

PRODUCTIVITY OF GRASSLANDS UNDER  
CONTINUOUS AND ROTATIONAL GRAZING



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STELLINGEN

1. In de formule van Linehan et al. (1947) voor berekening van de grasopname gedurende een omweidingsperiode wordt aangenomen dat een grasgewas altijd exponentieel groeit. Dit leidt in sommige situaties tot een aanzienlijke onderschatting van de grasopname.

Linehan, P.A., J. Lowe and R.H. Stewart. Journal of the British Grassland Society 2: 146-168 (1947).

Dit proefschrift.

2. Zelfs onder intensieve beweiding gaat bovengronds meer van de geproduceerde droge stof verloren via afsterving dan er door het vee wordt opgenomen.

Parsons, A.J., E.L. Leafe, B. Collett, P.D. Penning and J. Lewis. Journal of Applied Ecology 20: 127-139 (1983).

Dit proefschrift.

3. De zodekwaliteit bij het standweidesysteem is beter dan bij het omweidingssysteem. Bovendien is de produktie groter in perioden met vochttekorten.

Dit proefschrift.

4. De dagelijkse grasproduktie in Nederland neemt gemiddeld niet meer toe bij overschrijding van 60% van de maximaal mogelijke globale straling op die dag.

Dit proefschrift.

5. De lagere oogstbare grasproduktie bij sub-optimale stikstofvoorziening is niet het gevolg van een lagere gewasfotosynthese, maar van een verandering in het patroon van droge-stofverdeling.

Dit proefschrift.

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6. Onder beweiding bij hoge stikstofgiften is de circulatie van stikstof via urine en mest van weinig betekenis en werkt de uitgescheiden stikstof belastend voor het milieu. Het effect van stikstofbemesting op graslandproductie is daarom vrijwel gelijk onder intensief weiden en maaien bij overeenkomstige oogstintervallen in het traject rond de huidige adviesgift van 420 kg stikstof per hectare en per jaar.

Meer, H.G. van der. Landbouwkundig Tijdschrift 97 nr. 8: 25-28 (1985).

7. Bij vergelijkende opbrengstproeven van grasland is het beter de opbrengst uit te drukken in voedereenheden dan in droge stof.

Burg, P.F.J. van, W.H. Prins, D.J. den Boer en W.J. Sluiman. Proceedings No. 199. The Fertilizer Society, London (1981).

8. Het door De Vries e.a. (1942) toegekende waarderingscijfer aan ruwbeemdgras (*Poa trivialis*), dat nog steeds wordt gebruikt, is te hoog.

Vries, D.M. de, M.L. 't Hart en A.A. Kruijne. Landbouwkundig Tijdschrift 54: 245-265 (1942).

9. Het relatief hoge suikergehalte van tetraploïde raaigrassen is ongewenst voor een goede penswerking.
10. Regelmatige bespeling bevordert de bespeelbaarheid van grassportvelden. Het is daarom onjuist dit gedurende de zomerperiode geheel te verbieden.

Wijk, A.L.M. van. Proefschrift Landbouwhogeschool, Wageningen (1981).

11. Standweiden is beter dan omweiden.

Proefschrift van E.A. Lantinga

Productivity of grasslands under continuous and rotational grazing  
Wageningen, 23 oktober 1985

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## General introduction

Grazing is the most important method of utilization of grassland in the Netherlands. Zero-grazing, i.e. feeding of mown grass to housed cattle, is used only to a limited extent, and is not to be recommended, as the extra costs in comparison with grazing exceed the benefits resulting from the higher production per unit area (Laeven-Kloosterman and Overvest, 1983).

Grazing can be performed in many different ways. Nowadays, rotational grazing with grazing periods of 2 to 5 days is the most common system in the Netherlands (Van Burg et al., 1980). In some countries of North-western Europe there has been a move to continuous grazing, but this has not occurred in the Netherlands. Here, it is generally believed that this grazing system cannot supply an adequate amount of good quality herbage to the grazing cattle. This prejudice against continuous grazing, however, is not supported by the results of comparative trials, carried out in the 1970's with high stocking rates and high rates of nitrogen (reviewed by Ernst et al., 1980). There was on average only a 1.5% increase in animal production resulting from the use of rotational grazing for dairy cows. In these trials, however, little attention was paid to the primary production of herbage. Very little is known, therefore, about the physiological and environmental limitations to herbage production throughout the grazing season under these two grazing systems. Such knowledge is essential for explaining the results of comparative trials on grazing systems, and for the improvement of existing systems.

The main reason for this lack of understanding is that herbage production of a sward cannot be measured during grazing. However, a combination of carbon exchange measurements and herbage intake studies provides an opportunity to estimate herbage production in pastures.

The present study involves research on the seasonal totals and seasonal patterns of both  $\text{CO}_2$  assimilation and animal production using continuous and rotational grazing systems. With these data, predictive models for herbage production under grazing are developed; these appear to operate successfully. The models can be used in herbage intake studies with rotational grazing, to estimate the additional herbage production during the grazing period, and for management of the continuous grazing system.

This dissertation contains five chapters, of which the first four will also be published elsewhere.

- Chapter 1 describes the results of two experiments on the seasonal pattern of gross  $\text{CO}_2$  assimilation, herbage production and animal production under continuous and rotational grazing. Special attention is paid to the influence of nitrogen supply and water stress on sward assimilation and assimilate partitioning.
- Chapter 2 deals with herbage production and herbage intake during a rotational grazing period. A new formula is presented, to estimate the contribution of herbage production during the grazing period to the total herbage intake. Its validity is evaluated by means of dynamic simulation, with measured assimilation-light response curves as the main input.
- Chapter 3 presents a descriptive simulation model, to calculate the seasonal pattern of net herbage production under continuous grazing. The model is based on observed correlations between sward assimilation and respiration and herbage intake.
- Chapter 4 discusses the influence of the proportion of diffuse radiation on gross  $\text{CO}_2$  assimilation of leaf canopies and treats the relationship between the daily total radiation and the daily total gross assimilation. The leaf assimilation-light response curve in field-grown swards is also considered.

This dissertation ends with some final remarks (Chapter 5) on the practical implications of the use of the two grazing systems. Special attention is paid to the potential pattern of stocking density with continuous grazing throughout the grazing season. In addition, a procedure is given for estimation of the undisturbed production rate of grass swards at the grazing stage for rotational grazing, and a new approach is presented for the calculation of grazing losses.

# 1 CO<sub>2</sub> assimilation, herbage production and animal production under continuous and rotational grazing at two nitrogen levels

## Abstract

Studies were made on swards dominated by *Lolium perenne* to evaluate CO<sub>2</sub> assimilation, herbage production and animal production under continuous and rotational grazing with cattle at a low (125 kg ha<sup>-1</sup> yr<sup>-1</sup>) and a high (about 450 kg ha<sup>-1</sup> yr<sup>-1</sup>) nitrogen fertilization level.

At high nitrogen levels the cumulative gross assimilation over the grazing season was 9% higher with rotational than with continuous grazing, whereas there was no difference in animal production. The higher efficiency of utilization of gross assimilation products under continuous grazing was due to lower topping losses and lower costs for above-ground maintenance respiration.

The leaf area index under continuous grazing increased only marginally with sward height between 4 and 11 cm. The optimum mean sward height for continuous grazing with cattle is discussed with respect to the need to balance the herbage on offer with the animals' requirements.

The harvest-efficiency - the fraction of gross assimilation minus maintenance respiration harvested as animal intake - was on average 25% under continuous grazing with high nitrogen, and showed no clear seasonal differences. Its value was not affected by drought.

Gross CO<sub>2</sub> assimilation per unit leaf area was not depressed at low nitrogen, but there was a marked negative effect on the rate of leaf area development in the second half of the grazing season. Moreover, at low nitrogen more dry matter was allocated to the stubble beyond the reach of the grazing cattle. It is demonstrated that a small change in the carbon balance due to the nitrogen status of the sward has a large influence on pasture output.

## 1.1 Introduction

For centuries grazing was managed according to the extensive continuous grazing system. The main characteristics of this method of utilization are a low stocking rate, long grazing periods and no or little fertilization. Grass production levels are low and grazing losses high. Owing to low and variable

herbage production rates and poor quality, a high herbage allowance is required. Losses by death and decay, and by maintenance respiration in these physiologically old crops, are therefore high.

The disadvantages of extensive continuous grazing were already known in the eighteenth century, as noted by Johnstone-Wallace and Kennedy (1944). They quoted the writings of James Anderson (1797), who described certain grazing habits, and, as a result of his observations, proposed the adoption of a system of rotational grazing. But it still took a long time before rotational grazing became widely accepted. In the Netherlands the results of trials by, e.g., Frankena (1936) played an important role in the expansion of the rotational grazing system. In his experiments a significant higher annual milk production was found with rotational than with continuous grazing. However, this comparison is somewhat dubious, as there were differences in the pattern of nitrogen application.

A few decades ago the general opinion was that the application of nitrogen during grazing, even in pellet form, would cause problems with animal health. Thus for the long grazing periods under continuous grazing nitrogen was applied only once, whereas in case of rotational grazing nitrogen was applied at the end of each cycle. This discrepancy in nitrogen application pattern may have had a considerable effect on herbage production rates, certainly when expressed in fodder units. It is now known that there need be no problems with nitrogen application in the presence of cattle (Hood, 1974).

In the 1950's and 1960's rotational grazing became more and more common practice in the Netherlands. The three main reasons for the rapid expansion of this system were the introduction of cheap fertilizer and methods of fencing, and improved information to the farmers. In other countries continuous grazing was still applied in those years and was studied in experiments. For instance, McMeekan and Walshe (1963) concluded from experiments with milking cows under New Zealand conditions that stocking rate was a more important factor in determining the efficiency of pasture utilization than the grazing method. In their trials, however, fertilizer application was still far from the optimum level for grass production, and at the highest stocking rate (about 2 cows ha<sup>-1</sup>) rotational grazing had an average advantage of 8% over continuous grazing. At the time, however, this was attributed to a difference in forage conservation.

These results stimulated Hood (1974) to start experiments with continuous grazing for dairy cows in the UK, at high rates of nitrogen fertilizer and high stocking rates. He found that at a stocking rate of 4 cows ha<sup>-1</sup> throughout the grazing season and a fertilizer rate of about 500 kg N ha<sup>-1</sup>, milk production per head from continuously grazing cows was equal to that of rotationally grazing cows.

This result gave a new impulse to the discussion on grazing systems in the mid-seventies. In some countries, e.g. Germany, Belgium and the Netherlands, similar trials were started with rotational and continuous grazing with both milking cows and beef cattle. These experiments were under conditions of high N fertilizer rates and high stocking densities. In general, the results of the experiments on dairy cows were in agreement with those of Hood; for beef cattle, meat production was on average 6% higher using rotational grazing (Ernst et al., 1980; Schlepers et al., 1982).

In all of these trials, only data on animal production were obtained. No detailed measurements on herbage production were made since this is very difficult under continuous grazing. Three methods are given:

- The conventional method is to estimate dry matter production in areas which remain ungrazed for a short time. This method is described by Frame (1981). Herbage mass on grazed sward (A) is measured. Simultaneously, enclosure cages are placed and after a short period (e.g. 5-7 days) the herbage mass inside the cages is measured (C).

Herbage produced is estimated as (C-A). Because of the large variability in standing herbage mass in grazed swards it is difficult to find representative strips. Herbage production rates over a short period are small compared with the standing herbage mass, so this method is relatively inaccurate.

Another disadvantage is the fast change in structure of the sward when it is released from grazing (Parsons et al., 1981). Leaf area per tiller increases rapidly after placing the cages. Although this development is partly counterbalanced by an accelerated rate of tiller death: marked-tiller studies showed that the small and subordinate tillers are especially likely to die.

- Estimates of production in grazed swards by measuring rates of tissue turnover. This technique is described by Davies (1981). Net herbage

production is the difference between the increase in weight due to the formation of new tissue and the decrease in weight caused by death and decomposition of old tissue. These changes can be measured by close examination of a set of marked tillers. The rate of production of new tissue by individual tillers is computed on the basis of length increments of all leaf laminae, sheaths and stems. Weights per unit length are based on samples of the different tiller components. Rates of loss can be calculated from rates of disappearance of old leaf laminae and the weights of these laminae. Finally, net production per tiller must be multiplied by tiller density to give net herbage production per area. Though changes in tiller density can be extremely rapid (Hodgson et al., 1981), the time required for this kind of measurement is so short that changes in tiller number do not play an important role.

However, the method in itself is a cumbersome one. A large number of, usually small, tillers must be examined and the ultimate result is a combination of many different measurements, each with its own bias.

- Many of the considerable disadvantages of the two methods described above are avoided by making use of measurement of assimilation, respiration and transpiration with crop enclosures and using this information in crop growth simulators to compute crop growth. This method also provides a deeper insight into the process of herbage production in continuously grazed swards (Parsons et al., 1983a).

A disadvantage of crop enclosures is that the climatological conditions inside are different from those outside. The transparent cover absorbs a certain part of the short-wave radiation and there exists no wind profile in the thoroughly mixed air above the crop as in the open field. The latter effect has been examined by Goudriaan et al. (1984). They showed that the turbulence resistance, calculated on the basis of the logarithmic wind profile, does not impose a serious restriction on the assimilation rate. So it appears that the difference between the rate of assimilation in enclosures and in the field is small.

This latter method was used in the present study to obtain a better insight into the ecological basis of herbage growth under rotational and continuous grazing, and to develop predictive models of herbage growth under the different forms of management.

Continuous grazing and rotational grazing differ, not only in the way of herbage consumption, but also in the physiology of herbage production. Continuous grazing implies herbage production and consumption at the same time, whereas under rotational grazing these two processes are practically separated. But in spite of these differences, production under the two systems may be similar (Parsons et al., 1983c). The part of the study presented in this paper deals with the accumulated gross assimilation under the two grazing systems together with the animal performance and the carbon balance.

Two experiments were carried out. In the first experiment continuous grazing was compared with rotational grazing at two levels of nitrogen application. In this experiment yearling steers were used. These animals have the disadvantage that it is impossible to use a measured increase in liveweight as a reliable estimation for herbage intake, especially over short periods (Meijs, 1981). Therefore a second experiment was set up with lactating cows to obtain more accurate data about animal performance. In this experiment the measurements were restricted to the intensive continuous grazing system.

In both experiments the aim was to maximize herbage intake per unit area without restricting individual animal intake.

## 1.2 Materials and methods

### 1.2.1 Experiment 1

This study was carried out in 1981 on a 12-year old pasture on a fine-textured clay soil in Wageningen. The sward comprised more than 90% *Lolium perenne* and *Poa trivialis*. The pasture was divided into six paddocks (Table 1.1).

In both grazing treatments nitrogen was applied at intervals of about 3 weeks. Nitrogen was given as calcium-ammonium-nitrate (26% N). The difference in the quantity of applied nitrogen between C-HN and R-HN was 70 kg, but this is assumed not to have affected herbage production rates significantly since both doses were around the 'optimum' quantity of 420 kg N ha<sup>-1</sup> yr<sup>-1</sup> as determined by Prins (1983) under various cutting regimes. The supply of P and K was adequate and the paddocks were irrigated with sprinklers when necessary.

Table 1.1. Experiment 1. Description of the experimental plots. Continuous and Rotational grazing under Low and High Nitrogen fertilizer levels (C-LN, C-HN, R-LN and R-HN, respectively).

Treatment	Grazing method	area (ha)	number of paddocks	nitrogen application (kg N ha <sup>-1</sup> yr <sup>-1</sup> )
C - LN	continuous gr.	0.31	1	115
C - HN	continuous gr.	0.48	1	430
R - LN	rotational gr.	0.42	2	120
R - HN	rotational gr.	0.42	2	500

### Grazing

The paddocks were stocked with yearling steers.

*Rotational grazing* The grazing period was 4 to 7 days including one or two intervals of about 24 hours without grazing for measurements of assimilation in partially grazed paddocks.

In the rotational grazing system only one group of steers was used. Next to the experimental plot were situated two paddocks; these received a low and a high nitrogen application identical to the treatments R-LN and R-HN. Here the steers were stocked while the assimilation measurements were made.

Cleaning cuts of grazing residues were carried out when necessary, at a height of about 5.5 cm.

*Continuous grazing* The 'put and take' method was used. The aim was to maintain an average sward height of 8 cm throughout the grazing season. At this sward height no depression in herbage intake or animal weight gain are likely to occur (Ernst et al., 1980).

### Sward measurements

*Rotational grazing* In the rotationally grazed paddocks herbage dry mass was determined before and after grazing using a two-step harvesting system. The herbage samples were first cut with a motor scythe at a height of about 3.5 cm. Five strips of about 5 m<sup>2</sup> were cut. After removing the cut material two core samples of 90 cm<sup>2</sup> were taken in each strip and cut to ground level. The samples cut with the motor scythe were weighed and a subsample of approx. 150 g was taken to determine dry matter content. The stubble samples were so small that sub-sampling was not necessary to determine dry



matter weight. Three sub-samples of approx. 1.5 g dry weight were taken from both sward layers for division into live leaf, stem (including leaf sheaths) and dead material. The area of live leaf was measured using an electronic planimeter. All the material was oven-dried for 20 h at 105 °C.

The sward height was measured before and after each grazing period using a tempex disc with a diameter of 50 cm and a weight of 150 g. Thirty measurements were taken in each paddock.

*Continuous grazing* In the continuously grazed paddocks sward heights were measured at weekly intervals. Forty heights were taken in treatment C-LN and sixty in treatment C-HN. Herbage dry mass and its distribution over different plant parts were measured at monthly intervals. For this purpose core samples of 90 cm<sup>2</sup> were taken. The procedure of analysis was the same as for the stubble grass of rotationally grazed paddocks.

*Grass in assimilation chambers* Mean sward height of the chosen spot was measured before placing the assimilation chamber. Five heights were measured at random within the measuring area, using the tempex disc. After the period of measurements herbage dry mass and its distribution over different plant parts was estimated by taking three core samples of 90 cm<sup>2</sup> inside the experimental area. The procedure of analysis was as described before.

#### Assimilation and respiration measurements

During the trial, data were collected on CO<sub>2</sub> assimilation and respiration, radiation and temperature. Measurements were carried out with a mobile equipment, using two enclosures with an area of 100 x 100 cm and a height of 35 cm. The enclosures were screwed down into the ground with four large corkscrews. This was an improvement on earlier experiments (Deinum et al., 1983), in which metal frames were used, which were hammered into the soil. Air was circulated through the system at a rate of about 700 m<sup>3</sup> h<sup>-1</sup>. The temperature of the air inside the system followed the outside temperature. Fresh air was injected into the system at a rate of 50 m<sup>3</sup> h<sup>-1</sup>. The overpressure created inside the enclosures eliminated the effects of soil respiration. During the daytime the CO<sub>2</sub> concentration inside the chambers was kept as much as possible at a level of about 320 vppm, with the aid of an automatic CO<sub>2</sub> injector. The CO<sub>2</sub> concentration was higher than 320 vppm during most mornings because of accumulation of CO<sub>2</sub> in the lower air layers during the night.

Net CO<sub>2</sub> assimilation was determined by measuring the CO<sub>2</sub> concentration of the incoming fresh air and the outgoing chamber air and by measuring the CO<sub>2</sub> injection. Irradiance was measured with a Kipp solarimeter and corrected for absorption by the transparent chamber.

Respiration rates during daytime were estimated by covering the chambers with black plastic for about half an hour. The gross assimilation rate was obtained by adding the rate of respiration to the net assimilation rate. Justification of this procedure depends on the assumption that the rate of respiration is the same in darkened and illuminated conditions. Experimental evidence is contradictory, but recently developed methods for estimating the rate of respiration of green leaves in the light do support this assumption (Azcón-Bieto and Osmond, 1983).

The data were stored on paper tape and on magnetic tape, and used to compute light-assimilation response curves. Measurements were made simultaneously at two different sites. Usually one response curve was determined for the grass of a rotationally grazed paddock and one for a continuously grazed one. Each measuring period started in the early afternoon and lasted about 22 hours. Then the caravan was moved to another part of the trial. Thus 5-6 sets of response curves could be obtained each week. Measurements in the treatment 'rotational grazing' were made just before grazing, twice during grazing, and at various stages of regrowth. Two paddocks, one with each nitrogen treatment, were closely examined throughout the grazing season to follow the seasonal pattern of CO<sub>2</sub> uptake. In the continuously grazed sward, measurements were carried out at spots with different sward heights. Data were collected throughout the grazing period, which lasted from mid April till mid October. In addition, the steers were weighed 6 times during the period of experiments.

### 1.2.2 Experiment 2

This experiment was carried out in 1982 on a permanent grassland pasture on a fine-textured clay soil in Wageningen. The botanical composition of this pasture was less good than that in experiment 1, but throughout the grazing season highly valued grasses (*Lolium perenne*, *Poa trivialis*, *Poa pratensis*, *Phleum pratense* and *Dactylis glomerata*) still accounted for 80-90% of the standing herbage dry mass.

