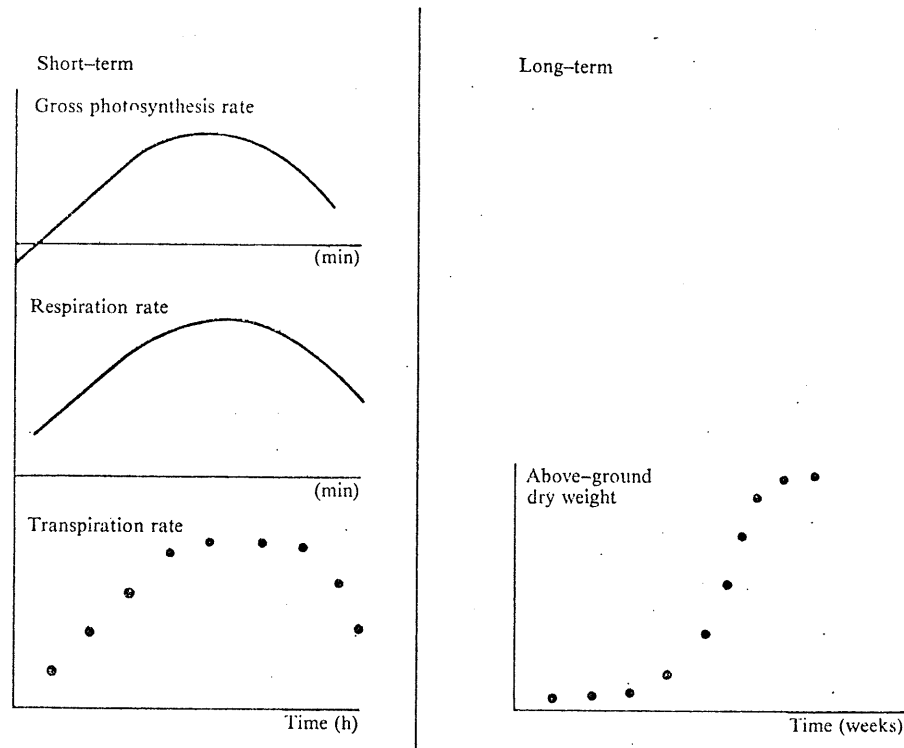


Fig. 28.2. The outputs of the short-term and the long-term simulation model, together with their time scale.

assuming the latter to be optimal (i.e. 0.1 bar). The conductivity is derived from the weight of the roots, assuming a ratio between weight and conductivity, that is dependent on soil temperature and on the degree of suberization of the roots. The growth of the roots is governed by the crop water status and the amount of available reserves. The temperature of the root zone is assumed to be constant with depth and follows the air temperature with a delay of four hours, taking into account a decrease in amplitude.



Some of the processes mentioned have a very short relaxation time and their dynamic behaviour can only be tested in short-term experiments, while other processes need long-term experiments for checking.

Two types of experiments are used to validate the model: short-term experiments with crop enclosures in which the measured and calculated rates of CO<sub>2</sub> exchange (or rates of photosynthesis and respiration) and the transpiration rates are compared, and long-term experiments with periodic harvest where a comparison is made between the measured and calculated above ground rate of biomass production. The outputs used for validation and their time scale are shown in Fig. 28.2.

### **Determination of crop growth and photosynthesis**

As has been explained in the preceding paragraph, it is necessary to test the model either by the measurement of photosynthetic performance of a plant or a crop in short-term experiments, or by the determination of dry matter increase over longer periods. The latter method has already been used in testing an earlier simulation model, devised by de Wit (1959) by measuring the rate of dry herbage production of a closed sward of perennial rye-grass (Alberda & Sibma, 1968). From this comparison it appeared that, apart from periods in early spring and late autumn when the temperature was too low, there was a good agreement between the actual and simulated growth rate of a young sward during the greater part of the growth period under the assumption that the herbage production amounts to 60% of the total dry matter production. There were, however, two situations in which there was a discrepancy between the two values. Firstly, the actual growth rate lagged behind the simulated one from the second half of August onwards, and, secondly, there was a rather sudden decline in the rate of dry herbage production as the sward became older, a decline that cannot be explained by a relative increase in the rate of respiration (Alberda & Sibma, 1968).