The whole area of 3 ha was continuously stocked with spring-calved cows from May until late October. Nitrogen application was  $500 \text{ kg ha}^{-1} \text{ yr}^{-1}$ . The P and K supply was adequate. Irrigation was not possible. Sward height was measured twice a week using the same disc as in experiment 1. Other herbage and assimilation measurements were carried out as described for continuous grazing in experiment 1. Milk yield was recorded for individual animals twice a day, and milk was analysed for fat every three weeks. The animals were weighed every two weeks after milking on Friday morning.

### 1.3 Theory

#### 1.3.1 Use of assimilation-light response data

The use of light by a canopy is much more efficient under an overcast sky than under a clear sky. This is due to the better distribution of diffuse light over the leaves, in comparison with direct sunlight. Goudriaan (1977) showed that at the same radiant flux density the gross assimilation of a full crop is up to 40% higher with diffuse light than under a clear sky. The magnitude of this difference depends on the height of the sun and the clarity of the sky. For this reason separate measurements of diffuse and direct radiation are almost as important as measurements of the total solar radiation (Goudriaan, 1977). Unfortunately these data are not available on a routine basis.

#### 1.3.2 Calculation of daily total of gross assimilation

To calculate the amount of gross assimilation accumulated over the season, daily totals are required. The most accurate method of obtaining the daily total gross assimilation is by integration of the sum of net assimilation and respiration over the part of the day that assimilation occurs. This involves measurements carried out without interruption throughout the grazing season, which is practically impossible.

Another procedure is to determine, at intervals through the growing cycle or season, a relation between radiant flux density and gross assimilation, and to use this relation as a basis for calculating the gross assimilation total each day in dependence of the daily radiation total and the daylength. For days

between two measuring dates the curves are obtained by interpolation. The main problem is to account for the influence of the fraction of diffuse light in the total radiation.

To solve this problem, the following measurement strategy and calculation procedure was followed. For determination of the relation between gross assimilation and radiant flux density only measurements during periods that the sun was shining were used. At midday the diffuse radiation was then, on average, 30% of the total radiation. This is about twice as high as the fraction observed on perfectly clear days. The difference is due to haziness, dust and reflection from clouds. The average radiant flux density is then calculated by dividing the measured daily radiation total by the effective daylength, and the corresponding rate of gross assimilation is read from the appropriate graph. A first estimate of the daily total gross assimilation is then obtained by multiplying this rate by the effective daylength. The effective daylength is here taken as the time for which the sun is above 8 °C (Goudriaan and Van Laar, 1978).

The value thus obtained is then corrected by a multiplication factor which depends on the average radiation throughout the day. This multiplication factor is calculated by means of the model PHOTON (De Wit et al., 1978) for the gross assimilation of a canopy. For this purpose daily assimilation rates were calculated (for crops with a spherical leaf distribution function, an LAI between 2 and 5 and a maximum gross assimilation rate of the leaf between 2.0 and 5.0 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>) in dependence of the relative daily radiation total and daylength for a latitude of 52° N. These daily totals are then expressed as a fraction of the daily totals for the situation in which the fraction of diffuse light at midday is 30%. The relative daily radiation total in these computations is here defined as:

$$R_r = \frac{R_m}{R_c} \tag{1.1}$$

in which  $R_m$  is the daily radiation total observed, and  $R_c$  this total on a perfectly clear day as defined by De Wit (1965). The multiplication factors obtained in this way are then averaged for each relative radiation level; the resulting relation is given in Fig. 1.1. The comparison (Fig. 1.2) of measured daily totals with daily totals calculated in this way shows that this calculation method gives satisfactory results.

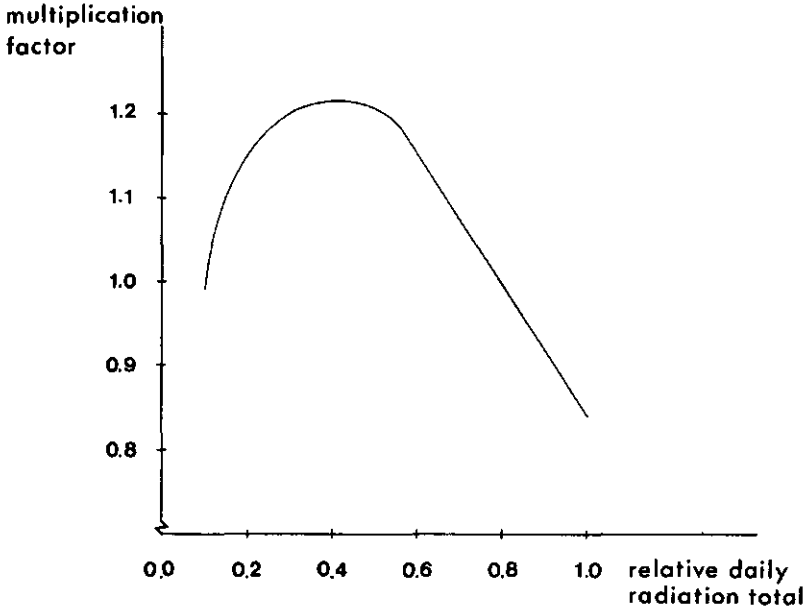


Fig. 1.1. Multiplication factor for calculation of the daily gross assimilation total. See text for further information.

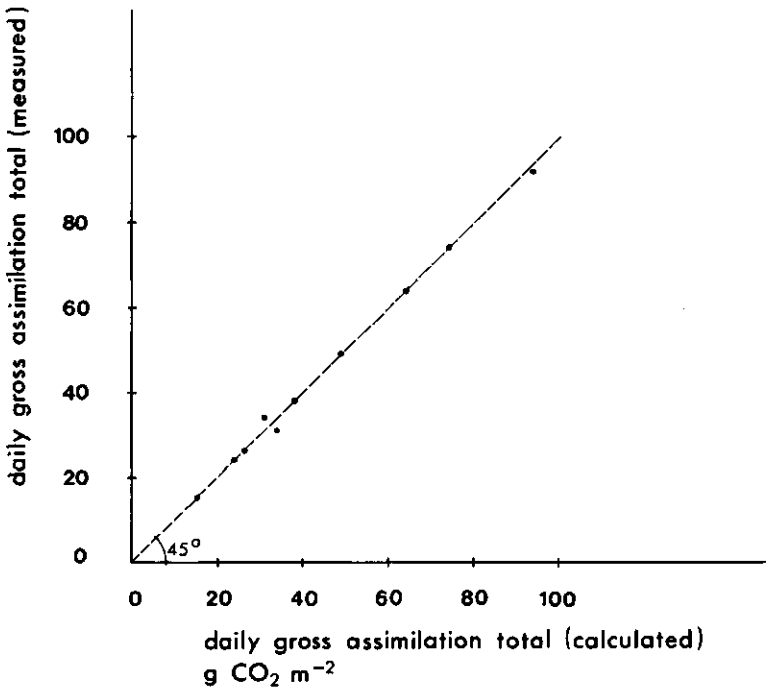


Fig. 1.2. Comparison between measured and calculated daily totals of gross assimilation. Period: 1 April - 7 May 1983.

This procedure was used for calculation of the daily gross assimilation in each grazing treatment throughout the season. In the rotationally grazed paddocks assimilation-light response curves were taken in patches which appeared representative of the whole paddock. The results from the continuously grazed paddocks were treated somewhat differently. First, the daily gross assimilation of each sward height class was calculated. Hereafter the daily total for the whole paddock was calculated using the relative contribution of each height class to the whole area. The following sward height classes were distinguished: 0.0-3.9 cm, 4.0-7.9 cm, 8.0-11.9 cm, 12.0-15.9 cm, 16.0 cm and higher.

#### 1.4 Results

##### 1.4.1 Experiment 1

###### Grazing days

The number of grazing days for the season is given in Table 1.2. The number of grazing days in treatment R-LN was lower than it might have been, since there remained a considerable amount of herbage at the end of the grazing season (Table 1.3). Had this been grazed down to the same level as in R-HN, the total number of grazing days in R-LN would have been between 1050 and 1100.

The average liveweight gain per steer was  $0.77 \text{ kg d}^{-1}$  with continuous grazing and  $0.80 \text{ kg d}^{-1}$  with rotational grazing. The low number of animals used and the small differences between continuous grazing and rotational grazing do not permit any conclusions to be drawn.

Table 1.2. Experiment 1. Total number of grazing days.

Treatment	grazing days $\text{ha}^{-1}$
C - LN	1039
C - HN	1528
R - LN	885
R - HN	1527

Sward height and herbage mass

*Rotational grazing* In Fig. 1.3 the sward height throughout the season is given for the rotationally grazed paddocks. A more detailed course cannot be given, because sward heights were only measured at the start and the end of each grazing period.

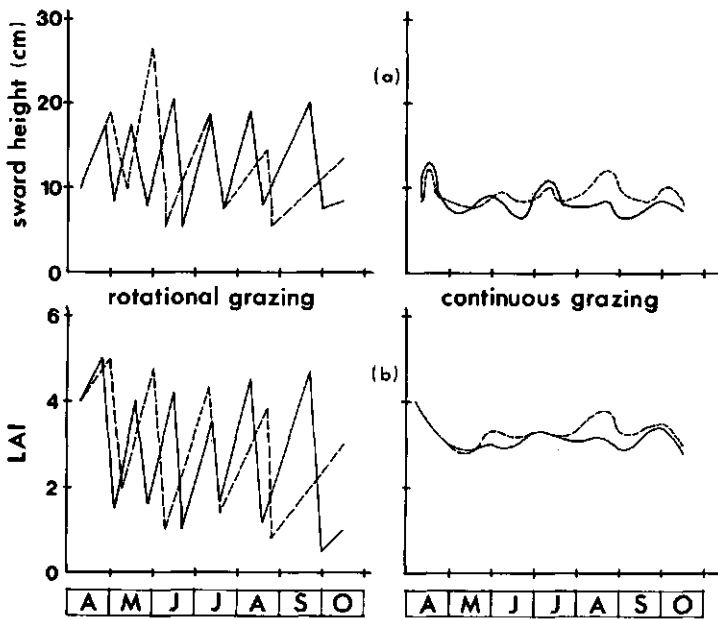


Fig. 1.3. Experiment 1. (a) Mean sward height and (b) leaf area index under continuous and rotational grazing. (—) high nitrogen; (----) low nitrogen.

Table 1.3. Experiment 1. Herbage dry mass (kg DM ha<sup>-1</sup>) in the rotationally grazed paddock above 3.5 cm at the start and at the end of the grazing periods. Between brackets amount of grass (kg DM ha<sup>-1</sup>) removed by cleaning cut afterwards.

Grazing period	R-HN		Grazing period	R-LN	
	pre-grazing	post-grazing		pre-grazing	post-grazing
28 April-4 May	3105	1140	6-11 May	3440	1160
19-26 May	2535	840	1- 7 June	3810	1570 (550)
16-23 June	2655	1330 (610)	16-23 July	2485	970
17-21 July	1860	1295	18-21 Aug.	2175	780 (110)
11-18 Aug.	2490	1030			
21-28 Sept.	2805	535			
rest at 12 Oct.	385		rest at 12 Oct.	1820	

Herbage yields harvested with the motor scythe are presented in Table 1.3. The values given for the post-grazing herbage mass are corrected for the increased stubble yield after grazing. This increase in the yield of the stubble grass left after cutting with the motor scythe is due to trampling and to poorer mowing results in the short and trodden grass (Meijs, 1981). The average difference between the stubble yields before and after grazing was 215 kg DM ha<sup>-1</sup> in R-HN and 204 kg DM ha<sup>-1</sup> in R-LN. In both paddocks these differences were highly significant. The pre-grazing stubble yield was on average 2529 kg DM ha<sup>-1</sup> in R-HN and 2764 kg DM ha<sup>-1</sup> in R-LN. In spring and early summer no influence of nitrogen on herbage growth could be established, but as the grazing season progressed the herbage production rates in the low nitrogen treatment gradually decreased in comparison to the high nitrogen treatment (Table 1.3, Fig. 1.3). This led to a smaller number of grazing cycles in the low nitrogen paddocks. The absence of an effect of nitrogen in spring and early summer was due probably to a residual effect of previously applied nitrogen fertilizer. This effect can be considerable on heavy clay soils (Prins, 1983).



*Continuous grazing* The mean sward heights recorded over the whole season were 8.3 and 9.1 cm for treatments C-H and C-L respectively. The time course of the sward heights is shown in Fig. 1.3. The whole area of both treatments was topped once in June/July at a height of about 10 cm. The mown grass was not removed immediately, but after about one week, to minimize topping losses. This method of utilization reduced the mass of grass lost by topping to 269 and 273 kg DM ha<sup>-1</sup> for treatments C-H and C-L respectively.

#### Leaf area and leaf weight

For calculations of the leaf area index (LAI) only laminae were measured. Despite a relative high contribution to the total photosynthetic area, especially in a hard grazed sward, the contribution of leaf sheaths to sward CO<sub>2</sub> assimilation is small (Parsons et al., 1983a). This is because sheaths have a very low assimilatory capacity and most of the sheaths are shaded. The sheath area is therefore neglected.

The specific leaf area, i.e. leaf area per unit leaf dry weight (Table 1.4), was fairly constant throughout the experimental period in all the treatments. This holds also for the leaf weight ratio, i.e. leaf dry weight as a fraction of total above-ground live dry weight. The specific leaf area was somewhat lower under continuous grazing than under rotational grazing, but this may have been because the leaves of the grass in the continuously grazed swards were so small that it was difficult to measure their area.

Table 1.4. Experiment 1. Specific leaf area (SLA) and leaf weight ratio (LWR). The presented values are seasonal averages with standard deviations between brackets.

Treatment	SLA cm <sup>2</sup> g <sup>-1</sup>	LWR g g <sup>-1</sup>
C-LN	221 (31)	0.46 (0.08)
C-HN	242 ( 6)	0.46 (0.12)
R-LN	254 (48)	0.47 (0.10)
R-HN	255 (35)	0.49 (0.10)

Fig. 1.3 also presents the pattern of LAI for all treatments. There was no effect of nitrogen application rate on the development of the LAI after a rotational grazing cycle until the middle of July. After that time there was a marked difference in this development.

The LAI in the continuously grazed paddocks fluctuated between 3 and 4. In both paddocks, the LAI of the short-grazed areas was about 2.5 throughout the grazing season, whereas the LAI of the uneaten grass around dung patches was between 4 and 5. The variation in the average LAI of the paddock was thus determined mainly by the variation in the area of ungrazed patches.

#### Gross CO<sub>2</sub> assimilation

*Rotational grazing* Fig. 1.4a presents assimilation-light response curves during a grazing cycle and subsequent regrowth in R-HN in May. Assimilation rates of the full grown sward were in close agreement with the measurements of Parsons and Robson (1982). At the end of the grazing period, the LAI of the chosen measuring spot was 0.9. Despite this low LAI, assimilation rates of the short-grazed herbage were rather high. This enabled a high rate of regrowth. Fig. 1.4b shows some curves constructed for August and September. A marked difference between Figs. 1.4a and 1.4b is the lower light response, at the same LAI, of the late summer grass. This is especially pronounced in the curves recorded during and just after grazing. Differences between spring and late summer are ascribed to leaf activity (Woledge and Leafe, 1976). In spring, the initial assimilatory capacity of all the expanding leaves up to the flag leaf is high and declines very slowly during ageing. In the vegetative late summer crop, only the first leaves to expand have high assimilatory capacities. Later leaves have progressively lower capacities.

The influence of the level of nitrogen fertilization on gross assimilation during regrowth was analysed during the second half of the grazing season, because before the middle of July there were no differences between R-LN and R-HN in herbage production (see Fig. 1.3). The results are given in Fig. 1.5, where the rate of gross assimilation during regrowth is plotted against LAI. It can be concluded from Fig. 1.5 that there is no experimental evidence for higher rates of gross assimilation per unit leaf area in R-HN.

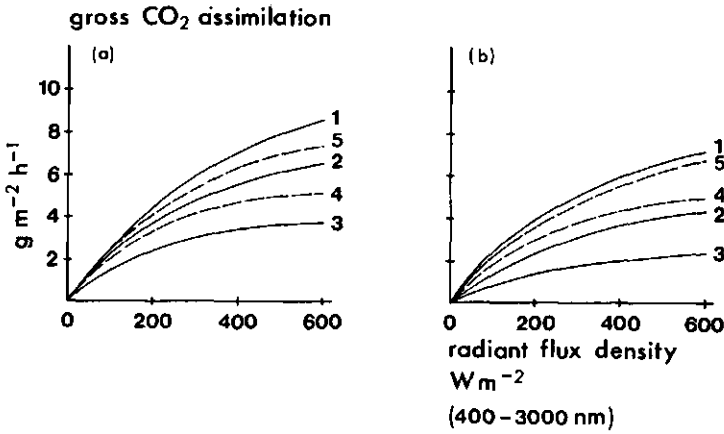


Fig. 1.4. Experiment 1. Some assimilation-light response curves under rotational grazing with high nitrogen in (a) spring and (b) late summer.

curve	date	crop stage	sward height (cm)	LAI
(a) 1	11 May	full crop	24.6	5.2
2	15 May	half grazed	12.7	3.0
3	19 May	short grazed	8.4	0.9
4	27 May	8 days regrowth	10.2	2.8
5	4 June	16 days regrowth	22.2	4.5
(b) 1	10 Aug.	full crop	20.4	4.7
2	12 Aug.	half grazed	13.0	3.0
3	19 Aug.	1 day regrowth	8.8	1.0
4	27 Aug.	9 days regrowth	12.2	2.9
5	21 Sept.	34 days regrowth	21.1	4.7

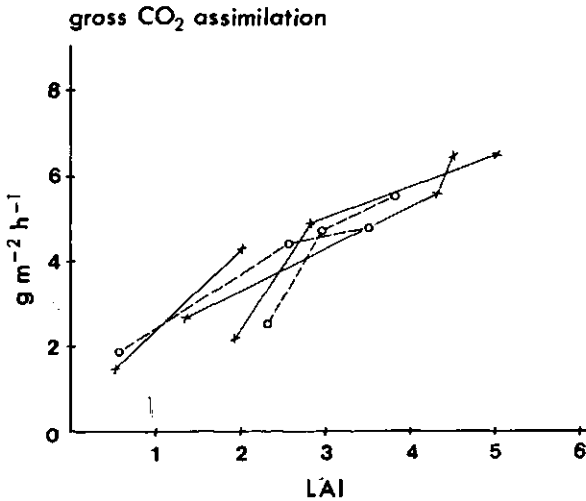


Fig. 1.5. Experiment 1. Relationship between gross assimilation and LAI during regrowth in the second half of the grazing season for rotational grazing with high nitrogen (x—x) and low nitrogen (o---o). Radiant flux density: 500 W m<sup>-2</sup> (400-3000 nm)

The higher rates of gross assimilation achieved in treatment R-HN at the end of a regrowth period resulted only from higher LAI.

The scattering in Fig. 1.5 below an LAI of 3 must be ascribed to a variation in LAI at the beginning of a regrowth period: at an initial LAI of 2 the rate of gross assimilation was only slightly higher than at an initial LAI of 0.5. Probably the sheaths contributed to the gross assimilation in paddocks with an initial LAI of about 0.5, whereas the assimilatory capacity of the leaves remaining after grazing was low.

*Continuous grazing* Fig. 1.6a presents a number of assimilation-light response curves for the treatment C-HN. Three results (curves 2, 4 and 5) are from areas with uneaten grass near dung patches; the others are from regularly grazed areas. In early summer the assimilation curve (2) for long grass with an LAI of 4.5 was much higher than the curve (1) for short grass with an LAI of 2.4. This difference between short and long grass was much smaller in autumn (curve 5 vs. curve 6). The reason may be that in autumn the long grass consisted of old leaves, as it had been only slightly grazed for a long period. This was not so in early summer. In regularly grazed areas the assimilation curve (1) in early summer was also higher than in autumn (curve 6).

In Fig. 1.6b several assimilation-light response curves are presented, for the treatment C-LN. These are similar to those measured in the treatment C-HN (Fig. 1.6a). This is also shown in Fig. 1.7 where gross assimilation rates at  $500 \text{ W m}^{-2}$  in C-HN are plotted against those for C-LN at the same LAI and measured in the same part of the season. Thus, the nitrogen deficiency created under continuous grazing was not sufficient to affect gross assimilation on a unit leaf area basis.

#### Cumulative gross assimilation

The cumulative gross assimilation in  $\text{kg CO}_2 \text{ ha}^{-1}$  in the four treatments was calculated over the experimental period (15 April - 12 October) by integrating daily gross assimilation totals as described in the introduction.

It can be seen from Table 1.5 that the highest cumulative gross assimilation was attained under rotational grazing with high nitrogen. However, the differences are less than 9%. The accumulation throughout the season for R-HN and C-HN, the two treatments that differ the most, is shown in Fig. 1.8.

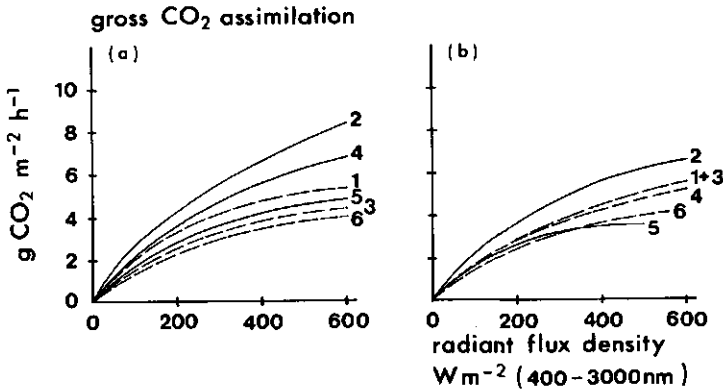


Fig. 1.6. Experiment 1. Some assimilation-light response curves under continuous grazing at high nitrogen (a) and low nitrogen (b).

curve	date	sward height (cm)	LAI
(a) 1	25 May	5.8	2.4
2	1 June	20.7	4.5
3	23 June	5.4	2.2
4	7 July	26.8	5.0
5	29 Sept.	20.5	4.0
6	5 Oct.	6.3	2.0
(b) 1	14 May	6.8	2.4
2	9 July	25.0	5.0
3	15 July	5.8	2.5
4	14 Aug.	5.7	2.2
5	16 Sept.	11.7	4.0
6	8 Oct.	6.0	2.0

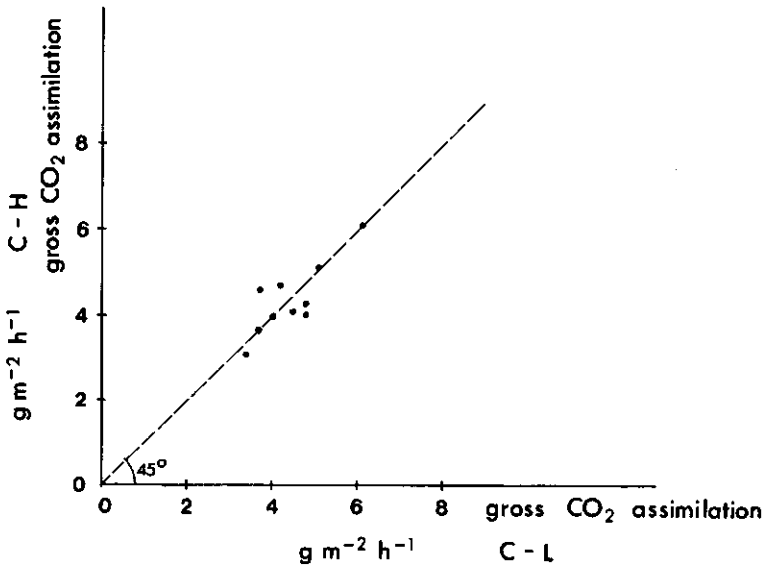


Fig. 1.7. Experiment 1. Relationship between gross assimilation at  $500 \text{ W m}^{-2}$  (400-3000 nm) in C-HN and C-LN at the same LAI and in the same part of the season.

Table 1.5. Experiment 1. Total gross assimilation over the period 15 April - 12 October. Relative figures between brackets.

Treatment	$10^3 \text{ kg CO}_2 \text{ ha}^{-1}$
C-LN	73.9 ( 93)
C-HN	72.7 ( 91)
R-LN	75.5 ( 95)
R-HN	79.7 (100)

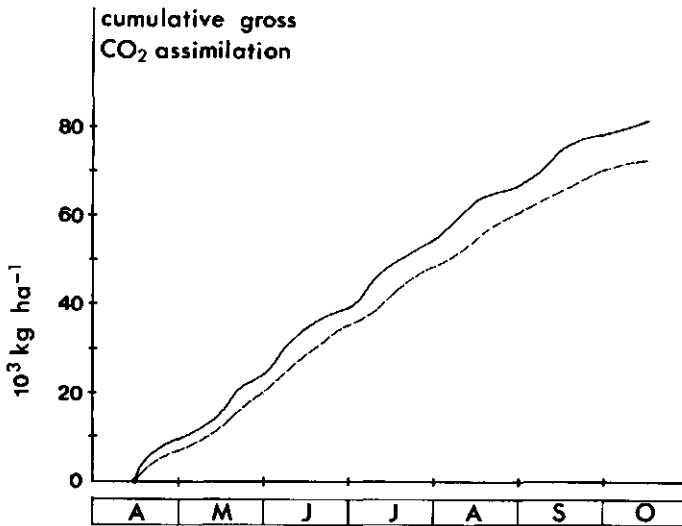


Fig. 1.8. Experiment 1. Cumulative pattern of gross assimilation under rotational grazing (—) and continuous grazing (----) at high nitrogen.

#### 1.4.2 Experiment 2

##### Sward height, herbage mass and LAI

The mean sward height of the continuously grazed paddock throughout the season is presented in Fig. 1.9a. During the first month of grazing the

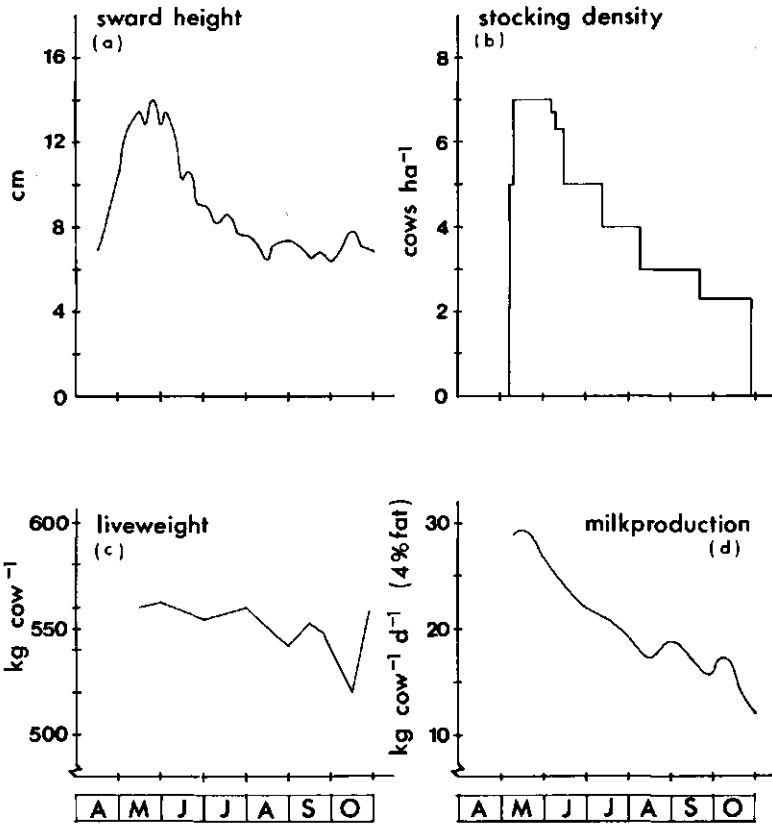


Fig. 1.9. Experiment 2. (a) Mean sward height, (b) stocking density, (c) average liveweight of the stock and (d) on 4% fat corrected milk production in the continuously grazed sward.

height was about 13 cm. This was due to the high sward at the start of the experiment and the decision to decrease sward height only gradually. The whole area was topped once in June/July at a height of about 9 cm. The mown grass was not removed from the paddock. From the middle of July onwards the mean sward height fluctuated between 6.5 and 8.5 cm. During that period the mean herbage mass above ground level was about 4000 kg DM ha<sup>-1</sup>.

The mean LAI decreased from 3.2 in May and early June to 2.1 in early August. From early August onwards there was very little variation in the mean LAI.

### Stocking density and grazing days

The stocking density throughout the season is shown in Fig. 1.9b. The experiment was started with 5 cows ha<sup>-1</sup>. This number was too low, as the mean sward height still increased (Fig. 1.9a). The stocking density was therefore set at 7 cows ha<sup>-1</sup> after 4 days. This stocking density was maintained for a period of 22 days. During the first week of June the stock decreased by 2 cows. One cow died suddenly and one cow was removed because of a leg abscess. Despite this decrease in stocking density the mean sward height decreased rapidly until mid-June. At that time the stocking density was further decreased to 5 cows ha<sup>-1</sup>. After this change, stocking density was reduced in three steps to the ultimate level of 2.3 cows ha<sup>-1</sup>, which was maintained from mid-September until the end of the experiment. This grazing strategy resulted in a total of 715 cow grazing days ha<sup>-1</sup>.

### Animal measurements

The mean liveweight of the milking cows throughout the grazing season is shown in Fig. 1.9c. Between half of May and early August, the mean liveweight was rather constant. The variation later in the season was due probably to a shortage of good grass (mid-August), and to bad weather (mid-October). At the end of the grazing period the mean liveweight was only 3 kg lower than that on 14 May, a change of no significance for pasture output calculations.

The milk production (4% fat-corrected) is shown in Fig. 1.9d. The recorded decline in milk production through the season is roughly in accordance with the normal pattern of spring-calving cows. There are, however, a few peculiarities. First of all, the rapid decline during late of May and early June. During this period the temperatures were extremely high, and this probably depressed herbage quality and herbage intake. Secondly, there were two periods in which the milk production reached a local minimum. Since in both cases this phenomenon occurred at the end of a long period with very low rainfall and high temperatures, it may be due to declining quality of the herbage on offer.



Net herbage production

The net pasture yield over the whole grazing season can be estimated from data about animal production using standards for nutrient requirements of grazing cows. Expressed in Dutch feed units (VEM) the total energy requirement  $\text{ha}^{-1}$  for the measured animal performance can be estimated by:

$$3000 G + 460 \text{ FCM} + 50.9 W^{0.75} n \quad (1.2)$$

with:      G = change in liveweight                      (kg  $\text{ha}^{-1}$ )  
             FCM = fat-corrected milk production              (kg  $\text{ha}^{-1}$ )  
             W = average liveweight                              (kg  $\text{cow}^{-1}$ )  
             n = number of cow grazing days              (cow days  $\text{ha}^{-1}$ )

The net pasture yield is the difference between the total energy requirement and the total energy consumption from concentrates (Table 1.6).

Based on chemical analyses it is estimated that the nutritive value of the consumed grass ranged from about 1000 VEM  $\text{kg}^{-1}$  DM in early summer to about 900 VEM  $\text{kg}^{-1}$  DM in midsummer and autumn. Using these values it follows that the total intake was about 10500 kg DM  $\text{ha}^{-1}$ . This corresponds to an average daily herbage intake of 14.7 kg DM  $\text{cow}^{-1}$ .

The seasonal pattern of herbage production in the continuously grazed paddock can also be derived from the animal data. During periods when there is no net change in sward height, net herbage production equals herbage intake per ha. Seven such periods of one week or longer were selected. The average daily net herbage production over these periods is presented in Table 1.7, column 4, together with the average radiation (column 2) and temperature (column 3). During the first experimental month net

Table 1.6. Experiment 2. Calculation of the net pasture yield in  $\text{kVEM ha}^{-1}$

	Conversion factor	$\text{kVEM ha}^{-1}$
Maintenance (715 cow d $\text{ha}^{-1}$ )	5.78 $\text{kVEM cow}^{-1} \text{d}^{-1}$	4133
Milk yield (15647 kg FCM $\text{ha}^{-1}$ )	0.46 $\text{kVEM kg}^{-1}$ FCM	<u>7198</u>
		11331
Concentrates (1430 kg $\text{ha}^{-1}$ )	0.94 $\text{kVEM kg}^{-1}$	<u>1344</u>
Net pasture yield		9987

Table 1.7. Experiment 2. Net herbage production, sward gross assimilation and maintenance respiration during different periods of the season.

Period (number)	Radiation ( $\text{J cm}^{-2} \text{d}^{-1}$ )	Temperature ( $^{\circ}\text{C}$ )	Net herbage production	Sward gross assimilation	Maintenance respiration (above-ground)
1	2	3	4	5	6
7 May - 9 June (1)	1958	15.4	100	622	70
16 June -24 June (2)	1270	14.2	72	441	53
9 July -21 July (3)	2054	20.0	64	465	62
26 July -24 Aug. (4)	1450	17.6	50	343	53
24 Aug. - 7 Sept. (5)	1226	14.6	41	295	44
17 Sept.- 2 Oct. (6)	874	15.1	32	213	44
5 Oct. - 27 Oct. (7)	476	11.2	23	138	35

Units for columns 5 and 6:  $\text{kg CO}_2 \text{ ha}^{-1} \text{d}^{-1}$ , units for column 4:  $\text{kg DM ha}^{-1} \text{d}^{-1}$ .

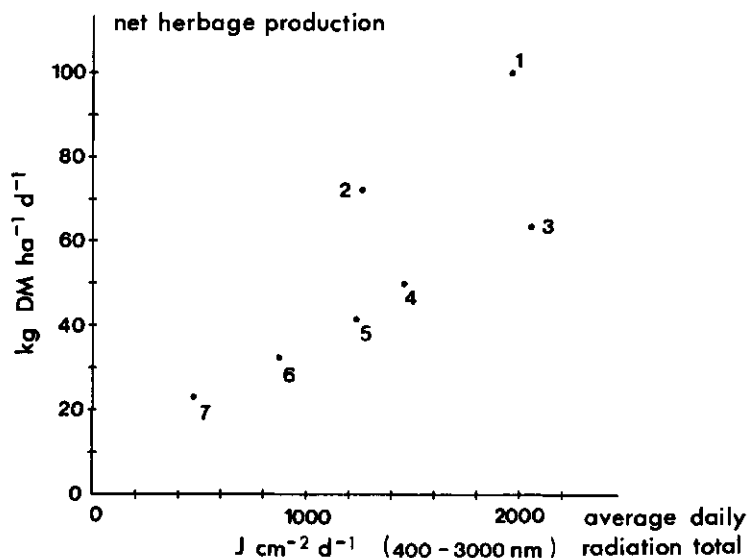


Fig. 1.10. Experiment 2. Relationship between average daily radiation and net herbage production. For periods see Table 1.7.

herbage production amounted to 100 kg DM ha<sup>-1</sup> d<sup>-1</sup>; this rate gradually decreased to about 25 kg DM ha<sup>-1</sup> d<sup>-1</sup> in October. The relation between radiation and net herbage production is shown in Fig. 1.10. During periods 1 and 2 the conversion of incoming solar energy was apparently more efficient than in the other periods. To explain this phenomenon the carbon balance of the paddock will be analysed in more detail below.

Table 1.8. Experiment 2. Gross assimilation at 500 W m<sup>-2</sup> (400-3000 nm) of areas with sward heights of 6 and 10 cm at different times of the season.

Date	Gross assimilation (g CO <sub>2</sub> m <sup>-2</sup> h <sup>-1</sup> )	
	6 cm	10 cm
11 June	4.7	4.7
26 July	3.0	4.7
2 September	3.7	4.1
10 October	3.4	4.1

### Gross CO<sub>2</sub> assimilation

The sward gross assimilation at four dates at the same radiant flux density and at two sward heights is given in Table 1.8.

The assimilatory capacity of the short-grazed grass with an average height of 6 cm was much lower on 26 July than on 11 June. No such a decline was observed at a sward height of 10 cm. The cause of this decline cannot be attributed to the leaf area index since all sward areas of Table 1.8 had an LAI of about 2. It was probably the vertical distribution of leaf age classes which depressed the CO<sub>2</sub> assimilation. In July there was very little rainfall, and this may have retarded the growth of young leaves, which are frequently removed in short-grazed areas. When leaf growth is restricted, relatively more light is intercepted by older leaves with lower assimilatory capacities, resulting in a lower assimilation rate in the sward. In areas which are only slightly grazed, most of the incoming light is still intercepted by the youngest leaves, even if leaf growth is reduced. This may explain why the assimilation rates of short and relatively tall grass differed so much at the end of July.

The average daily gross assimilation is calculated for the seven selected periods with no net change in sward height (Table 1.7, column 5). The relation between daily gross assimilation and net herbage production is much better than that between radiation and net herbage production. This is due to the differences in the efficiency of solar energy utilization, as described above.

### Maintenance respiration

For carbon balance studies it is desired to consider the pool of assimilates which is derived from gross assimilation minus maintenance respiration, since these carbohydrates can be used for structural growth above ground (De Wit et al., 1979). Unfortunately, the losses by maintenance processes in plants are still insufficiently quantified (Penning de Vries and Van Laar, 1982).

In the present study, respiration rates were measured throughout the night. Based on the few available data on the contribution of maintenance and growth respiration to the total respiratory losses, it was estimated that at the end of the night, maintenance respiration was about half of the measured respiration rate (Chapter 3). Using this estimation and a Q<sub>10</sub>-value of 2.0 (Penning de Vries and Van Laar, 1982), the average daily losses by above-ground maintenance respiration were calculated for the seven periods (Table 1.7, column 6).

### Cumulative gross assimilation

The sward height of the pasture was approximately the same on 15 April as on 27 October, the last grazing day. Between these two dates cumulative gross assimilation amounted to  $77230 \text{ kg CO}_2 \text{ ha}^{-1}$ . This sum is a little higher than the accumulated gross assimilation in treatment C-HN of experiment 1 (Table 1.5), but in all probability this must be attributed to the longer calculation period in experiment 2.

### 1.5 Discussion

The present study was set up to evaluate  $\text{CO}_2$  assimilation, and herbage and animal production, under continuous and rotational grazing with cattle. Although the data collected from experiment 1 do not permit statistical analysis it appears that, with the same number of grazing days cumulative gross assimilation was higher under rotational grazing (Table 1.5). This difference in assimilatory performance between rotational and continuous grazing was greater at high than at low nitrogen levels. The reason may have been a difference in the average LAI, a difference in assimilatory activity per unit LAI, or a combination of both. This is evaluated below for high nitrogen.

By combination of Figs. 1.3b, 1.4 and 1.6 the relationship between LAI and gross assimilation in Fig. 1.11 is obtained. In May and August the gross assimilation rate under continuous grazing equalled the average value under rotational grazing at an LAI of 2.5. This was also found for the other grazing cycles. With the exception of the first rotational grazing cycle (May), assimilation at a given LAI was lower during grazing than during subsequent regrowth. This was caused by differences in the assimilatory potential of the leaves, owing to differences in the average leaf age. The reverse pattern observed during the first grazing cycle was due probably to the persistence of the high leaf assimilatory capacity up to and including the grazing period. This is characteristic of the early spring growth (Woledge and Leafe, 1976). Throughout the grazing season the LAI in treatment C-HN was 2.5 on about 80% of the area. The rest of the area consisted of uneaten grass around dung patches, with a sward height of 12 cm or more. In May, the LAI of these areas was about 5.0 and the gross assimilation rate was equal to that measured under rotational grazing at the same LAI. In August the LAI of the patches with uneaten grass was about 4.0, and at this LAI the gross

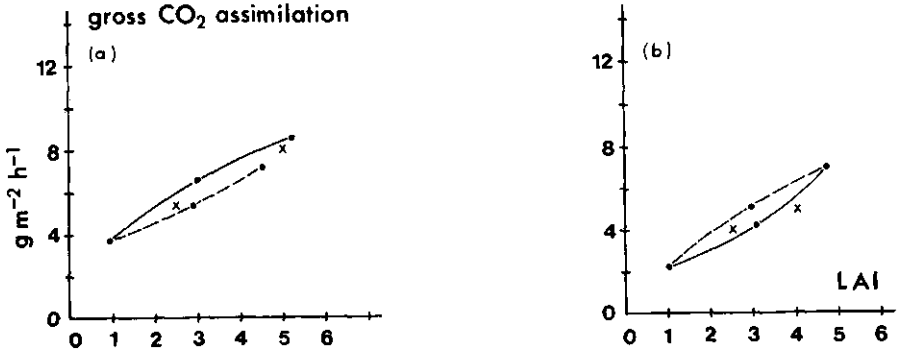


Fig. 1.11. Experiment 1. Relationship between LAI and gross assimilation at  $600 \text{ W m}^{-2}$  (400-3000 nm) under rotational grazing (—) with subsequent regrowth (---) and continuous grazing (x). Measurements are from high nitrogen treatments. (a) May; (b) August.

assimilation rate was higher in the rotationally grazed paddocks. (This is of less importance because of the relatively small area with refused grass). These observations indicate that the small differences in cumulative gross assimilation between the two grazing systems were not due to differences in assimilatory activity per leaf area, so they may be attributed to a difference

Table 1.9. The effect of management on cumulative gross assimilation and herbage intake. Treatments: H - hard continuously-grazed sward (LAI=1.0); L - leniently continuously-grazed sward (LAI=3.0); L/H - continuously-grazed sward in which LAI fluctuated between 1.0 and 3.0; R - rotationally grazed sward with a fixed rotation of 21 days growth followed by 3 days grazing; 4-CUT = sward cut four times. Cumulative gross assimilation is expressed in relative figures (rotational grazing = 100) (from Parsons et al., 1983a,b,c).