In trying to get some more information about the latter discrepancy, an experiment was designed in which the following items were measured at four-weekly intervals throughout the season: (i) the rate of dry herbage production of a grass sward of an age of three to four weeks, seven to eight weeks and eleven to twelve weeks; (ii) the rate of photosynthesis of the same swards measured by putting a 2 m<sup>2</sup> enclosure over them; (iii) the rate of photosynthesis of just fully expanded leaves of these swards at different light intensities. A short description of each

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technique will be given here, with references to more detailed information.

The field experiment was carried out on a permanent pasture, consisting mainly of perennial rye-grass (*Lolium perenne*) mixed with some timothy (*Phleum pratense*). In the absence of nitrogen fertilizer there was hardly any growth. A rapid growth of a particular experimental strip could be started by nitrogen application. By choosing the appropriate times, it could be arranged that at four-weekly intervals there was one week for measurements in which closed swards were available which were three, seven and eleven weeks old, respectively at the beginning of the week. The growth rate of the herbage was measured by cutting an area of 8 m<sup>2</sup> at the beginning and the end of the measuring week and calculating the difference in dry weight. A more detailed description of the technique is given elsewhere (Alberda, 1962).

The rate of photosynthesis was determined by placing a 2 m<sup>2</sup> iron frame in the sward before fertilizer application and by putting a transparent enclosure over this frame during the measurement week. The rate of net photosynthesis was measured with a mobile installation, similar to that described by Stiles & Leafe (1969). Details of our method are given elsewhere (Louwerse & Eikhoudt, 1975). Usually a measurement on a particular sward took one or two 24-hour periods. On each measuring day two swards of different age were always compared by measuring them simultaneously.

The light response curve of individual leaves was measured in a laboratory set-up, described by Louwerse & van Oorschot (1969). To bring the leaves into the laboratory blocks of an area of 20 cm × 20 cm and 40 cm deep were dug out of the sward. These blocks were placed in a plastic bucket of the same shape, well watered and placed beside the leaf chamber. A sufficient number of just fully expanded leaves was placed between thin nylon wires in the leaf chamber and exposed to a series of light intensities.

### **Experimental results**

#### *The rate of herbage growth*

The results of the growth rate measurements are presented in Fig. 28.3 in which the dry herbage weights are plotted against time. As was found earlier (Alberda, 1962), the growth curves are somewhat irregular and, therefore, growth rates calculated from weight differences between the successive cuts show usually rather large variations. These calculated

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growth rates during the measuring week are given in Table 28.2, columns 6, 11 and 15.

*The rate of photosynthesis*

An example of the measurement of the rate of canopy photosynthesis during a period of a little over twenty-four hours is presented in Fig. 28.4. In the upper half of the figure the course of temperature and light intensity are plotted against time, and in the lower half the same is done for the rate of photosynthesis of two swards of different age, calculated from the air speed and the difference in ingoing and outgoing carbon dioxide concentration. The sharp depression in light intensity and

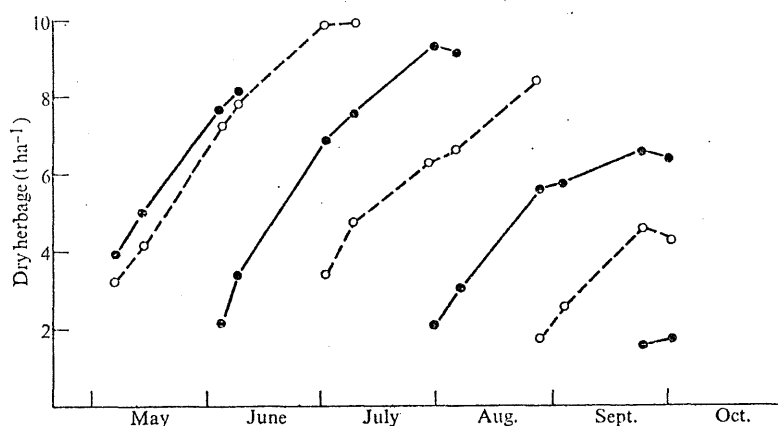


Fig. 28.3. Measured dry herbage weights at different stages of uninterrupted growth of closed swards at successive periods during the growing season.