Treatment	relative gross assimilation	average stocking density (sheep $\text{ha}^{-1}$ )	herbage intake (kg DM $\text{ha}^{-1} \text{yr}^{-1}$ )
H	63	47	9600
L	95	24	6900
L/H	87	50	not measured
R	100	45	9800
4-CUT	105	-	-

in the average LAI over the season. But this has not been analysed further. Parsons et al. (1983 a,b,c) also compared continuous grazing with rotational grazing, using sheep. Three grazing pressures were applied. In the hard-grazed paddock an LAI of about 1 was maintained, in the leniently-grazed paddock the LAI was close to 3 and in the intermediate-grazed paddock the LAI fluctuated between 1 and 3. The results are summarized in Table 1.9.

As judged by the sward dry weights, which are not given here, the intermediate-grazed paddock is comparable with treatment C-HN of experiment 1. This is in accordance with the cumulative gross assimilation, which is also about 10% lower than under rotational grazing (Table 1.5).

#### 1.5.1 Sward height and herbage production under continuous grazing

In the present study an attempt was made to maintain a mean sward height of about 8 cm under continuous grazing, as recommended by Ernst et al. (1980). The question is whether this is really the optimum height for continuous grazing with cattle. There has been some British' research on the relation between sward height and net herbage production, but nearly all of these trials were carried out with sheep. For instance, Parsons et al. (1983 a, b, c) found that, despite lower rates of gross assimilation, the total intake by sheep was greater in the hard-grazed treatment than in the leniently-grazed treatment (Table 1.9). They do not present the sward heights, but judging from the sward dry weights this was not more than a few centimeters in the hard-grazed treatment. Such a sward height is not relevant for cattle grazing, as the intake per head would be too far below its maximum (Ernst et al., 1980). Besides, from the work of Arosteguy et al. (1983) it is known that at a height of about 3 cm the net herbage production (i.e. gross herbage production minus senescence) is about one-third lower in cattle-grazed swards than in sheep-grazed swards.

The effect of sward height on net herbage production was investigated further by Bircham and Hodgson (1983) and Grant et al. (1983). In both experiments it was found that under continuous defoliation, with sheep, the rate of net herbage production was remarkably stable across a range of sward heights from 2.5 to 7 cm. Hence, there will be no benefit in terms of net herbage production per area at sward heights that are maintained lower than 7 cm. Despite these findings, Bircham and Hodgson (1983) suggested

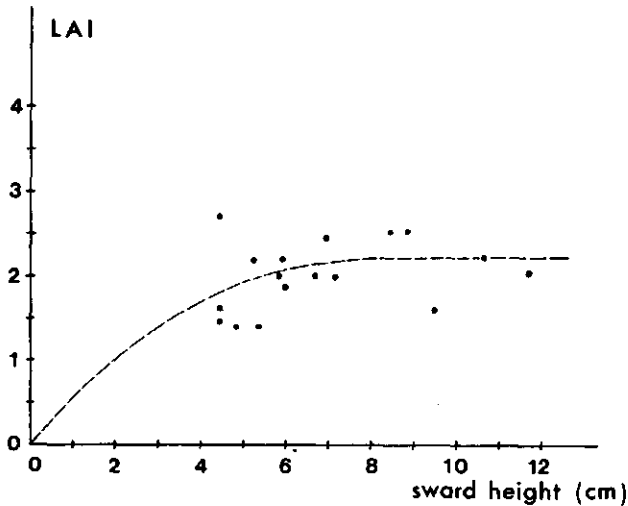


Fig. 1.12. Experiments 1 and 2. Relationship between sward height and LAI under continuous grazing in regularly grazed areas.

that under continuous grazing there exists an almost linear relationship between sward height (range 1-9 cm) and LAI (range 1-5). This suggestion is in contrast with the findings of the present study (Fig. 1.12). It appears that the LAI of regularly grazed areas hardly increases with sward height between 4 and 11 cm. This is supported also by the assimilation measurements (not presented here), which showed no increase within this range. Only the measurements made during the period of prolonged drought in experiment 2 disagree with this figure. The morphological background of this adaptation of LAI was examined by Jackson (1974). He showed that harvesting at a constant height (3,6,9 or 12 cm) effected a rise in the level of the lowest green leaf towards harvesting height. The result was that after a few cuts the total dry weight of green leaf was the same at all sward heights. Under-grazing of a sward under continuous grazing, leading to mean sward heights in excess of 8 cm, may have adverse effects on herbage production and sward quality (Ernst et al., 1980). Under-grazed areas are characterised by a lower tiller density and by the production of aerial tillers. Subsequent defoliation can remove these tillers, further reducing tiller density and in extreme cases leaving open patches in the pasture. Moreover, the net herbage production in the lightly-grazed areas is low, especially late in the season. In the autumn, the gross assimilation rate in these areas is no



Table 1.10. Experiment 2. Harvest-efficiency ( $\text{kg DM kg}^{-1} \text{CH}_2\text{O}$ ) under continuous grazing during different periods of the season. For periods see Table 1.7.

Period	harvest-efficiency
1	0.27
2	0.27
3	0.23
4	0.25
5	0.24
6	0.28
7	0.33

higher than that in the short-grazed areas (Fig. 1.6), whereas the losses by respiration and senescence are higher because of the greater herbage mass. Thus, all things considered, it appears that a mean sward height of 7 to 8 cm is the optimum for continuous grazing with cattle.

#### 1.5.2 Harvest-efficiency under continuous grazing

The 'efficiency of harvest' is defined by Parsons et al. (1983c) as the fraction of gross assimilation harvested as animal intake. Using this definition, its value is dependent on the temperature. This is because the losses via maintenance respiration are controlled by the temperature. It is better therefore to relate the intake to the gross assimilation minus maintenance respiration of the above-ground herbage mass. The harvest-efficiency, expressed in this way, has been calculated for the seven periods of experiment 2, when no net change in mean sward height occurred (Table 1.10).

The average harvest-efficiency over the first six periods was 25%, with only slight variation. In period 7 (5-27 October) the harvest-efficiency was above this average value. This may have been caused by a decrease in the proportion of carbohydrates invested in root and stubble as a result of the very low light intensities during October 1982 (compare Parsons and Robson, 1981). However, it may also have been a consequence of the very low level of production, since the value of the harvest-efficiency is then very sensitive to changes in the estimates of herbage intake, gross assimilation and maintenance respiration.

Table 1.10 suggests that the low net herbage production during the period of prolonged drought in July and August (periods 3 and 4) was not caused by any change in the pattern of assimilate distribution. This is in contrast with the assumption made by Van Keulen (1982), that water stress reduces shoot growth more than root growth. Studies by Wardlaw (1969) and Gales (1979) on the influence of water stress on the distribution of assimilates were also unable to establish a shift.

### 1.5.3 Carbon balance under continuous grazing

Some of the pattern of flow of carbon under continuous grazing is shown in Table 1.7 for experiment 2. This figure could be completed if the losses by shoot growth respiration and the partition of assimilates to root were known. The uneaten shoot is then the remainder in the carbon balance. The losses due to growth respiration can be estimated by assuming that 0.7 g of plant dry matter with 40% C is synthesized from 1 g of carbohydrates. The production of 1 g carbon in plant dry matter then results in a loss of 0.33 g carbon as growth respiration.

The proportion of gross  $\text{CO}_2$  uptake consumed in the growth and respiration of root is very difficult to measure. Parsons et al. (1983b) used radioactive  $^{14}\text{CO}_2$  to study assimilate partitioning. They assumed that 48 hours after labelling the proportion of the total  $^{14}\text{C}$  content of the whole sward that is present in the roots reflects the proportion of gross  $\text{CO}_2$  uptake consumed in both the growth and respiration of root. This assumption was based on the hypothesis that in the above-ground as well as the below-ground parts one half of the carbon invested is consumed in the respiration of these tissues. There is evidence from the literature (e.g. Overgaard Mogensen, 1977; Hansen, 1978), however, that in the roots of graminous plants the respiration losses exceed the investment in growth.

Parsons et al. (1983b) concluded that under continuous grazing with optimal supply of N about 10% of the gross assimilation was partitioned to the root, irrespective of season. Using this value, it follows that over the year, in the present experiments, not more than about  $5000 \text{ kg CH}_2\text{O ha}^{-1}$  had been translocated to the roots. This seems far too low a figure, since the seasonal root production can be estimated at  $5000 \text{ kg DM yr}^{-1}$ . The underestimation may be due to higher respiration losses than assumed, but also to losses of

Table 1.11. Experiment 2. The carbon balance under continuous grazing between gross assimilation, animal intake and losses of carbon. Relative figures with gross assimilation = 100. For more information about periods see Table 1.7.

	Period	
	7 May - 9 June	17 Sept. - 2 Oct.
Intake	21	19
Uneaten shoot	28	24
Shoot maintenance respiration	11	19
Shoot growth respiration	15	13
Root growth and respiration	<u>25</u>	<u>25</u>
	100	100

<sup>14</sup>C-labelled tissue during washing and to leaching. A more realistic estimate of the proportion of assimilates consumed in the growth and respiration of root, with an optimal supply of nutrients, is 25% (Deinum, pers. comm.). A similar value was also found by Overgaard Mogensen (1977) in field experiments with *Lolium multiflorum*.

The balance between gross assimilation, animal intake and the losses of carbon in two periods of experiment 2 is summarized in Table 1.11. The shoot maintenance respiration in this balance is somewhat higher than given in Table 1.7. This is due to the inclusion of the maintenance respiration of the below-ground shoot, which is based on estimates made by Parsons et al. (1983b).

The most striking feature of the balance in Table 1.11 is the large quantity of assimilates that ends up in shoot tissue that is not eaten, and that will be lost to death in the equilibrium situation. These losses can be decreased by increasing the stocking density, but this action ultimately results in a reduction of herbage intake per animal (Parsons et al., 1983b). It seems, therefore, that the losses via death under continuous grazing cannot be reduced without affecting individual animal performance.

#### 1.5.4 Gross assimilation and net herbage production under both grazing systems

In experiment 1 it was found that at high nitrogen levels the cumulative gross assimilation was 9% lower under continuous grazing than under rotational grazing. From a practical viewpoint, this result should be considered in relation to the net herbage production in both grazing systems. Taking into account that the number of grazing days (Table 1.2), the liveweight gain per animal and the sward height at the end of the grazing season (Fig. 1.3a) were roughly equal in the two systems, there can have been only minor differences in net herbage production. This implies that the efficiency of utilization of the gross assimilation products was higher under continuous grazing. This was caused partly by lower topping losses under continuous grazing, but this effect was relatively small (269 vs. 610 kg DM ha<sup>-1</sup>). A more important factor seems to be the higher maintenance respiration losses under rotational grazing due to the larger amount of standing live dry matter throughout the season (unpublished results). Since it is impossible to calculate the exact amount of these losses, it is estimated that throughout the grazing season the respiration rate was about 20% lower in the continuously stocked sward. This may account for the observed difference in utilization efficiency, as about one third of the gross assimilation products is ultimately lost via respiration processes (Table 1.11; Parsons, 1983b).

#### 1.5.5 Influence of nitrogen on assimilation, partition and growth

The different rates of nitrogen supply in experiment 1 affected gross assimilation per unit leaf area neither under continuous grazing (Fig. 1.7) nor under rotational grazing (Fig. 1.5). The nitrogen deficiency at the low nitrogen supply was thus not so large that it restricted the rate of gross assimilation. The absence of any N-effect may be explained as follows. The nitrogen content of the dry matter above stubble height at the end of a regrowth period was on average 3.5% in the rotational grazing treatment with high nitrogen and 2.6% with low nitrogen. The maximum rate of gross assimilation is positively related to leaf nitrogen percentage (Wilson, 1975), but the initial light use efficiency is virtually unaffected by nitrogen status (Robson and Parsons, 1978). The nitrogen concentrations of the various leaf

layers were not determined in the present study, but there may well have been a gradient of the same extent as was found in wheat by Spiertz and Ellen (1978). At one measuring date they found that at an average nitrogen level in the leaves of 2.8%, the nitrogen concentration in the upper leaf was 3.9%, and that in the lowest leaf 1.6%. In such a crop the assimilation at common radiant flux densities will scarcely be influenced by nitrogen shortage, since the upper leaves contain enough nitrogen and the lower leaves receive little light. Accordingly, in a crop with an average nitrogen content in the leaves and stems (which contain less nitrogen than the leaves) of 2.6%, as in the present treatment R-LN, it is not to be expected that there will be any significant reduction in the gross assimilation per leaf area.

Yet the question remains as to how the herbage production rates could have been depressed to such a large extent in summer and autumn in the swards which received the low nitrogen rate. To understand this it is necessary to look at the sward carbon balance.

The main effect of nitrogen shortage in grass plants is reduction of leaf expansion and concurrent stimulation of root production (Robson and Parsons, 1978). The mature size of individual leaves can be nearly doubled by nitrogen fertilization without a reduction in the number of leaves in the canopy (Wilman and Wright, 1983). Wilman and Mohamed (1981) found that the rate of leaf expansion still increased with applied N towards rates of 500 kg ha<sup>-1</sup> yr<sup>-1</sup>, whereas there was virtually no effect of applied N on the specific leaf area, as in the present investigation (Table 1.4).

These findings indicate that within the range of nitrogen application rates which is of interest for the present study, there is a strong effect on the proportion of assimilates devoted to leaf production. Since the leaf weight ratio was insensitive to applied N (Table 1.4), stem production was also depressed at low nitrogen.

Furthermore, the division of dry matter among the different sward layers is important. Here, it was found in experiment 1 that significantly more dry matter was allocated to the stubble in the low-nitrogen treatments (Table 1.12). Thus, in the swards with low nitrogen less of the shoot produced was accessible to the grazing cattle.

In addition, it should be noted that only about 20% of the assimilated carbon was harvested by the grazing cattle under continuous grazing at high nitrogen (Table 1.11). If, for example, as a consequence of nitrogen shortage

Table 1.12. Experiment 1. Dry matter yields of the above-ground stubble under rotational (sward layer below 3.5 cm) and continuous grazing (sward layer below 4.0 cm). The presented values are averages of the records made in the second half of the grazing season, with standard deviations between brackets.

Treatment	kg DM ha <sup>-1</sup>
C-LN	3850 (396)
C-HN	2855 (114)
R-LN	3025 (325)
R-HN	2613 (220)

10% more assimilates are allocated to root and stubble at the expense of the sward layer above the maintained height, the herbage production in this last fraction will be nearly halved.

#### 1.5.6 Practical implications

From a physiological viewpoint there is no advantage in the adoption of one particular grazing system, so other points, related to farm management, must be considered. It is often claimed that continuously stocked pastures may need less frequent reseeding since their denser swards are more resilient to weed ingress, damage and deterioration (Ernst et al., 1980). A parallel study in the present one-year trials showed that under continuous grazing at high nitrogen the good botanical composition of the pasture in experiment 1 was maintained and the poorer composition of that in experiment 2 was improved. In experiment 2 it was found that during the grazing season the contribution of couch grass (*Elymus repens*) to the total standing dry weight decreased while that of perennial ryegrass (*Lolium perenne*) increased. Another important point is labour input for nitrogen fertilization, fodder conservation, pasture topping and fencing. This is considerably less under continuous grazing than under rotational grazing (Luten and Schlepers, 1981; Ernst et al., 1980).

On the other hand, it should be stressed that continuous grazing requires considerable management skill to maintain pasture and animal in equilibrium with each other (Ernst et al., 1980).

## 2 Simulation of herbage production and herbage intake during a rotational grazing period

### An evaluation of Linehan's formula

#### Abstract

The herbage intake under rotational grazing is often estimated using Linehan's formula (Linehan et al., 1947) which takes into account the herbage production during grazing. In the present study this formula was evaluated by means of dynamic simulation, with measured assimilation-light response curves as the main input. There was a close agreement between the intake figures found using the simulation and Linehan's formula for a common rotational grazing system, i.e. a mean sward height of about 18 cm at the start of a 3 day's grazing period and an average daily herbage allowance between 20 and 25 kg DM cow<sup>-1</sup>d<sup>-1</sup>. This result was obtained when herbage mass was measured above a 4 cm stubble. In other practical situations the agreement was less good. This was mainly because Linehan's formula assumes exponential growth of the sward at all stages of growth. Since this is not correct for a sward in the absence of grazing, a new comprehensive formula is developed using the assumption that at the start of grazing the sward is in the linear growth phase.

Comparisons with the simulation output show that this new formula for estimating herbage intake is valid for all situations of rotational grazing.

#### 2.1 Introduction

In the Netherlands, herbage intake by grazing cattle in a rotational grazing system is generally estimated by the sward-cutting technique, i.e. estimating the amount of herbage before and after a grazing period (Meijs, 1981). If the grazing period is longer than one day, as is common practice in the Netherlands, it is desirable to take into account the herbage production during the grazing period.

To estimate the magnitude of this herbage production, Linehan et al. (1947) developed a formula which was validated by means of a large set of estimates of herbage consumption by livestock. Although this formula is widely used,

only one article has described a validation test (Iwasaki, 1972), in which grazing was simulated by hand-plucking.

In this chapter the problem of estimating herbage intake during rotational grazing is reconsidered by simulating the herbage production during grazing. Since assimilation is one of the main controlling factors, it is calculated not from an assumed leaf assimilation curve, leaf distribution and leaf area index, but from measured assimilation-light response curves of the sward in the presence and absence of grazing. Linehan's formula is discussed, then the simulation program is presented and discussed. The herbage intake calculated with Linehan's formula is compared with that obtained from the simulation program for different sward growth stages. The influence of radiation level is also studied. Although it appears that under the most common situation of rotational grazing the differences are slight, the agreement is less good in some other situations that occur in practice. A new comprehensive formula is therefore developed and tested; this can be seen as an improved version of Linehan's equation.

## 2.2 Linehan's formula

Linehan et al. (1947) assumed that at every moment of a rotational grazing period both the rate of consumption of herbage and the rate of herbage production are proportional to the quantity of uneaten herbage at that moment. Thus, they arrived at the following equation for the consumption of herbage:

$$C = (Y_s - Y_e) \frac{\ln (Y_u/Y_e)}{\ln (Y_s/Y_e)} \quad (2.1)$$

in which

$C$  is herbage consumed ( $\text{kg DM ha}^{-1}$ );

$Y_s$  is herbage mass at start of the grazing period ( $\text{kg DM ha}^{-1}$ );

$Y_e$  is herbage mass at the end of the grazing period ( $\text{kg DM ha}^{-1}$ );

$Y_u$  is herbage mass at the end of the grazing period in an ungrazed area ( $\text{kg DM ha}^{-1}$ ).

Herbage mass refers to the sward layer above a cutting height of approximately 4 cm (Meijs, 1981). The herbage mass  $Y_u$  can be measured in a fen-



ced part of the area to be grazed. The difference between  $Y_u$  and  $Y_s$  is sometimes termed the "undisturbed accumulation" (Meijs, 1981).

The herbage production in the grazed paddock can be expressed as a fraction of this "undisturbed accumulation". In the case of Linehan's formula this is:

$$f_L = \frac{(Y_s - Y_e)}{(Y_u - Y_s)} \left\{ \frac{\ln(Y_u/Y_e)}{\ln(Y_s/Y_e)} - 1 \right\} \quad (2.2)$$

Accordingly:

$$C = (Y_s - Y_e) + f_L (Y_u - Y_s) \quad (2.3)$$

where  $f_L$  is Linehan's accumulation factor.

In fact, Linehan's formula is based on four simplifying assumptions about the rate of herbage production and the rate of herbage intake. These are:

- Growth of the ungrazed sward at all stages of growth is exponential. It is now known that this assumption is not correct. Already in the 1950's it had been found that during regrowth the rate of herbage production increases more or less exponentially until complete light interception is approached, and that thereafter this rate is almost constant (Brougham, 1956).
- The rate of herbage production during grazing is proportional to the quantity of uneaten herbage above cutting height. Although for the greater part of the grazing period there is a nearly closed canopy, this is more or less correct because the leaves with the greatest assimilatory capacity are grazed first.
- There is no net contribution of the stubble to the production capacity since only the herbage yield above cutting height is taken into account. In Linehan's experiments the cutting height was between 3 and 4 cm. In reality the assimilatory capacity of the stubble below this cutting height can be considerable, especially in spring, and its carbon balance may be positive.
- There is a negative exponential intake pattern over the grazing period. This assumption seems reasonable, except at extreme high levels of herbage allowance.

These four assumptions are further evaluated in this chapter.