photosynthesis during the first light period is caused by artificial darkening of the enclosure to measure the rate of respiration during the day. The temperature inside the enclosure was always kept at ambient. The younger and older swards show a very large difference both in net photosynthesis during the day and in respiration during the night. From these curves the net dry matter production during a 24-hour period can be calculated, as shown in the figure, and that of the eleven weeks old sward proves to be only about one-eighth of that of the three weeks old sward. For each measuring week, a few days with a rather regular distribution of light intensity during the day have been selected, and the net dry matter production over a 24-hour period, calculated from this data, is presented in Table 28.2, columns 3, 8 and 12, together

Table 28.2. Comparison of measured photosynthesis, simulated photosynthesis, measured dry herbage production and calculated dry herbage production of different age and at different times during the season

Date	Age 3-4 weeks						Age 7-8 weeks				Age 11-12 weeks			
	Radiation ( $J\text{ cm}^{-2}\text{ d}^{-1}$ )	Measured net photosynthesis in enclosure	Simulated net photosynthesis in enclosure	Calculated net herbage production column $3 \times 0.6$	Measured net herbage production from sward growth	Calculated mean net herbage production of young swards	Measured net photosynthesis in enclosure	Simulated net photosynthesis in enclosure	Calculated net herbage production column $8 \times 0.6$	Measured net herbage production from sward growth	Measured net photosynthesis in enclosure	Simulated net photosynthesis in enclosure	Calculated net herbage production column $12 \times 0.6$	Measured net herbage production from sward growth
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
7 May	1782	262	225	157	133	170	264	218	158	148	-	-	-	-
4 June	2845	359	-	215	312	200	238	181	143	148	-	-	-	-
6 June	2356	325	-	195	312	200	-	-	-	-	144	129	86	117
2 July	2569	-	-	-	-	-	130	-	78	101	41	-	25	6
4 July	2351	321	300	193	190	185	-	-	-	-	39	-	23	6
30 July	971	-	-	-	-	-	111	72	67	37	33	12	20	-21
1 Aug.	1648	238	-	143	136	147	113	-	68	37	-	-	-	-21
28 Aug.	858	123	-	73	106	116	-	-	-	-	25	-	14	n.d.
29 Aug.	1276	184	-	110	106	116	111	-	67	-	-	-	-	-
24 Sept.	849	-	-	-	-	-	74* 88†	49	44	19	-	-	-	-
26 Sept.	611	73	50	43	27	66	-	-	-	-47	11	-	7	-20

\* Rather prostrate leaves.

† Leaves put into a more upright position.

n.d., not determined.

(Units for columns 3, 4, 8, 9, 12, 13:  $\text{kg CH}_2\text{O}$  or  $\text{kg total dry matter ha}^{-1}\text{ d}^{-1}$ , units for columns 5, 6, 7, 10, 11, 14, 15:  $\text{kg dry matter above cutting level ha}^{-1}\text{ d}^{-1}$ ).

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with the total radiation (column 2). The large differences in the rate of net photosynthesis between swards of different age are evident.

From the data as presented in Fig. 28.4 the relation between light intensity and photosynthesis can also be constructed. This is done in Fig. 28.5 for a number of measurements, and again shows the large difference in photosynthetic performance between swards of different age, except at the beginning of the season (5 May). At this date a real difference in age was not yet established because the oldest sward only started to grow at the beginning of April and was therefore only four to five weeks old at the time of measurement, although nitrogen had already been applied much earlier.

#### *The rate of photosynthesis of individual leaves*

The detailed measurements of the rate of photosynthesis of individual leaves are not presented here. In all cases, the light response curves had approximately the same size and shape, whether the leaves were taken early or late in the season or from a young or an old sward. The saturation level was always around  $80 \mu\text{l CO}_2 \text{ cm}^{-2} \text{ h}^{-1}$ , a value much lower than is found for leaves of plants grown on nutrient solution in the climate room. This lack of variation in light response curves of plants taken from the field is also at variance with data obtained on individual leaves *in situ* (Deinum, personal communication). These measurements showed that the saturation level of leaves *in situ* in young swards was similar to that found for leaves of plants grown in climate rooms, and that it dropped progressively with age. Calculations with the simulation program, using the light response curve of individual leaves taken from the field as found by us, gave values much lower than those calculated from photosynthesis measurements in the corresponding enclosure. For this reason, the aim to simulate the daily growth rate from the light response curve of a single leaf taken from the field failed. The alternative possibility was to simulate the daily growth rate of a young sward using the light response curve, as found for leaves of growth room plants on nutrient solution, to compare the outcome with the values calculated from the data obtained for photosynthesis and respiration in the enclosure and, if these agreed well, to vary the plant parameters in the simulation program within reasonable limits and to compare the outcome with the photosynthesis data obtained from the older swards. This should provide information on the factors that are most likely to be responsible for the ageing effect in swards.