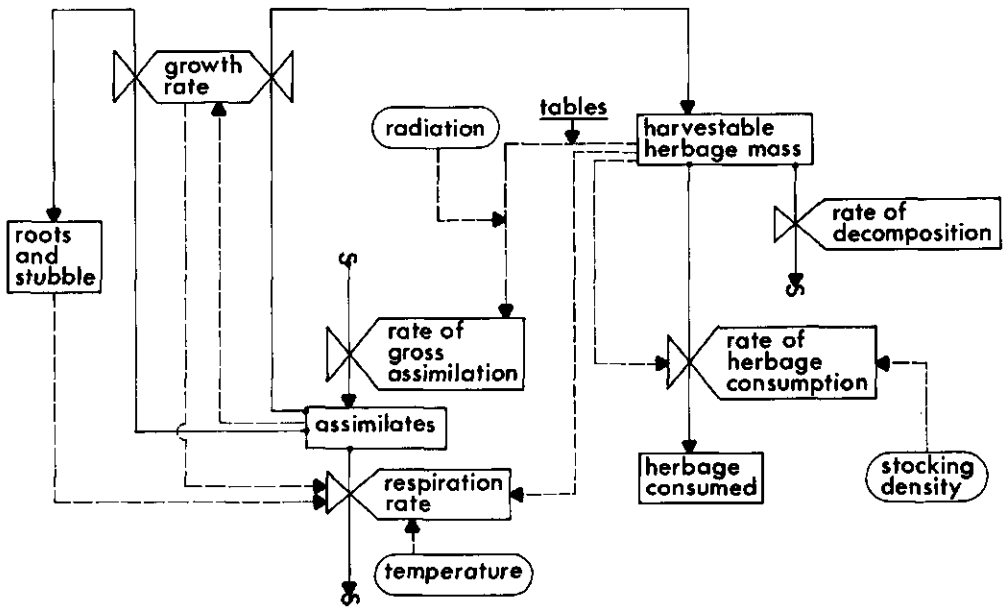


Fig. 2.1. Relational diagram of the simulation model for the production and consumption of herbage during grazing. Rectangles represent state variables, valves represent rates and ellipses are driving variables.

### 2.3 The model

In Fig. 2.1 is shown a relational diagram of the simulation model for the production and consumption of herbage during a rotational grazing period. It is a dynamic, dry matter-budget model with the state variables "harvestable herbage mass" and "herbage consumed" being expressed in units of dry matter per unit ground area ( $\text{kg DM ha}^{-1}$ ). The model is written in the language CSMP, and the rectilinear method of integration is used. The time interval for the calculations is set at 1 hour, which is short enough to cover the diurnal pattern of temperature and radiant flux density in a satisfactory way.

The average daily temperature was set at 15 °C with a diurnal amplitude of 10 °C. Calculations were carried out for eight radiation levels (equidistant steps between and including 20% and 90% of maximum radiation). The daily pattern of maximum radiant flux density is calculated by means of the procedure described by De Wit et al. (1978) and assumed to be the same for all radiation levels.

### 2.3.1 Grazing periods and gross assimilation

The rate of gross assimilation at any moment of a grazing period is calculated using sets of assimilation-light response curves, which were measured at varying amounts of herbage in rotationally grazed paddocks fertilized with  $500 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ . These sets are used in such a way that in the simulation program the herbage mass controls the assimilatory capacity of the sward. The experimental plots, grazing management, herbage and assimilation measurements are described in Chapter 1. From this experiment the results of the first and fifth grazing periods were taken (spring and summer swards respectively, see Table 2.1). During both periods the daily global radiation total was about  $2750 \text{ J cm}^{-2} \text{ d}^{-1}$  for a standard clear sky (Goudriaan and Van Laar, 1978).

In both swards the mean sward height at the onset of grazing was around 18 cm (Table 2.1). This is often assumed to be the optimum height for rotational grazing. The corresponding yields are high compared with values reported elsewhere for that sward height. For instance, at a sward height of 18 cm Meijs (1981) found on average  $2000 \text{ kg DM ha}^{-1}$  above a 4 cm stubble, irrespective of season. These differences in herbage mass density, i.e. kg DM per cm herbage, must be attributed to tiller density. In the spring sward the tiller density was extremely high (about  $20.000 \text{ tillers m}^{-2}$ ). This resulted in the very high herbage mass density. In the summer sward the tiller density had decreased to about  $10.000 \text{ tillers m}^{-2}$ . This is a more common density in rotationally grazed paddocks.

The assimilation-light response curves which were used in the simulation model are shown in Fig. 2.2. The curves concern ungrazed, partly-grazed and completely-grazed herbage. These grazing stages refer to the fractions of the initial herbage mass above a 4 cm stubble removed by grazing cattle,

Table 2.1. Description of the swards at the start of grazing.

Grazing period	Sward height (cm)	LAI	Herbage mass above a 4 cm stubble ( $\text{kg DM ha}^{-1}$ )
April/May (spring sward)	17.1	5.0	3105
August (summer sward)	19.1	4.5	2490



which are quantified in the subscript to Fig. 2.2. For intermediate values of the herbage mass the required curves are obtained via linear interpolation. This procedure is justified by measurements (Lantinga, unpublished data). A similar approximately linear relationship between herbage mass and assimilation rate under grazing has also been reported by King et al. (1984). The reason is that with the onset of grazing the leaves with the highest assimilation potential are removed first, thus causing a greater decrease in gross assimilation than would be expected on the basis of light interception. The choice of a reference herbage height of 4 cm is not fortuitous; this is the average cutting height of the motor scythes often used in grassland research.

Fig. 2.2 shows that, especially in the spring sward, the stubble below this cutting height has some assimilatory capacity. However, this capacity does not reflect the large amount of herbage present here. In normally treated, rotationally grazed grassland, this sward layer contains about 3000 kg DM ha<sup>-1</sup> (Chapter 1). The amount of green leaves is very small, however, especially in autumn, and moreover, these leaves and the sheaths show little activity.

For the construction of the curves in Fig. 2.2, only measurements collected under a clear sky with about 90% of maximum radiation were used. At lower relative radiation levels the approach of the saturation level with increasing radiant flux density is faster, owing to the higher proportion of diffuse radiation in the incoming light (Goudriaan, 1977). This effect is corrected for by the multiplication factors of Table 2.2, which are experimentally and theoretically justified in another publication (Chapter 4). Table 2.2 holds for an LAI of 5. At lower values of the LAI the required multiplication factor is somewhat lower, but the differences are slight. For reasons of simplicity only one correction table is used.

### 2.3.2 Respiration and growth

Respiration includes maintenance and growth components. The losses due to maintenance respiration are set at 0.03 g glucose g<sup>-1</sup> live dry biomass at 25 °C with a Q<sub>10</sub>-value of 2.0 (Penning de Vries and Van Laar, 1982). For the conversion of primary assimilates into structural material an average conversion factor of 0.7 g g<sup>-1</sup> is used (Penning de Vries and Van Laar, 1982).

In the model it is assumed that all, and only, current assimilates are used for maintenance and growth purposes. This assumption is based on observations made by Grant et al. (1981) in grazed and cut *Lolium perenne* swards. They found that in swards which were grazed for 12 d-periods in summer and autumn, the level of carbohydrate reserves showed a sharp decline *after* the end of the grazing period. In the cutting experiment it was observed that it took more than two days before the carbohydrate concentration in the tiller bases started to decline.

### 2.3.3 Distribution of assimilates

Growth is divided among two biomass fractions: harvestable crop, and stubble and roots (Fig. 2.1). The stubble is the shoot layer below a sward height of 4 cm.

Very little is known at present about the influence of the gradual herbage removal by grazing cattle on the distribution of assimilates during a rotational grazing period of a few days.

St-Pierre and Wright (1972) working with *Phleum pratense*, found only minor effects on assimilate distribution 24 hours after defoliation. Ryle and Powell (1975), by contrast, found that after defoliation the proportion of labelled assimilates translocated to meristematic leaf tissue of unculm barley increased immediately at the expense of the allocation to the roots. But since most of the meristematic leaf tissue (shoot apex plus leaf primordia and unemerged leaves) is located in the stubble, such a change in the distribution pattern has no important influence on the carbon balance according to Fig. 2.1. It is assumed therefore, that in both ungrazed and grazed herbage a constant proportion of the assimilates derived from gross assimilation minus maintenance respiration of the above-ground material is incorporated into the harvestable sward layer. This proportion is set at 70% for the spring sward and at 60% for the summer sward (Lantinga, in prep.). The remainder is used below ground and in the stubble.

### 2.3.4 Death of plant tissue

In a grass sward there are on average three to four living leaves per tiller (Alberda and Sibma, 1968; Sheehy et al., 1979). Thus the production of a new leaf is generally balanced by the death of an old one. In addition, a small part of the tiller population dies every day. A certain part of this dead plant material accumulates in the harvestable sward layer and eventually decomposes. In the model the rate of disappearance of dead plant tissue from the harvestable sward layer, as a result of decomposition, is set at 50 kg DM ha<sup>-1</sup> d<sup>-1</sup> (Sheehy et al., 1979).

### 2.3.5 Herbage intake

The rate of herbage intake at any time of the grazing period is calculated using the relationship between average herbage allowance and average herbage consumption as found by Meijs (1983) for a rotational grazing period of 3 days with an additional daily intake of 1 kg of concentrate-supplement per cow. This relationship can be described with the formula of Zemmeling (1980):

$$I = I_m \left\{ 1 - e^{-\left(\frac{A}{I_m}\right)h} \right\} 1/h \quad (2.4)$$

in which

$I$  is average daily herbage intake (kg DM cow<sup>-1</sup> d<sup>-1</sup>);

$I_m$  is the maximum daily herbage intake (kg DM cow<sup>-1</sup> d<sup>-1</sup>);

$A$  is average daily herbage allowance (kg DM cow<sup>-1</sup> d<sup>-1</sup>) defined as the herbage mass at the start of grazing, plus the amount of herbage accumulated during the grazing period (kg DM ha<sup>-1</sup>), divided by the number of cows per hectare and by the length of the grazing period;

$p$  is the fraction of herbage allowance which can be considered consumable;

$h$  is a shape parameter.

It was found by Meijs (1981) that  $p = 1$  on aftermath for a cutting height of 4.5 cm. This value is also used here in the simulation model, where the assumed cutting height is only slightly lower (4 cm). The maximum daily her-

bage intake ( $I_m$ ) is set at  $18 \text{ kg DM cow}^{-1} \text{ d}^{-1}$  (Van der Honing, pers. comm.). The best fit was then obtained by setting  $h$  at a value of 1.23. The resulting relation is given in Fig. 2.3.

In the model it is assumed that Eq. (2.4) holds throughout the grazing period. The pattern of herbage intake is then calculated as follows. At the start of the grazing period the (average) rate of herbage intake per cow is  $I_m$ . This rate is realized over the chosen time interval of 1 hour. Together with the number of cows per hectare and the calculated rate of herbage production over the same time interval, this results in a new value of the herbage mass in the grazed area. All rates are then recalculated. For the calculation of the rate of herbage intake, the level of herbage allowance ( $A$ ) is required. This is obtained following the definition for  $A$  in Eq. (2.4) for the duration of grazing so far. This gives a new value for the average rate of herbage intake so far. The instantaneous rate of herbage intake is calculated by comparing this value with the value one time interval earlier. This procedure is repeated until the end of the grazing cycle.

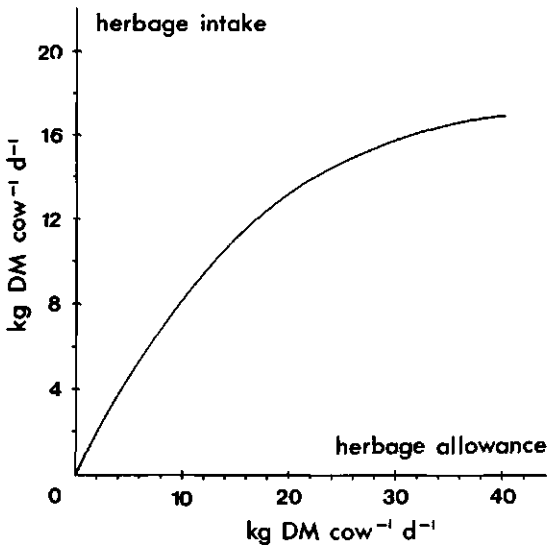


Fig. 2.3. Relationship between daily herbage allowance and daily herbage intake according to Eq. (2.4) with the parameter values given in the text.



In the model it is assumed that grazing takes place 24 hours per day. This simplified approach is permissible, since it was found that the ultimate difference with more realistic grazing patterns, e.g. 8 hours per day spread over 24 hours, was very small.

### 2.3.6 Harvestable herbage production

As stated above, all, and only, current assimilates are assumed to be used for maintenance and growth. For simple simulation approaches, the rate of harvestable herbage production is then adequately defined as:

$$HP = (P_g - M) * EC * F - DR \quad (2.5)$$

where

HP is the rate of harvestable herbage production (kg DM ha<sup>-1</sup> h<sup>-1</sup>);

P<sub>g</sub> is the rate of gross assimilation (kg CH<sub>2</sub>O ha<sup>-1</sup> h<sup>-1</sup>);

M is the maintenance respiration of the above-ground material (kg CH<sub>2</sub>O ha<sup>-1</sup> h<sup>-1</sup>);

EC is the efficiency of conversion of assimilates into structural material (kg DM kg<sup>-1</sup> CH<sub>2</sub>O);

F is a distribution factor for the accumulated dry matter;

DR is the decomposition rate of the harvestable shoots (kg DM ha<sup>-1</sup> h<sup>-1</sup>).

Eq. (2.5) was proposed by Van Keulen (1976) as a simple method to calculate the potential crop production with time steps of one day or more. However, it can also be used in calculation procedures with shorter time steps without affecting the daily total of accumulated dry matter.

## 2.4 Results and discussion

Calculations were performed for a rotational grazing period of 3 days and a range of average herbage allowances between 10 and 50 kg DM cow<sup>-1</sup> d<sup>-1</sup>. In order to compare the simulation approach with Linehan's formula the values for herbage mass used in this formula were taken from the results of the simulation.

#### 2.4.1 Undisturbed herbage production

The simulated rates of undisturbed herbage production in spring and summer were approximately linearly dependent on time. This was because the assimilatory capacity of the ungrazed sward remained unchanged during the calculation periods.

In both periods it was found that the relation between the daily radiation total and the undisturbed herbage production was almost linear up to a relative radiation level of 0.5, and levelled off between this level and 0.6 (Fig. 2.4). At higher relative radiation levels the rates were almost constant. This must be ascribed to the influence of the changing composition of the incoming light on crop gross assimilation. Clearly, in the range of increasing daily radiation totals above a relative radiation level of 0.6, the effect of the increase in the amount of direct radiation is offset by the (smaller) decrease in the amount of diffuse radiation, which is used in a much more efficient way by the sward (see Table 2.2).

#### 2.4.2 Pattern of herbage intake

In one run of the model, in which the rate of herbage production was set at zero, the pattern of herbage intake over the grazing period was studied. This was done for three levels of average herbage allowance: 13.3, 22.2 and 33.3 kg DM cow<sup>-1</sup> d<sup>-1</sup>. The results are shown in Fig. 2.5, where the simulated pattern is compared with the negative exponential pattern according to Linehan for these average allowance levels. It can be concluded that the differences between the two intake functions are so small that only minor effects on the rate of herbage production during grazing can be expected as a result of using either one or the other function.

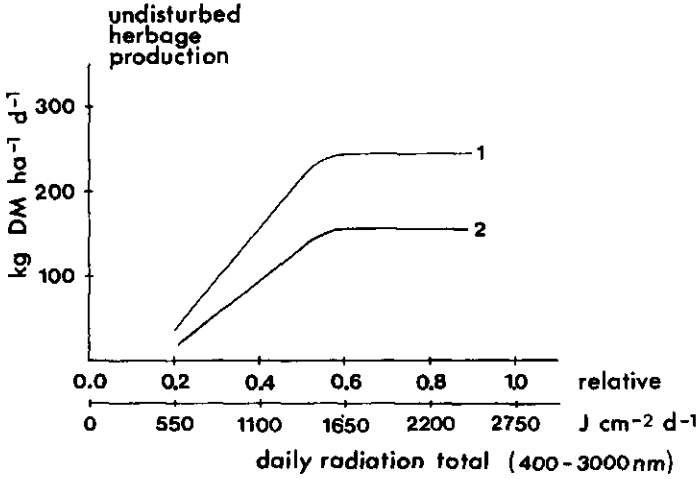


Fig. 2.4. Simulated rate of undisturbed herbage production in spring (1) and summer (2) as a function of the daily radiation total.

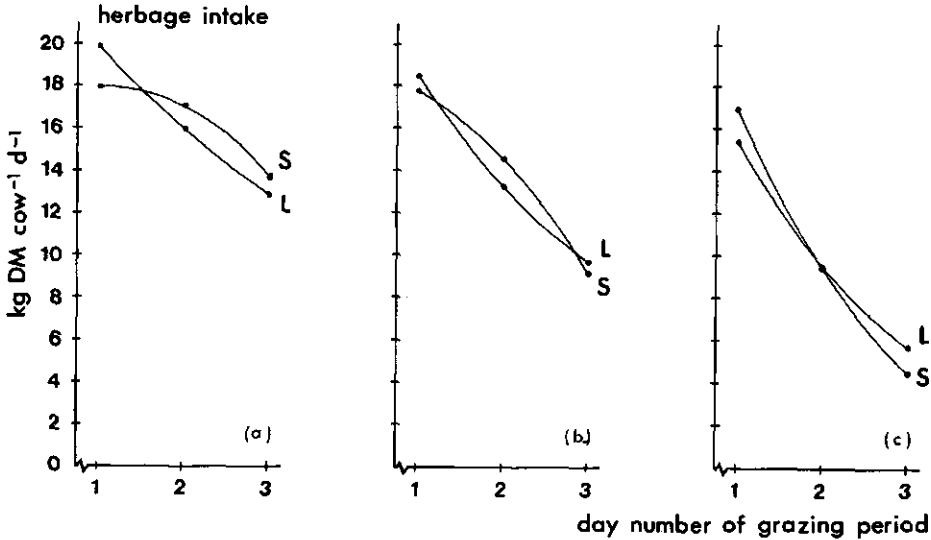


Fig. 2.5. Pattern of herbage intake over the grazing period according to the simulation model (S) and Linehan (L). The rate of herbage intake is given as a daily average. Herbage allowances: 33.3(a), 22.2(b) and 13.3(c) kg DM cow<sup>-1</sup> d<sup>-1</sup>.

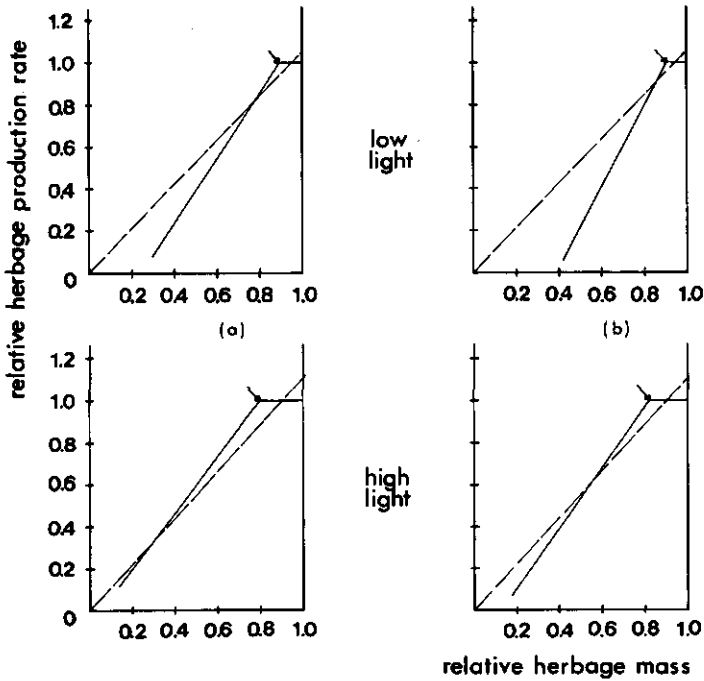


Fig. 2.6. Relationship between the relative herbage mass and the relative herbage production rate during grazing in spring (a) and summer (b) at low light (30% of maximum radiation) and high light (60% of maximum radiation and more). Broken lines: relationship according to Linehan; solid lines: relationship found with the simulation model.

#### 2.4.3 Pattern of herbage production under grazing

In Fig. 2.6 the simulated relative herbage production rates under grazing are shown together with Linehan's values, as a function of the relative herbage mass at a given moment of the grazing period for two radiation levels: 30% ("low light") and 60% ("high light") of maximum radiation. The relative herbage production rate under grazing is here the ratio between the rates of herbage production in grazed and ungrazed swards on the same day.

The relative herbage mass in Fig. 2.6 is defined as the actual herbage mass as a fraction of the herbage mass at the end of the grazing period in the undisturbed situation. In all cases the simulated rates of herbage production at the start of a grazing period (indicated with an arrow) were higher than assumed by Linehan. This discrepancy was caused by the difference in the assumed growth pattern of the undisturbed sward (linear vs. exponential growth). For the grazing cycles of the present study the discrepancies were only slight, but it will be clear that these increase with the difference between the herbage mass at the start of grazing ( $Y_s$ ) and that at the end of grazing in an ungrazed area ( $Y_u$ ).

With low light intensity it was found that, in both periods, soon after the onset of grazing the relative herbage production rate under grazing was lower than that predicted by the Linehan equation. At low relative herbage masses this ratio even became negative. This is because the assimilatory capacity of the sward was not high enough to compensate for the losses due to maintenance respiration and decomposition.

With high light intensities the agreement improved. This is an interesting finding because, especially at high light intensity, the herbage production during grazing can introduce a bias in estimating herbage intake by the sward-cutting technique.

It can be seen from Fig. 2.6 that at both light levels the simulated performance in spring was somewhat better than that in summer. This is caused by the higher assimilatory capacity of the stubble in spring (see Fig. 2.2).

#### 2.4.4 Herbage accumulation factor

In accordance with Eq. (2.3) the herbage accumulation factor is defined as the total herbage production during the grazing period divided by the total herbage production in the absence of grazing. Here, the radiation level had a large effect on the simulated value of the herbage accumulation factor: the lower the radiation level during the period of grazing, the lower was the simulated herbage accumulation factor (Fig. 2.7). This is not surprising, as the relative carbon losses via maintenance respiration and decomposition increase more with decreasing light in a grazed than in an ungrazed sward. In both periods it was found that at high light intensities ( $\geq 60\%$  of maximum radiation) the differences between the simulated value and Linehan's value of the herbage accumulation factor were slight over the range that was studied.

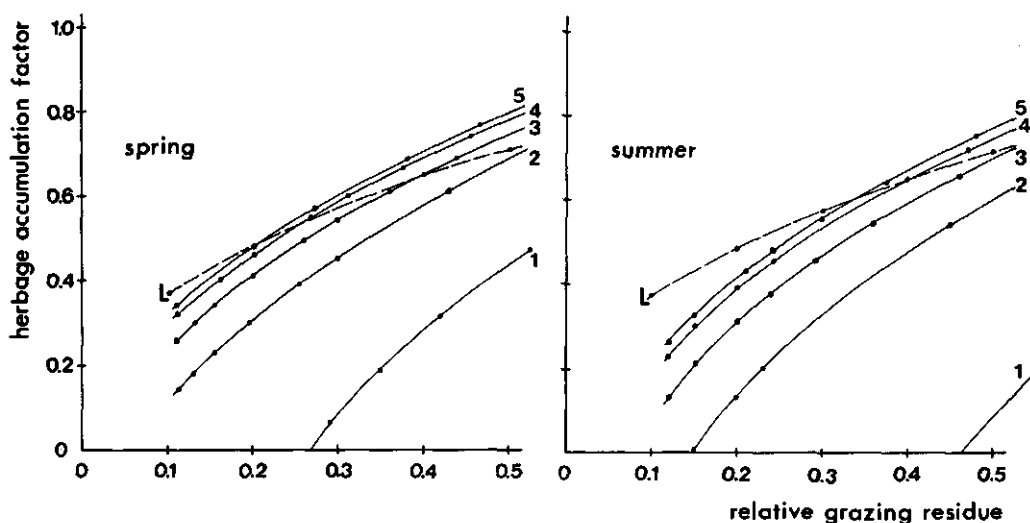


Fig. 2.7. Relationship between the relative grazing residue and the herbage accumulation factor as a function of the radiation level. Relative grazing residue is  $Y/Y_u$  (see Eq. (2.1)).  
 L = Linehan; 1-5 = Simulated at respectively 20, 30, 40, 50 and 60% and more of maximum radiation during the day.

The differences were never greater than about 0.10 units. Fig. 2.7 shows that, at this light level, identical results were obtained with relative herbage masses (at the end of grazing) of 0.2 in spring and of 0.35 in summer. With higher grazing residues the simulated values were slightly greater than those indicated by Linehan. Important effects on the calculated rate of herbage intake are to be expected, especially in this range, because the contribution of the herbage production during grazing to the total intake may be considerable.

#### 2.4.5 Total herbage consumption

The total amount of herbage consumed is calculated as a daily average per cow over the whole grazing period. This average rate of herbage intake is of great interest in the comparison of the two calculation procedures.

It was found that at high light intensities the differences between the results of the simulation model and Linehan's formula were generally small (Fig. 2.8). At herbage allowance levels of practical significance, i.e. between 20 and 25 kg DM cow<sup>-1</sup> d<sup>-1</sup>, the average level of daily herbage intake is about 14 kg DM cow<sup>-1</sup> d<sup>-1</sup> (Fig. 2.3). It can be seen in Fig. 2.8 that in this situation the simulation model and Linehan's formula agree very closely. According to Fig. 2.7, differences of any importance at this light level are to be expected only at very low and very high grazing residues. With very low grazing residues there also appeared to be a close agreement in both periods (Fig. 2.8). This is not surprising, because in case of a very low relative herbage mass at the end of grazing, the contribution of the accumulated herbage during the grazing period to the total amount of consumed herbage is small. For instance, the simulation showed that in both periods at an average herbage intake rate of 8 kg DM cow<sup>-1</sup> d<sup>-1</sup> not more than about 10% of the total intake was derived from additionally grown herbage. In such a situation, of course, a change in the value of the herbage accumulation factor has hardly any effect on the total rate of herbage intake.

Differences increase at higher herbage allowances. For instance, it was found in spring that at an average herbage allowance of 40 kg DM cow<sup>-1</sup> d<sup>-1</sup>, the average herbage intake according to Linehan's formula was 16.2 kg DM cow<sup>-1</sup> d<sup>-1</sup>, whereas the simulation model calculated 16.9 kg DM cow<sup>-1</sup> d<sup>-1</sup>. However, taking into account the accuracy of the estimation of herbage production in the absence of grazing (Meijs, 1981), such differences can be ignored. Moreover, such a level of herbage allowance is not of practical significance in intensive grassland farming.

At low light intensities the differences in herbage intake between the simulation program and Linehan's formula were never greater than a few percent (Lantinga, unpublished data), despite the fact that in both periods the simulated value of the herbage accumulation factor was always lower than that given by Linehan (Fig. 2.7). But since the contribution of the herbage accumulated during the grazing period to the total intake was very small, owing to the low production rates, the calculated herbage intake was only slightly affected.

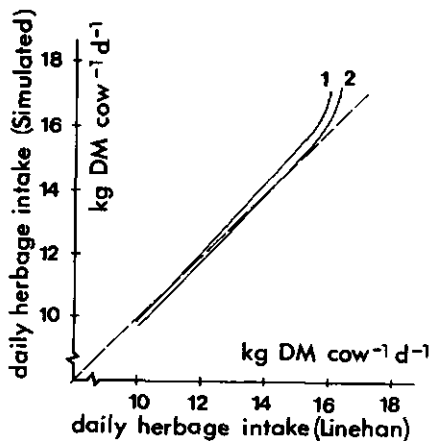


Fig. 2.8. Comparison of the simulated and Linehan's daily herbage intake at high light intensity. 1 = spring; 2 = summer.

#### 2.4.6 Validity in other situations

The above results show that for common rotational grazing systems, irrespective of season and radiation level, there is a close agreement between the herbage intake figures found with Linehan's formula and those yielded by a simulation approach based on measured assimilation-light response curves. A common rotational grazing system is here defined as a system with a grazing period of 3 days, a mean sward height at the start of grazing of about 18 cm and an average herbage allowance between 20 and 25 kg DM cow<sup>-1</sup> d<sup>-1</sup> measured above 4 cm stubble.

The question remains whether Linehan's formula is also of value for longer grazing periods and for other growth stages of the sward.

It was found that the larger the relative difference between the herbage mass at the start of grazing ( $Y_s$ ) and the herbage grown in the absence of grazing during the grazing period ( $Y_u$ ), the less accurately can Linehan's formula describe the herbage production during grazing. This is because of the assumed exponential growth pattern of the ungrazed herbage, which may lead to serious underestimations of the herbage production during grazing, and therefore of the herbage intake. For this reason it is concluded that Linehan's formula may lose its validity for grazing periods longer than 3 days.



Another situation in which the difference between  $Y_s$  and  $Y_u$  can be relatively large, even during short grazing periods, occurs when the herbage mass at the start of grazing is low. To investigate this effect of growth stage, appropriate assimilation-light response curves, derived from measurements done in other paddocks of the same experiment, were used as input in the simulation model. For this purpose grazing cycles were selected with a mean sward height at the start of grazing of about 13 cm. It was found that in that case the value of the simulated herbage accumulation factor at all radiation levels was up to 0.20 units higher than that in the simulated curves in Fig. 2.7. The simulated values of the herbage accumulation factor were highest for young spring swards and for summer swards that were repeatedly grazed at a mean initial sward height of about 13 cm. For these swards rather large differences in the calculated rates of herbage intake occurred. For instance, for a young spring sward it was found that at a herbage allowance of  $29.5 \text{ kg DM cow}^{-1} \text{ d}^{-1}$  the herbage intake according to Linehan's formula was  $13.9 \text{ kg DM cow}^{-1} \text{ d}^{-1}$ , whereas the simulation model predicted  $15.5 \text{ kg DM cow}^{-1} \text{ d}^{-1}$ . Such discrepancies are unacceptable. A new comprehensive formula has therefore been developed to calculate the total herbage consumption correctly even in these conditions.

#### 2.5 A new formula for estimating herbage intake under rotational grazing with the sward-cutting technique

For the derivation of this new formula, which can be seen as an improved version of Linehan's equation (Eq. (2.1)), it is assumed that in the ungrazed situation herbage production proceeds linearly and that at the same time in the grazed situation herbage production is proportional to the amount of herbage that is present, as is illustrated in Fig. 2.9. The difference between these cases is that in the latter, the young leaves with the highest potential assimilation are grazed in preference, as explained earlier. Both assumptions have been confirmed by experiment. In accordance with Linehan it is further assumed that the intake is proportional to the amount of standing herbage. The derivation proceeds now as follows.

If  $kY$  is the rate of herbage production and  $hY$  is the amount of herbage consumed per day when an amount  $Y$  of herbage is available (the dimension of  $k$  and  $h$  is  $\text{day}^{-1}$ ), then the rate of net herbage production is

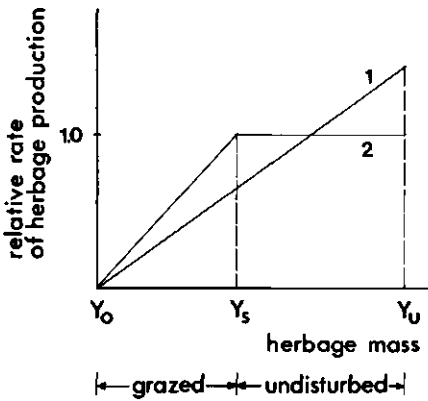


Fig. 2.9. Relationship of the relative rate of herbage production to the herbage mass as assumed by Linehan (1) and as used in the new approach (2). For the definitions of the herbage mass above a 4 cm stubble see Eq. (2.1).

$$\frac{dY}{dt} = (k-h)Y \quad , \quad \text{so} \quad (2.6)$$

$$Y = Y_s e^{(k-h)t} \quad ,$$

in which  $Y_s$  is the amount of herbage at the beginning of grazing.  
If  $b$  is the number of grazing days, then

$$Y_e = Y_s e^{(k-h)b} \quad , \quad (2.7)$$

in which  $Y_e$  is the amount of herbage at the end of the grazing period in the grazed area.

In the ungrazed area, linear growth is assumed. Consequently, the rate of undisturbed herbage production during the period of grazing is

$$\frac{Y_u - Y_s}{b} \quad ,$$

in which  $Y_u$  is the yield after  $b$  days in the undisturbed area.

When  $t=0$ ,  $Y=Y_s$  (Fig. 2.9), so at that moment the rate of herbage production is  $kY_s$ .

Thus

$$k = \frac{Y_u - Y_s}{bY_s} \quad (2.8)$$

Substituting Eq. (2.8) in Eq. (2.7):

$$Y_e = Y_s e^{(\frac{Y_u - Y_s}{bY_s} - h)b},$$

so that

$$h = \frac{Y_u/Y_s - 1 - \ln(Y_e/Y_s)}{b} \quad (2.9)$$

The amount of herbage consumed in  $b$  days is now

$$\begin{aligned} h \int_0^b Y dt &= \frac{Y_u/Y_s - 1 - \ln(Y_e/Y_s)}{b} \int_0^b Y_s e^{(\frac{\ln(Y_e/Y_s)}{b} - h)t} dt \\ &= (Y_s - Y_e) \frac{(Y_u/Y_s - 1 + \ln(Y_s/Y_e))}{\ln(Y_s/Y_e)} \end{aligned} \quad (2.10)$$

If  $Y_u$  and  $Y_s$  differ only slightly, then Eq. (2.10) approaches Linehan's formula (Eq. 2.1), since

$$\lim_{Y_u \rightarrow Y_s} \left\{ \ln(Y_u/Y_s) \right\} = Y_u/Y_s - 1.$$

This can also be seen in Fig. 2.9, since when  $Y_u$  equals  $Y_s$  the relationship between the relative herbage mass and the relative rate of herbage production is the same for both formulae.

The validity of Eq. (2.10) was investigated by comparing its results with the model output in the same way as has been done for Linehan's formula. This was done first for the two swards described in Table 2.1, for which Linehan's formula was satisfactory for herbage allowance levels of practical significance and for short grazing periods. Then two swards were considered for which Linehan's formula underestimated the herbage production: a young spring sward and a summer sward repeatedly grazed at a young stage. In addition, a tall spring sward with elongating stems was considered. Finally, the effect of the length of the grazing period was studied.

The results obtained at high light and a grazing period of 3 days are shown in Fig. 2.10. In all cases the agreement between the herbage intake calculated with Eq. (2.10) and that from the simulation model is excellent. In comparison with Fig. 2.8 it can be concluded that the deviations at high herbage allowances have disappeared. This is due to the better description of the herbage production at the beginning of the grazing period.

It may be concluded therefore that the herbage intake during short grazing periods is estimated well by Eq. (2.10), not only over the range of herbage allowances for which Linehan's formula is of value, but also at the high levels of herbage allowance, where Linehan's formula is less good.

The validity of Eq. (2.10) is compared with that of the formula of Linehan, for grazing periods longer than 3 days, in Table 2.3. The results presented were obtained with the spring sward (see Table 2.1) at high light intensity. For the comparison, grazing periods were considered of 3 and 7 days, respectively. In both cases the average level of herbage allowance was  $32.5 \text{ kg DM cow}^{-1} \text{ d}^{-1}$ .

As was to be expected, Linehan's formula led to a markedly lower value of the herbage intake for the 7 days' grazing period than was found with the simulation model. The new equation, however, yielded herbage intake figures which were very close to the simulated values.

The same was found for the other swards of Fig. 2.10, and at lower light levels (data not presented). Clearly, even for long grazing periods the validity of Eq. (2.10) for estimation of the herbage production during grazing is very good.

We can thus conclude that Eq. (2.10) is to be preferred to Linehan's formula for estimation of the herbage intake under rotational grazing using the sward-cutting technique.

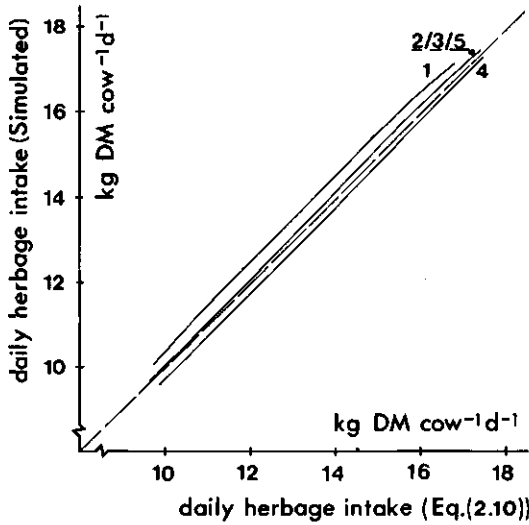


Fig. 2.10. Comparison of the daily herbage intake at high light calculated with the simulation program and Eq. (2.10).

Curve	Sward conditions at the onset of grazing		
	Stage	Sward height (cm)	Herbage mass above a 4 cm stubble (kg DM ha <sup>-1</sup> )
1	Spring	13.7	2000 <sup>*)</sup>
2	Spring	17.1	3105
3	Spring	23.5	3522
4	Summer	19.1	2490
5	Summer	12.1	1160

<sup>\*)</sup> Estimated value.

Table 2.3. Influence of the length of the grazing period on the rate of herbage intake calculated with the simulation model, Eq. (2.10) and Linehan's formula. Conditions: spring sward (see Table 2.1); high light intensity; herbage allowance = 32.5 kg DM cow<sup>-1</sup> d<sup>-1</sup>.

Length of the grazing period (days)	Herbage intake (kg DM cow <sup>-1</sup> d <sup>-1</sup> )		
	Simulation model	Eq. (2.10)	Linehan
3	16.1	16.1	15.5
7	16.1	16.0	13.9

### 3 Seasonal pattern of gross assimilation and net herbage production under continuous grazing

#### Abstract

The seasonal pattern of net herbage production under continuous grazing with optimal supply of nutrients is studied with a descriptive simulation model. The net herbage production is calculated as a constant fraction of the gross assimilation minus the above-ground maintenance respiration.

The model demonstrates that, although there is a gradual decline of the assimilatory capacity from spring to autumn, the highest potential rates occur in June.

The model is used to investigate the impact of sward height and water stress on net herbage production. It is concluded that during prolonged periods of drought the optimum sward height for cattle grazing is 6 cm, whereas under normal conditions this is 7 to 8 cm. On clay soils there is thus actually no need for irrigation of continuously-grazed swards to achieve high pasture outputs.

Continuous grazing is preferable to rotational grazing, to withstand periods with low rainfall.

#### 3.1 Introduction

Recent studies have shown that the annual totals of herbage and animal production on rotationally and continuously grazed pastures can be very similar at nitrogen fertilization rates of about  $400 \text{ kg N ha}^{-1} \text{ yr}^{-1}$  (Ernst et al., 1980; Parsons et al., 1983c; Chapter 1). From a practical viewpoint, however, it is important to consider not only the yearly total, but also the pattern of production over the grazing season. The seasonal pattern of herbage production has been thoroughly studied by Alberda and Sibma (1968) and by Parsons and Robson (1982) for systems of infrequent harvesting, as is the case with 3- to 4-weekly cutting and rotational grazing. In contrast, very little is known about the seasonal pattern of herbage production under continuous grazing. This knowledge is indispensable for the management of a continuous grazing system.

This chapter attempts to describe the pattern of production in a continuously-grazed sward throughout the grazing season. This is done with the aid of a descriptive simulation model centered around the relation between the daily radiation total and net herbage production under continuous grazing between April and October. The net herbage production is defined here as the herbage intake in a continuously-grazed sward when there is no net change in standing herbage dry mass. The results of the model, which includes a temperature correction for maintenance respiration, are verified with experimental data. The impact of water stress and sward height on net herbage production is then discussed. Sward height was measured using a tempex disc with a diameter of 50 cm and a weight of 150 g.

Many of the basic data for the model were taken from recent studies of carbon balance under continuous grazing (Parsons et al., 1983b; Chapter 1).

### 3.2 Modelling of the carbon balance under continuous grazing

It is widely accepted that the optimum mean sward height of perennial ryegrass pastures for continuous grazing with cattle is between 7 and 8 cm (e.g. Ernst et al., 1980). As long as this situation is maintained there is little net change in the standing herbage dry mass. There is thus an equilibrium in the carbon balance between gross assimilation, herbage intake and the losses due to respiration, translocation of assimilates to below-ground parts and death.

From a modeller's viewpoint it is a challenge to simulate the flow of matter in a continuously-grazed sward by means of an explanatory model. Some attempts have been made (e.g. Sibbald, unpublished; Lantinga, unpublished), but these models have the shortcoming that the losses of matter via tiller and leaf turnover are treated in an unsatisfactory way. This is due to the inadequate understanding of the losses by death in a grass sward. Since these losses are greater than the amount of the intake, at equilibrium with a mean sward height of 7 to 8 cm (Chapter 1), they are of over-riding importance.

For this reason it is necessary to seek another approach. Other items of the carbon balance can be measured or estimated with more accuracy; it has been shown (Chapter 1) that at equilibrium, with an optimal supply of

nutrients, about 25% of the gross assimilation minus the above-ground maintenance respiration is harvested by the grazing cattle, irrespective of season. Such an observation is very useful, because with the present knowledge both gross assimilation and maintenance respiration can be simulated satisfactorily. The remainder (75%) reflects the allocation of carbohydrates to roots, the conversion efficiency of carbohydrates into structural material and the losses by death.

As mentioned above, the utilization efficiency of carbohydrates under continuous grazing is not liable to seasonal fluctuations. One of the processes that may affect this efficiency is the allocation of assimilates to roots. In Chapter 1 it was demonstrated that a small change in this allocation can have large effects on the harvestable shoot production. For instance, one of the reasons that spring swards with elongating stems are superior in terms of harvestable shoot production is that the transport of assimilates to roots is reduced (Parsons and Robson, 1981). However, such a reduction has never been found in continuously-grazed swards, where stem elongation is suppressed by the grazing animals (Corrall, 1984). This may explain the constancy throughout the grazing season of the fraction of carbohydrates that is translocated below ground.