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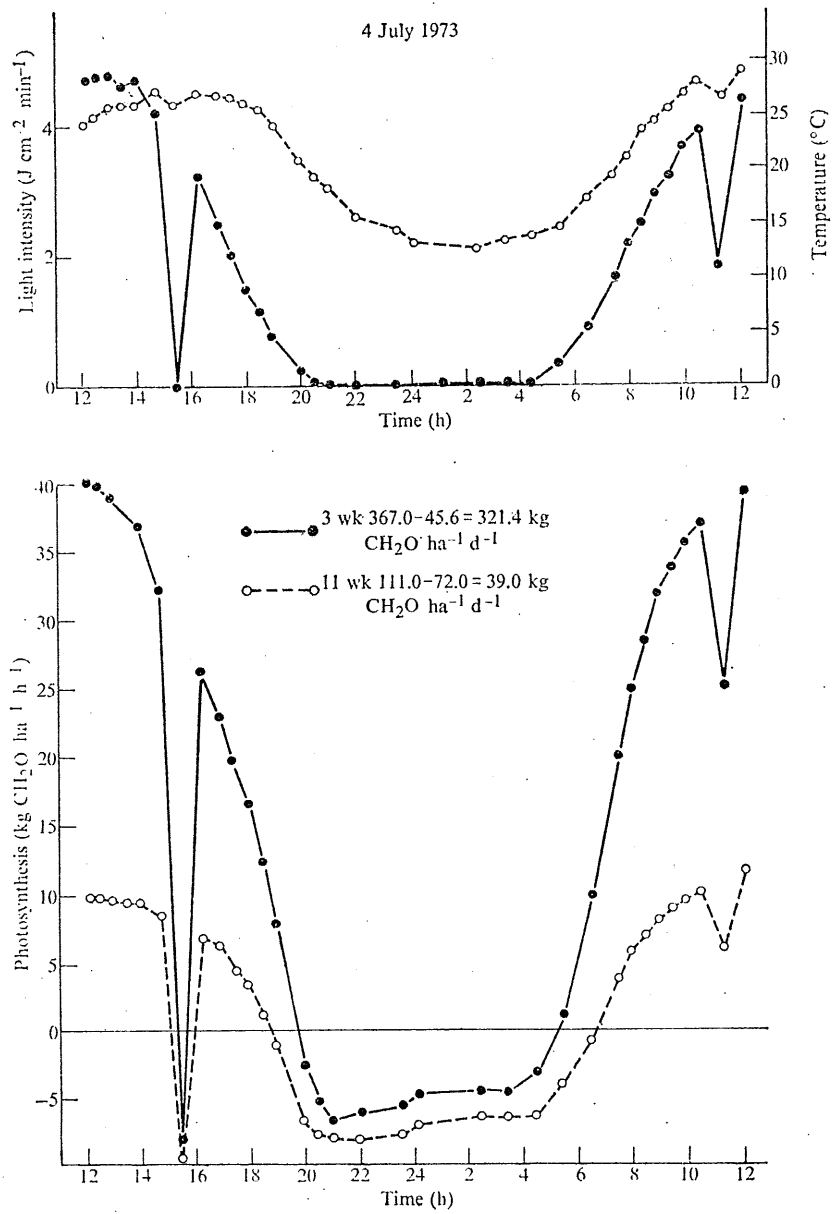


Fig. 28.4. Record of temperature and light intensity over a 24-h period (4 July 1973) together with the measured net photosynthesis values of two swards of different age.

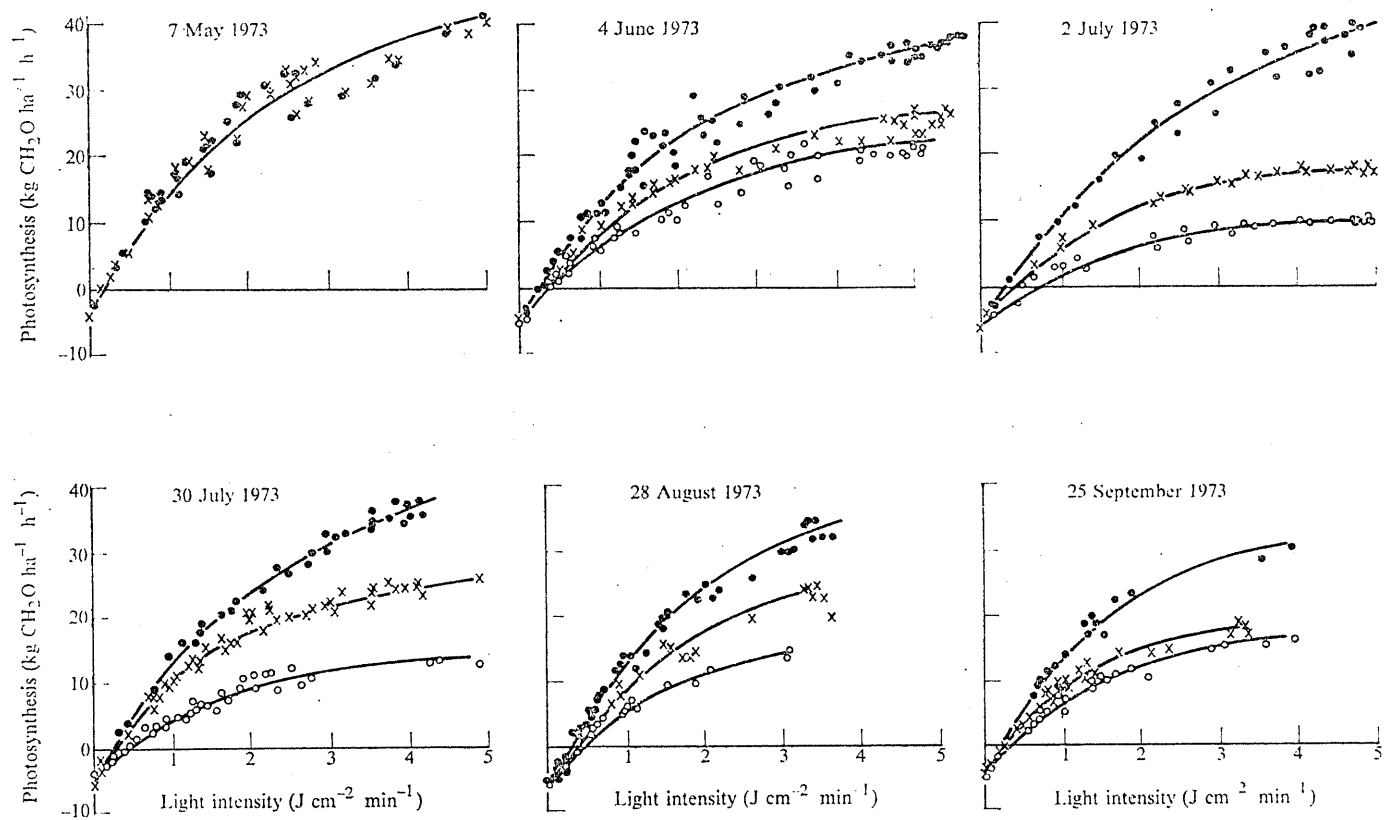


Fig. 28.5. The relation between net photosynthesis and light intensity at different times during the growing season for swards of different age. (●) 3-4 weeks old sward; (×) 7-8 weeks old sward; (○) 11-12 weeks old sward.

### **Comparison of actual and simulated production values**

The relevant data obtained are presented in Table 28.2. The third vertical column represents the net daily total dry matter production on a sunny day at approximately monthly intervals throughout the growth season, as measured in the enclosure with a young sward. The measured total radiation is given in column 2.

The fourth column gives the simulated values for a young sward. As has been pointed out before, the data for the light response curve of the just fully expanded leaves of that sward were too low to be used in the program. Therefore, for a young sward, the light response curve for leaves grown in the climate room was used, and with this reasonable values were obtained. However, if the same light response curve were used to simulate the net daily photosynthesis of swards which are seven or eleven weeks old, the calculated values would be much too high. As the measurements of leaf photosynthesis failed methodologically to show any change with sward age, the simulation program was used to indicate the most plausible cause by varying the factors that change during the experiment one by one, and calculating the effect on net photosynthesis of the sward. Changes in crop architecture from an erectophile canopy, when the sward is young, to a planophile when the sward gets older (Alberda, 1966) create only slight differences in the simulated light response curve of the sward and virtually no difference in cumulative gross photosynthesis (Fig. 28.6). As might be expected, the planophile position was more advantageous than the erectophile position at low light intensities, because of the low altitude of the sun, but at high light intensities, i.e. high altitudes of the sun, the situation was reversed.