The net herbage production (NHP) under continuous grazing ( $\text{kg dry matter ha}^{-1} \text{d}^{-1}$ ), with an optimal supply of nutrients, is now calculated simply as

$$\text{NHP} = 0.25 * (P_g - R_m), \quad (3.1)$$

where  $P_g$  is the gross assimilation and  $R_m$  the maintenance respiration of the above-ground parts, both expressed in  $\text{kg CH}_2\text{O ha}^{-1} \text{d}^{-1}$ . The simulation of these two processes is described below.

### 3.2.1 Sward and leaf gross assimilation

During the years 1979-1984 many data were collected relating to the seasonal pattern of gross assimilation of pastures under continuous grazing. These data show that there is a gradual decline in the assimilatory capacity from mid-April to late October. This is illustrated in Fig. 3.1, where three typical curves are given from continuously-grazed swards with a mean sward height of 7 to 8 cm and a corresponding LAI of 2. The assimilation data were selec-



ted in such a way that for all curves the diffuse light fraction was about 0.5 at an incoming radiant flux density of  $200 \text{ W m}^{-2}$  or more (400-3000 nm). Up to this radiation level the proportion of diffuse light was always higher than 50%. This selection of data was necessary to enable comparison throughout the season, since the gross assimilation rate of leaf canopies is dependent on the ratio of diffuse to direct light (Goudriaan, 1977).

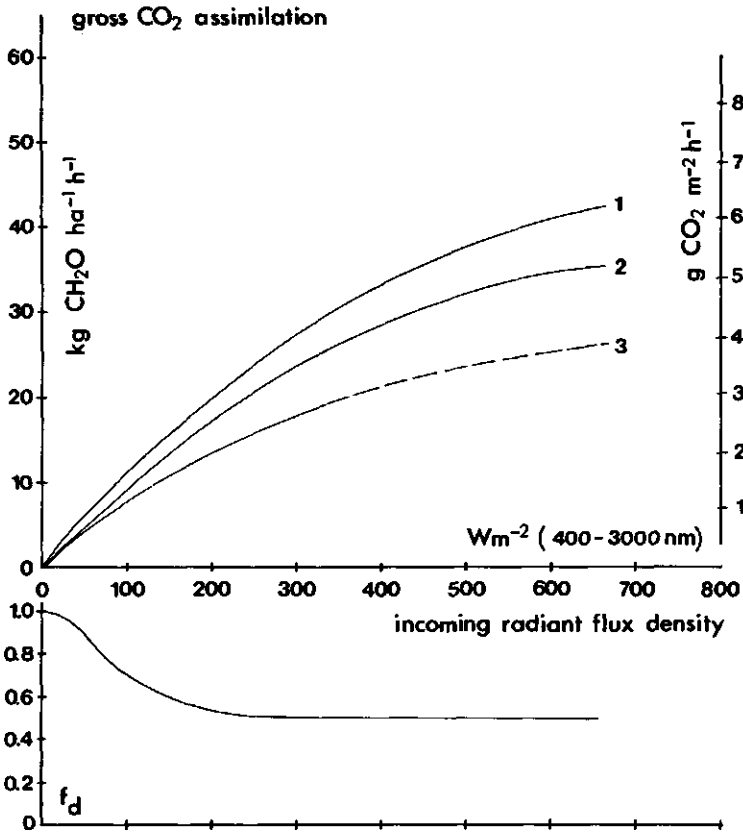


Fig. 3.1. A general relationship of gross assimilation to incoming radiant flux density under continuous grazing. The fraction of diffuse radiation is given in the lower part of the graph.  
1 = mid-April; 2 = mid-July; 3 = end of October.

To understand the seasonal decline in Fig. 3.1, it is necessary to consider in detail the initial light-use efficiency ( $\epsilon$ ) and the maximum rate of gross assimilation ( $A_m$ ) of the individual leaves. Since very few data were collected in the field on individual leaf assimilation, the simulation model PHOTON (De Wit et al., 1978; see also Chapter 4) was used to derive these parameters from sward assimilation measurements. For this purpose, the original version of the model was slightly modified. The most important adjustment was the introduction of the Blackman curve for the relation between absorbed radiation and leaf gross assimilation. This was done because this curve appears more realistic for grass swards in the field than the asymptotic exponential curve (Chapter 4). Besides, measured values of the diffuse light fraction were used.

With the modified version of the model PHOTON the values of the parameters  $\epsilon$  and  $A_m$  were found by matching the simulated curves to the measured curves in Fig. 3.1, by trial and error. In accordance with the measurements, LAI was set at 2. In addition, it was assumed that all leaves had the same assimilatory capacity. The results are given in Table 3.1.

As expected, the maximum rate of leaf gross assimilation was highest for the April sward ( $4.0 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ), and decreased to  $2.0 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$  for the October sward. This drop in assimilatory capacity of leaves during the season is sometimes related to a decrease in the demand for assimilates by the tiller population (Deinum, 1976), since during late summer and autumn relatively less carbohydrate is spent on growth than in spring and early summer (Behaeghe, 1979). This brings about a decline in the demand for assimilates through the season. Moreover, the poor light conditions in autumn

Table 3.1. Estimated values of the maximum rate of leaf gross assimilation ( $A_m$ ) and the initial light-use efficiency ( $\epsilon$ ).

period	$A_m$ ( $\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ )	$\epsilon$ ( $10^{-5} \text{ g CO}_2 \text{ J}^{-1}$ ; 400-700 nm)
mid-April	4.0	1.11
mid-July	3.0	1.11
late October	2.0	0.97

restrict the development of a high assimilatory capacity (Sheehy et al., 1980).

The initial light-use efficiency was the same in April and July and showed only a small decline in October (Table 3.1). Other observations show also hardly any seasonal influence of internal plant factors (Woledge and Leafe, 1976) or environmental factors (Monteith, 1965). The only exception is the effect of carbon dioxide on the initial slope of the assimilation-light response curve (Goudriaan et al., 1984).

To apply Eq. (3.1), daily totals of gross assimilation are required. These are obtained following the procedure proposed in a previous paper (Chapter 1). This procedure calculates an average rate of gross assimilation over the day from measured assimilation-light response curves, which is then adjusted for the non-linearity of the response curve and the composition of the incoming light (direct vs. diffuse light). For the present study the curves in Fig. 3.1 were used, with a linear interpolation for the days in between, and a new set of multiplication factors to allow for changing proportions of diffuse radiation.

### 3.2.2 Maintenance respiration

Maintenance processes are normally programmed as respiration rate per unit biomass (Penning de Vries, 1983). An average value of  $0.03 \text{ g glucose g}^{-1} \text{ dry matter d}^{-1}$  is given in the literature for tissues containing about  $0.04 \text{ g nitrogen g}^{-1} \text{ dry matter}$  at a temperature of  $25 \text{ }^\circ\text{C}$  (Jones et al., 1978; McCree, 1982; Moser et al., 1982; Penning de Vries and Van Laar, 1982). In continuously-grazed swards with a mean height between 7 and 8 cm, the above-ground live herbage dry mass is roughly  $2000\text{-}2500 \text{ kg DM ha}^{-1}$  (Fig. 3.2). In such swards, therefore, above-ground maintenance processes require about  $70 \text{ kg CH}_2\text{O ha}^{-1} \text{ d}^{-1}$  at  $25 \text{ }^\circ\text{C}$  and, with a  $Q_{10}$ -value of 2, about  $1.5 \text{ kg CH}_2\text{O ha}^{-1} \text{ h}^{-1}$  at  $15 \text{ }^\circ\text{C}$ . Experimental evidence for this estimate is problematical, since maintenance respiration is confounded with other respiratory processes (growth; decay of standing dead material and litter). This is illustrated in Fig. 3.3, which shows the seasonal course of the measured respiration rates during the last part of the night. The data presented were collected at a temperature close to  $15 \text{ }^\circ\text{C}$  in patches with a mean sward height of 7 to 8 cm. It can be seen from Fig. 3.3 that there is fairly wide

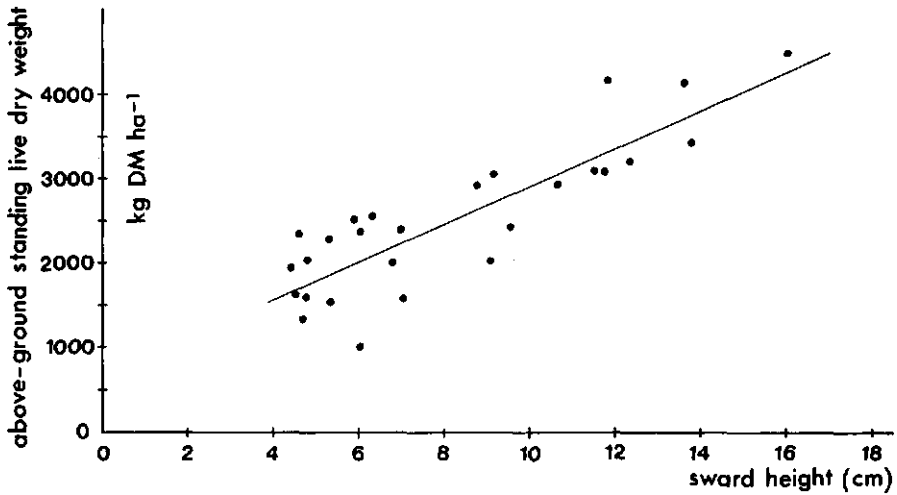


Fig. 3.2. Relationship between sward height and live herbage dry mass under continuous grazing. Wageningen, 1982.

variation, with a tendency to higher respiration rates in spring. This latter phenomenon may be due partly to the higher growth rate, at a given temperature, of a spring sward than of a summer sward (Peacock, 1976).

The carbon dioxide production due to the decay of standing dead material and litter is very small when these fractions are dry (Redmann and Abouguendia, 1978). In assimilation chambers this situation is approached rapidly, as a result of the high drying power of the ventilating air. It may be assumed, therefore, that during the later part of the night, after a measuring period of at least 12 h, the living shoots are the only significant source of carbon dioxide. The contributions of maintenance and growth processes to the total CO<sub>2</sub> efflux can then be estimated by measuring its pattern during an artificially extended period of darkness of 2 days (Jones et al., 1978). It is then assumed that the value of CO<sub>2</sub> efflux at the end of this period represents the maintenance component of respiration. Using this method, Jones et al. (1978) found that in a spring sward the value of maintenance respiration was equivalent to a loss of about 0.015 g CH<sub>2</sub>O g<sup>-1</sup> dry matter d<sup>-1</sup> at

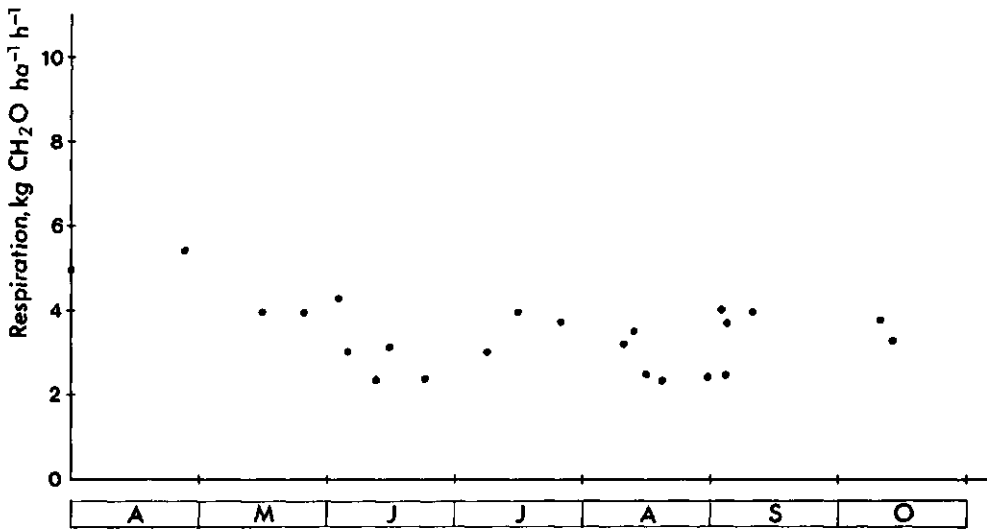


Fig. 3.3. Measured seasonal course of respiration rates at the end of the night under continuous grazing at 15 °C. Wageningen, 1979-1983; Swifterbant, 1984. Nitrogen fertilization 400-520 N ha<sup>-1</sup> yr<sup>-1</sup>.

a nitrogen content of 4% and a temperature of 15 °C. The same result was found in Wageningen in a vegetative sward in August (Fig. 3.4).

Although these data are not from continuously-grazed swards, they match the previous estimate. The model uses, therefore, for the rate of above-ground maintenance respiration a value of 70 kg CH<sub>2</sub>O ha<sup>-1</sup> d<sup>-1</sup> at 25 °C and a Q<sub>10</sub> of 2. It is interesting to note that, with this value, on average about 50% of the measured respiration at the end of the night is due to maintenance processes (see Fig. 3.3).

### 3.3 Results and discussion

The calculated seasonal pattern of net herbage production under continuous stocking is shown in Fig. 3.5, for a number of radiation levels. For the calculations the following conditions were assumed to exist:

- mean daily temperature of 15 °C;
- mean sward height of 7 to 8 cm;
- optimal supply of water and nutrients.

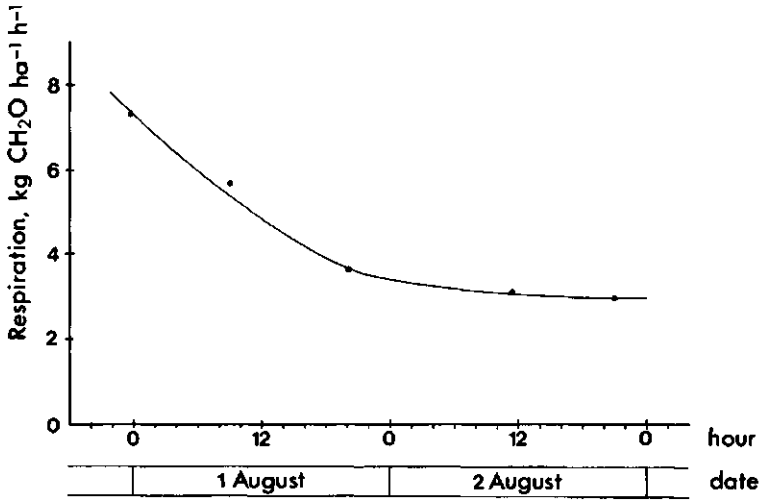


Fig. 3.4. Respiration rate of a vegetative sward (4000 kg live DM ha<sup>-1</sup> with 3.5% N) during two days of continuous darkness. Temperature was about 17.5 °C in all cases. Wageningen, 1981.

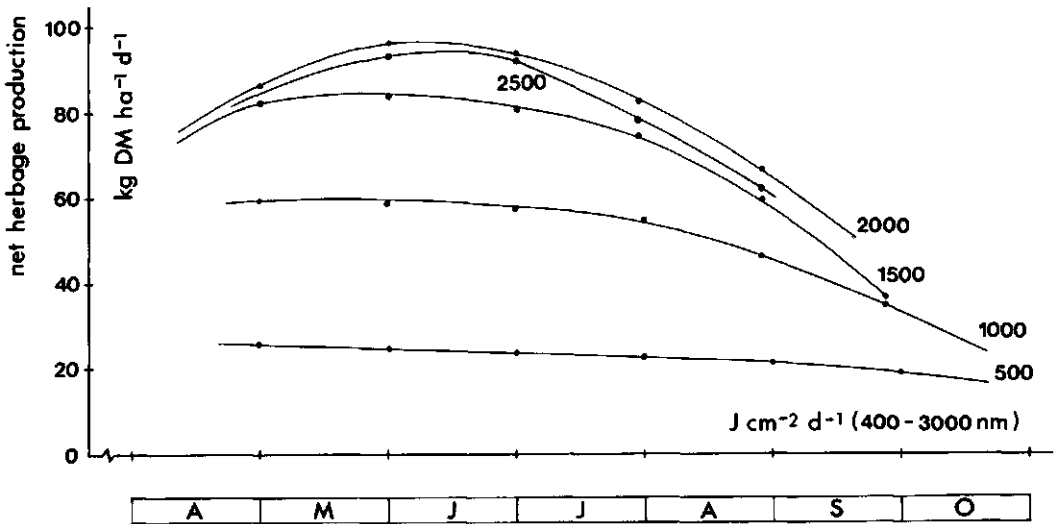


Fig. 3.5. Seasonal pattern of net herbage production under continuous grazing for five levels of daily radiation total at 15 °C.

The curves in Fig. 3.5 are therefore of value only for this production situation.

The effects of deviating temperatures and sward heights and of water shortage will be discussed below.

The seasonal pattern of herbage production generated by the model differs from that normally found where cutting takes place every 3-4 weeks. In the latter case, the curves are characterised by a sharp peak of production in May (Corrall, 1984). This is due to stem elongation, a feature that is suppressed under intensive continuous grazing. Consequently, it is to be expected that under continuous grazing the seasonal pattern of production will more closely reflect the radiation and the assimilation potential.

Using the model, the highest production rates at a given radiation level were found to occur in June (Fig. 3.5). This is slightly surprising, since the assimilation potential of the sward is then lower than in April and May. The present model, however, emphasizes not only the amount of radiation but also its composition (direct/diffuse). In June, when the maximum daily radiation total reaches its highest value, the amount of diffuse radiation, for a given daily total, is higher than in spring. Since diffuse light is utilized much more efficiently by a canopy than direct light (Goudriaan, 1977), this more than compensates the lower assimilatory capacity.

Another characteristic of the curves given in Fig. 3.5 is that there is hardly any increase in net herbage production above a daily radiation total of  $1500 \text{ J cm}^{-2} \text{ d}^{-1}$ . This also is due to the composition of the incoming light. In the range of increasing daily radiation totals above about  $1500 \text{ J cm}^{-2} \text{ d}^{-1}$ , the effect of the increase in direct radiation on gross assimilation is more or less offset by the (smaller) decrease in the amount of diffuse radiation (Chapter 4).

The model output can be verified by comparison with experimental data. For this purpose, data were used from three experiments with milking cows (Schlepers et al., 1982; Chapter 1 and unpublished results). In all cases the realized herbage intake per cow must have been very close to  $15 \text{ kg DM d}^{-1}$  throughout the grazing season, given the animal production data and the level of concentrate-supplementation. The net herbage production could then be calculated by multiplying this intake rate by the stocking density. Ten periods were found in which the sward height, water supply and nutrient conditions were satisfied. For periods with mean daily temperatures different

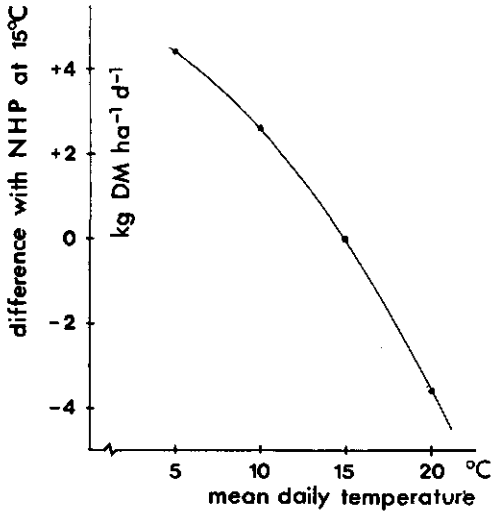


Fig. 3.6. Effect of temperature on the rate of net herbage production (NHP) due to its influence on the rate of maintenance respiration according to Eq. (3.1).

from 15 °C the model output was corrected according to Fig. 3.6.

Fig. 3.7 shows that although there is some variation, the agreement between the model output and the experimental data is good. It can be concluded, therefore, that the model describes satisfactorily the seasonal pattern of the production capacity of a continuously-grazed sward. Figs. 3.5 and 3.6 can therefore be used to construct the average seasonal pattern of net herbage production under continuous grazing, using data on average radiation and temperature. For this purpose it is not correct to use the average radiation values themselves, since the relationship between daily radiation total and net herbage production is not linear (see Fig. 3.5). To account for this, a normal distribution pattern is assumed for the daily radiation total, with an estimated coefficient of variation of 0.40. Together with the average daily radiation totals and temperatures of De Bilt (1961-1980), the average production pattern was calculated (Fig. 3.8). The corresponding stocking densities are also given, assuming an intake rate of 15 kg DM cow<sup>-1</sup> d<sup>-1</sup>.

The integrated net herbage production over the whole grazing season (Fig. 3.8) is 11300 kg DM ha<sup>-1</sup>.