A change in maintenance respiration from 50.0 mg CO<sub>2</sub> per g dry matter per day for the young protein-rich sward to 22.5 mg for an old one (Penning de Vries, 1974) also led to a negligible change in net photosynthesis.

However, when the photosynthesis-light response curve of the individual leaves of a sward was determined from the sward photosynthesis curve of a particular day and then used to simulate the net photosynthesis on another day, close agreement with the measured values could be found (Table 28.2, columns 8 and 9, 12 and 13). As all other parameters used in the program are equal throughout the season, it can be concluded from this comparison that a reduction in the photosynthetic performance of the leaves seems to be the only possible cause for the observed reduction in canopy photosynthesis with age.



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Although the leaf position has no effect on the daily photosynthesis of a sward, a sudden change in leaf position during measurement has a distinct influence. Bringing upright leaves into a more flat position by means of a wide-meshed gauze resulted in a reduction in photosynthesis of up to 40%, leaving respiration unaffected. When the rate of photosynthesis is simulated with a sward of the same leaf area index but with all the leaves in a horizontal position and in separate layers, each with a leaf area index of 1, a reduction in photosynthesis of about 40% as compared with normal positions is also obtained. As the photosynthesis of the individual leaves is unaffected by the manipulation, because nearly normal values were obtained when the leaves were returned to their normal position, it can reasonably be assumed that using the gauze a practically horizontal leaf position was achieved.

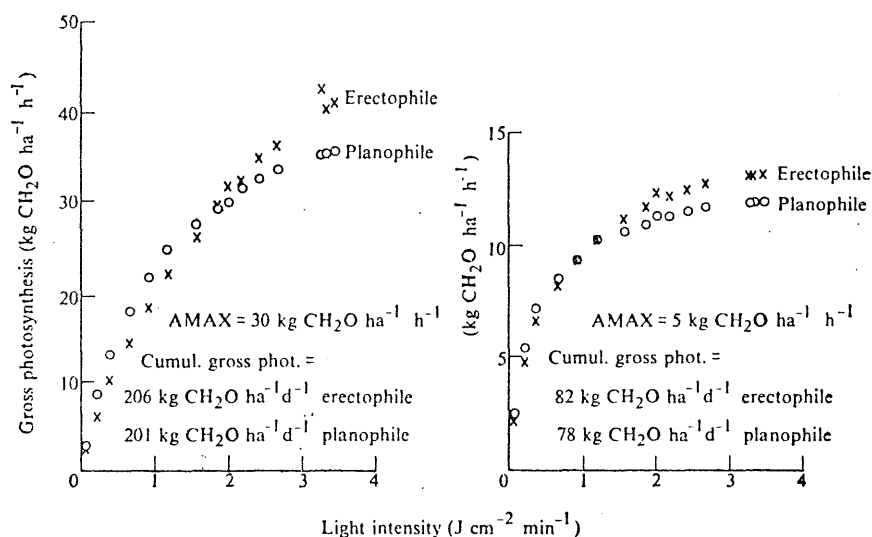


Fig. 28.6. The relation between gross photosynthesis and light intensity, simulated for a sward with planophile and erectophile leaf positions and for different saturation values (AMAX) of the single leaf photosynthesis.

Changing the rather flat leaves of an older sward into a more upright position, also by means of a wide meshed gauze, had no effect. This fits quite well with the results of the simulation program in which a shift in leaf position over the observed range had also no influence on total photosynthesis during the day (Fig. 28.6). If, however, during ageing of a sward the leaves were kept in an upright position, the diminution in photosynthesis was less than with a normal sward, the difference

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being nearly 20% (see Table 28.2, column 8 for 24 Sept.). This suggests that it is the effect of micro-climatological influences on the photosynthetic performance of lower leaves rather than canopy structure that reduces the rate of photosynthesis with age. More insight into the effect of lodging on leaf performance and crop architecture is needed before any definite conclusions can be drawn.

The fifth column in Table 28.2 gives the dry herbage production calculated from column 3 by multiplying it with 0.6, on the assumption that the herbage weight is 60% of the total plant weight, a proportion found in many growth room experiments. This growth rate can then be compared with that calculated from the herbage yield difference between the beginning and the end of the measuring week (column 6), and also with the mean daily growth rate calculated from five-year measurements of growth rates of young rye-grass swards (Alberda & Sibma, 1968) (column 7). The latter figure was taken because the *mean* growth rate values, although not directly comparable to the photosynthesis data because of differences in the amount of light energy received, are less erratic than the actual determinations of the growth rate. There is a particularly good agreement between columns 5 and 7. Using the actual growth measurements, however, the agreement is less, especially in the beginning of June when a very high actual growth rate was found, due to some irregularities in the experimental plot (see also Fig. 28.3).

For the older swards, no mean growth rate data are available; a comparison between the growth rate and the rate of photosynthesis on the same plot shows less agreement, as the yields become smaller and thereby more uncertain (compare columns 10 and 11, 14 and 15).

### **Discussion**

#### *Comparison between the rate of growth and the rate of photosynthesis*

The calculated rate of dry herbage production fitted reasonably well with the mean growth rates for the first two experimental periods, and with both mean and actual growth rate for the rest of the season. When the sward grows older both the growth rate and the rate of photosynthesis drop, but the smaller the production values, the larger the inaccuracy and the more difficult the comparison. When growth rates of herbage are below  $100 \text{ kg ha}^{-1} \text{ d}^{-1}$ , a comparison becomes impossible. Nevertheless the experimental evidence clearly indicates that the reduction in growth rate with age of the sward is caused by a reduction in the rate of net photosynthesis and not by an increase in the rate of respira-

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tion, as has been suggested in the conception of optimum growth rate and ceiling value (Donald, 1961; see also McCree & Troughton, 1966).

Fig. 28.4 clearly indicates the large differences in net photosynthesis as compared to respiration. As the dry weight increases the respiration per g dry weight decreases, as can be seen when the respiration data are related to the dry herbage weight at the end of the measuring week:

Age of sward (wks)	Wt of dry herbage (kg ha <sup>-1</sup> )	Respiration rate (kg CH <sub>2</sub> O ha <sup>-1</sup> d <sup>-1</sup> )	Respiration rate (g kg <sup>-1</sup> d <sup>-1</sup> )
4	3400	45.6	13.41
11	8130	72.0	8.86

*The role of the simulation model in analysing crop production factors*

The aim of the present study was to gain a better insight into the performance of a closed grass sward of different ages throughout the season, and especially to analyse the factors that are responsible for the observed reduction in the rate of dry herbage production of the sward with age. For this purpose the increase in dry weight over a certain period, and the rate of crop photosynthesis, were determined. The photosynthetic performance of the youngest fully expanded leaves of that sward was also measured to use in the simulation program in order to test the validity of the program. To analyse the relative importance of the yield-determining factors the crop simulation model was used to calculate either the daily crop growth rate or the daily photosynthesis rate. For crop parameters, basic physiological knowledge was used together with known data on leaf density and leaf position and their change with age of the sward. Using the prevailing weather data, it was then possible to compare the actual and calculated values. A reasonable agreement between measured and simulated dry matter production and measured and simulated photosynthesis rate under varying outdoor conditions and at different ages of the sward, would indicate that the simulation model could now be used satisfactorily to predict the effect of various climatic and canopy factors on dry matter production.

Unfortunately, the present measurements of leaf photosynthesis on plants removed from the sward failed to demonstrate any influence of the season or the age of the sward on the light response curve, and, in addition, all measurements were much lower than those found for plants grown in growth rooms on nutrient solution, or than field

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measurements of individual leaves *in situ*. It must be concluded that the removal of small swards from the field to the laboratory has influenced the photosynthetic performance of the leaf. When, however, the light response curve of leaves of plants grown indoors was used in the simulation program, the agreement between calculated and measured sward photosynthesis was reasonably good. For older swards, the simulated values based on the values for leaf photosynthetic capacity estimated as described earlier, also agree well with the actual values determined under a range of climatic conditions. It can therefore be concluded that it is the reduction in leaf photosynthetic performance with age that is mainly responsible for the reduction in photosynthesis and growth rate of the sward with age, and also that the simulation program developed so far is able to calculate the rate of dry matter production with reasonable accuracy under various conditions of climate and sward architecture.

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