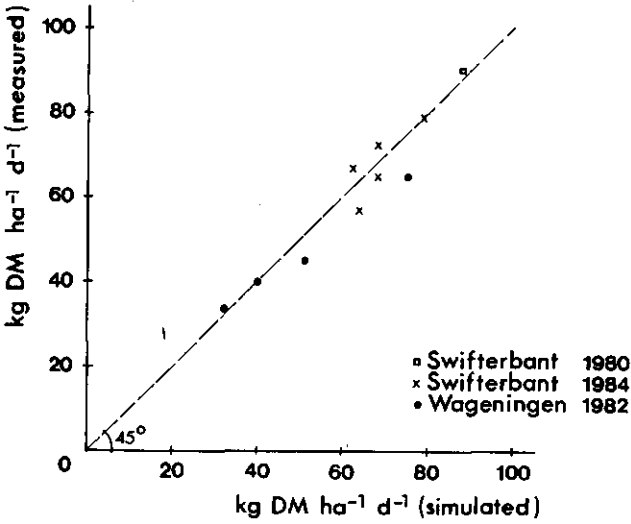


Fig. 3.7. Comparison of measured and calculated rates of net herbage production under continuous grazing. Wageningen, 1982 (●); Swifterbant, 1980 (□) and 1984 (x).

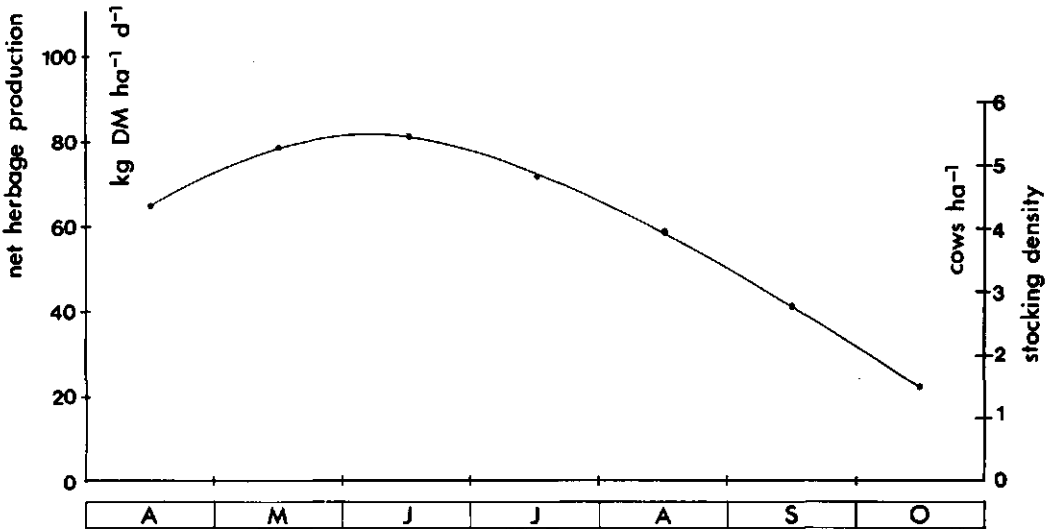


Fig. 3.8. Average seasonal pattern of net herbage production and potential stocking density for a maintained sward height of 7 to 8 cm.

### 3.3.1 Impact of sward height

In one experiment (Chapter 1) the mean sward height during the first month of continuous grazing (early May till early June) was maintained at about 13 cm. Over this period, the measured net herbage production was on average 100 kg DM ha<sup>-1</sup> d<sup>-1</sup>. According to the model, this would not have been more than 85 kg DM ha<sup>-1</sup> d<sup>-1</sup> during the same period at a sward height maintained between 7 and 8 cm. This difference could be attributed to an LAI of 3 in the field instead of 2 in the calculation.

These rates suggest that it may seem profitable to commence with grazing at a higher initial sward height than the recommended 7 to 8 cm.

However:

- In a normal spring it takes about two weeks for the grass to grow from a height of 8 cm to 13 cm; this implies that the start of the grazing season would be delayed by two weeks.
- During these two weeks the average net herbage production in a continuously-grazed sward is about 70 kg DM ha<sup>-1</sup> d<sup>-1</sup> (Fig. 3.8). In total this loss of 980 kg DM ha<sup>-1</sup> is much greater than the benefit of 450 kg DM ha<sup>-1</sup> obtained by maintaining the sward height at a higher level for one month.
- In the long term, tiller density and LAI will decrease in a tall sward. This may have adverse effects on herbage production in mid-summer when the sward height is reduced to about 8 cm again. This is necessary to preserve the capacity of the sward to produce grass of good quality at a high production rate.
- Much of the grass produced between 8 and 13 cm will be lost by death before it can be consumed when the sward height is lowered.

In the present experiment the herbage intake was almost 2600 kg DM ha<sup>-1</sup> between early June and early July, when the sward height was gradually reduced from 13 to 8 cm. According to the model the accumulated net herbage production during the same period would have been close to 2500 kg DM ha<sup>-1</sup>. This shows the importance of the latter two observations.

It is concluded, therefore, that under continuous grazing, not only in late summer and autumn but also in spring and early summer the optimal mean sward height is between 7 and 8 cm.

### 3.3.2 Impact of water stress

During periods of water stress grass production can be restricted. Except in cases of severe stress this is, in swards regrowing from a cut or a rotational grazing cycle, due to a reduction of leaf area expansion, resulting from a reduced leaf extension and leaf appearance (Jones et al., 1980). Hence, to ensure high production rates, irrigation is necessary.

It was also found, however, that in continuously-grazed dense swards during periods with less rainfall, herbage intake rates remained rather high without irrigation, provided the grass in the regularly grazed areas was not higher than about 5 cm (Chapter 1). This can be explained as follows. When water stress occurs, dry matter is produced mainly in the sward layer close to ground level as a result of reduced leaf extension. Consequently, in order to utilize this production, grazing must take place in this lower sward layer. Otherwise, the produced grass will die off. For this purpose the mean sward height has to be maintained at about 6 cm instead of 8 cm. The individual intake is then not restricted, since the dry matter content of the grass consumed is relatively high. Hence, if during periods of water stress the strategy of grazing is not adapted, one might conclude wrongly that the

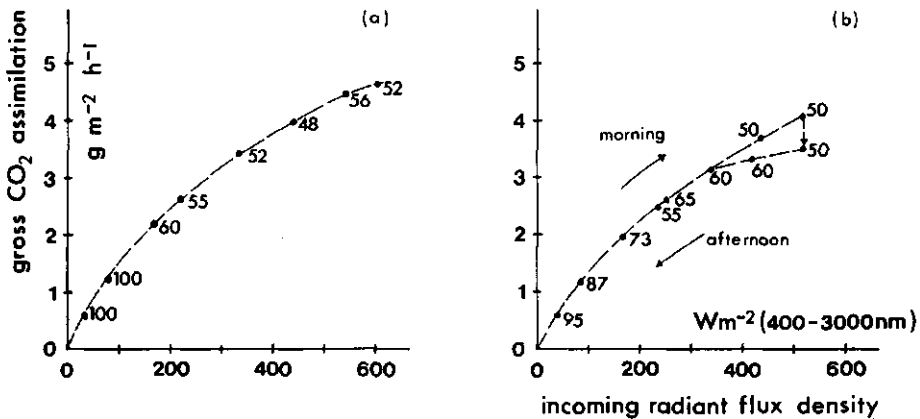


Fig. 3.9. Light response of gross assimilation under continuous grazing without (a) and with (b) water stress. The percentage of diffuse radiation is given for each measuring point. Swifterbant, 1984, (a) on 8 August and (b) on 23 August.

Table 3.2. Effect of water shortage on the net herbage production (NHP) under continuous grazing. Swifterbant, 1984.

Period	water shortage	mean sward height (cm)	NHP (kg DM ha <sup>-1</sup> d <sup>-1</sup> )		
			measured	calculated standard curves	calculated actual curves
2 Aug. - 8 Aug.	no	7.3	65	67	67
20 Aug. - 25 Aug.	yes	6.3	50	64	51

above-ground dry matter production is severely restricted, while in reality it is the poor utilization of the produced grass and the higher losses that are mainly responsible for the reduction in pasture output. In cases of severe stress, however, production rates will be severely reduced because of a decrease in the number of live tillers and a continued decrease in the rate of assimilation per unit leaf area.

It is often suggested that water stress causes a shift in the distribution of assimilates in favour of the roots (Van Keulen, 1982). However, this was not found in the experiment described above. There, the decline in net herbage production could be explained fully by the reduced assimilatory capacity of the sward (Chapter 1). The same was found in an experiment carried out during August 1984 on a silty clay loam in the new land of the Flevopolders with a nitrogen fertilization of 520 kg N ha<sup>-1</sup> yr<sup>-1</sup> and a total rainfall of 13 mm between 20 July and 31 August. This led to a progressively increasing water stress during August. It appeared here that there was some reduction in gross assimilation in the early afternoon of 23 August (Fig. 3.9b). This was due probably to increased stomatal resistance. No such a reduction was observed on 8 August (Fig. 3.9a). Moreover, the assimilatory capacity of the sward was somewhat lower on 23 August. Using the actual weather data it was found that during early August there was a very good agreement between the measured net herbage production and the model (Table 3.2). At the end of August, when the mean sward height of the paddock was 6.3 cm, the net herbage production was overestimated using the standard curves of Fig. 3.1. However, when measured assimilation-light response data were used in Eq. (3.1), the agreement was again good (Table 3.2).

Both experiments were carried out on clay soils, where during periods of water shortage the capillary rise from groundwater supplies a considerable part of the transpiration demand of the sward. It is estimated that in both cases the actual net herbage production was about 20% below its potential value. On sandy soils without capillary rise from groundwater, a greater reduction is to be expected.

Therefore it may be concluded that:

- In continuously-grazed swards on clay soils there is actually no need for irrigation to achieve high pasture outputs, but this may not be extrapolated to sandy soils.
- Continuous grazing seems to be the best system to withstand periods of low rainfall, since with rotational grazing the length of the regrowth period is greatly extended owing to the reduction in leaf area expansion.

#### 4 Influence of the proportion of diffuse radiation on gross assimilation of leaf canopies

##### Abstract

The influence of the proportion of diffuse radiation on gross assimilation and dry matter production in leaf canopies was studied. This influence was shown to be considerable and, over a wide range of radiation levels, the diffuse component is significantly underestimated by the crop production models BACROS and PHOTON (De Wit et al., 1978). Radiation measurements were used to improve the section in these models describing the separation between diffuse and direct radiation. With this improvement it emerged that the relationship between daily total radiation and daily total gross assimilation (and dry matter production) is approximately a Blackman curve, with the intersection at 60% of the maximum radiation total on that day, i.e. that under a perfectly clear sky.

It is concluded that the leaf assimilation-light response in field-grown grass swards can be best calculated from a Blackman curve.

##### 4.1 Introduction

The  $\text{CO}_2$  assimilation of a canopy depends not only on radiant flux density and the assimilatory capacity of the single leaves, but also on factors affecting the distribution of radiation over the leaves in the canopy (De Wit, 1965). The most important of these factors is the ratio between diffuse and direct radiation. This factor is much more important than, for instance, the leaf angle distribution (Goudriaan, 1977). With an increasing percentage of the diffuse component, at a given radiant flux density, the distribution of radiation over the leaves improves and the assimilation rate of the canopy increases.

Nevertheless, in many crop production models no distinction is made between diffuse and direct radiation. In the models BACROS and PHOTON (De Wit et al., 1978) this problem is tackled by assuming that during the time interval of calculation the sky is overcast for a certain period and clear for the rest of the interval. BACROS and PHOTON are simulation programs for the seasonal gross assimilation, respiration and transpiration of crops and the daily

course of these processes, respectively. This procedure yields a linear relationship between the rate of dry matter production and the total intercepted radiation. Although this may be correct for the whole growing season (Monteith, 1977), it does not fit field measurements over periods of a few days, which do show a curvilinear relation (Meijs, unpublished measurements). This may be due to an underestimation of the fraction of diffuse radiation over a range of radiation levels (Goudriaan, pers. comm.). In this paper this hypothesis will be investigated using experimental results and simulation.

Further, data on the assimilation response of single leaves to irradiance will be re-examined, since there are indications that the approach to saturation in field-grown plants is faster than that predicted by the frequently used asymptotic exponential curve.

#### 4.2 Incoming diffuse and direct radiation

The diffuse flux is the difference between the total global irradiance and the direct solar flux, which can be measured separately. When the diffuse flux is measured with a solarimeter provided with a shadow band or a revolving shadow disc, as was the case in the present study, corrections must be applied for the interception of part of the diffuse radiation. Under a clear sky, however, much of this diffuse radiation comes from the sky region surrounding the sun. Since this diffuse radiation reaches the earth at the same angle of incidence as the direct solar radiation, it seems more realistic to treat it as direct radiation in crop production models. In this article, therefore, the diffuse radiation data are not corrected. A consequence of this is, that, under largely cloudy and overcast conditions, the proportion of diffuse radiation is underestimated. Under these conditions, however, small changes in the proportion of diffuse radiation in the total flux have no influence on the rate of  $\text{CO}_2$  assimilation in leaf canopies (Chapter 2).

This study does not take account of the fact that for a clear sky the fraction of photosynthetically active radiation is larger in (diffuse) blue skylight than in the total global radiation (Spitters, pers. comm.; Lantinga, unpublished measurements). This is partly compensated, however, by the lower energy-efficiency for photosynthesis in the blue part of the spectrum than in the red part, so that omission of the two effects leads only to marginal deviations.

Unfortunately, diffuse radiation is still not measured on a routine basis. In nearly all situations, therefore, the division into diffuse and direct components must be approximated. In the models BACROS and PHOTON this is done in a fairly sophisticated way: the measured daily radiation total (in BACROS) or the actual radiant flux density (in PHOTON) are used to calculate the fraction of time that the sky is overcast. This is done by comparing the measured radiation level to that on a completely clear and on a fully overcast day. Thus, it is assumed in BACROS that the clouds are evenly distributed over the day. The actual rate of CO<sub>2</sub> assimilation of the canopy is then calculated as the average of the assimilation rates under these sky conditions, weighted according to the fraction of time the sky is overcast. The consequences of this procedure for the division into diffuse and direct components will be discussed for the model BACROS, which does not differ essentially from the model PHOTON.

In BACROS, the fraction of time that the sky is overcast ( $f_o$ ) is computed as

$$f_o = \frac{R_c - R_m}{R_c - R_o} \quad (4.1)$$

where  $R_m$  is the measured daily global radiation total, and  $R_c$  and  $R_o$  are the daily totals for a very clear and a fully overcast day, respectively. The yearly pattern of  $R_c$  for Wageningen is shown in Fig. 4.1.

The radiant flux density under fully overcast skies, when all radiation is diffuse, depends on the density of the clouds, but it is reasonable to assume that the visible radiant flux density (400-700 nm) is about 20% of that under very clear skies. Since under a fully overcast sky the ratio of the incoming visible to the near-infrared radiation is 0.6 : 0.4 (Goudriaan, 1977; Stigter and Musabilha, 1982), it follows that, for wavelengths between 400 and 3000 nm, the radiant flux density under a fully overcast sky is about 17% of that under a very clear sky.

Thus, if the relative daily radiation total ( $R_r$ ) is defined as

$$R_r = \frac{R_m}{R_c} \quad (4.2)$$



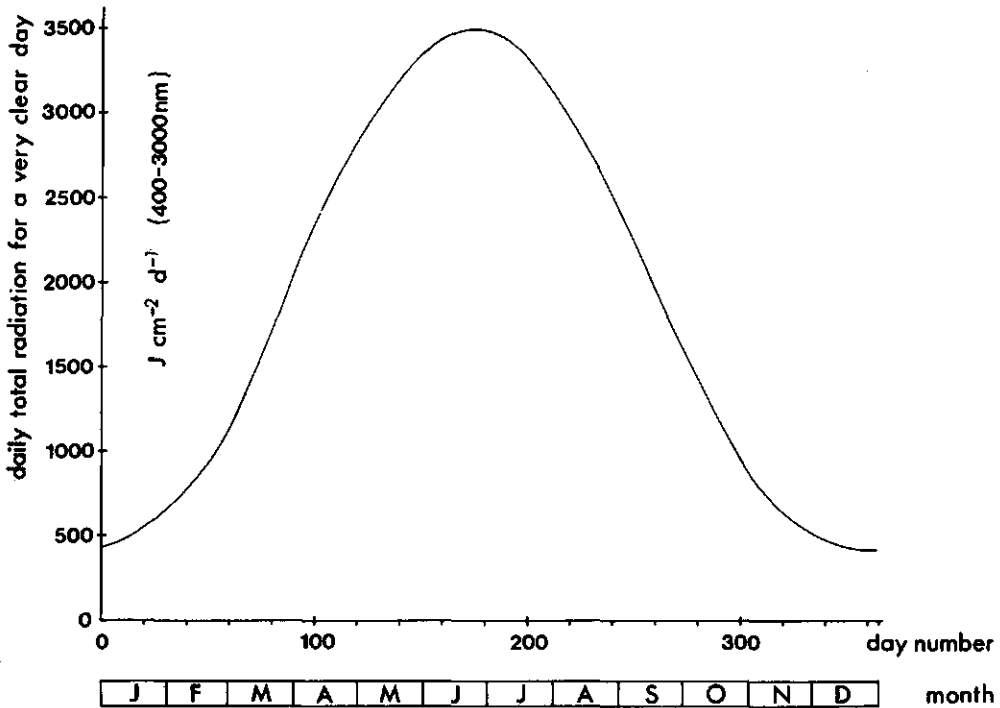


Fig. 4.1. Yearly pattern of the daily global radiation total under a very clear sky. Location: Wageningen ( $52^\circ$  N.lat.).

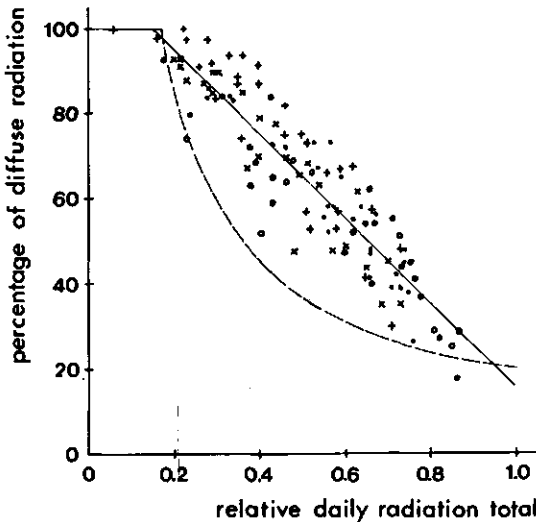


Fig. 4.2. The relation between percentage of diffuse radiation ( $f_d$ ) and relative daily radiation total ( $R_d$ ) at Wageningen. (o = April 1982; x = July 1981; • = August 1984; + = October 1982). The broken line indicates the relationship as used in BACROS, according to Eq. (4.4).

substitution into Eq. (4.1) gives

$$f_o = \frac{1 - R_r}{0.83} . \quad (4.3)$$

The proportion of diffuse radiation for a very clear sky is a function of the height of the sun above the horizon. On such a day, the integrated diffuse flux is approximately 20% of the total daily radiation, depending on the day of the year. Consequently, according to the procedure used in BACROS, the fraction of diffuse radiation ( $f_d$ ) is given by

$$f_d = \frac{0.17 \times f_o + (1-f_o) \times 0.2}{R_r} \quad (4.4)$$

Substitution of Eq. (4.3) into Eq. (4.4) yields

$$f_d = \frac{0.164}{R_r} + 0.036 \quad (0.17 \leq R_r \leq 1.00) \quad (4.5)$$

The validity of Eq. (4.5) can be investigated by comparison with measured radiation data. This has been done for four arbitrarily selected months in the 1980's at Wageningen, where both the total global radiation and the diffuse radiation were measured (Fig. 4.2). It appears that in nearly all cases the fraction of diffuse radiation is greatly underestimated in BACROS. This has important consequences for the rate of  $CO_2$  assimilation, as will be shown later.

A regression analysis on the data in Fig. 4.2 yielded the equation

$$f_d = 1.16 - 1.01 \times R_r . \quad (0.17 \leq R_r \leq 1.00) \quad (4.6)$$

( $r^2=0.92$ )

To improve the radiation section in BACROS, Eq. (4.6) may be incorporated. The absence of a daily pattern is, however, a disadvantage. Moreover, this results in some overestimation of the proportion of diffuse radiation at higher relative radiation levels.

For this reason a new set of forcing functions has been developed for the relations between sun height, relative daily radiation total and the proportion

Table 4.1. The proportion of diffuse radiation for various relative daily radiation totals ( $R_r$ ) and some solar heights.

$R_r$	inclination of the sun ( $^\circ$ )					
	5	15	25	35	45	90
0.17	1.00	1.00	1.00	1.00	1.00	1.00
0.30	1.00	0.94	0.92	0.91	0.90	0.89
0.80	1.00	0.38	0.30	0.27	0.25	0.22
0.90	1.00	0.33	0.24	0.20	0.18	0.15
1.00	1.00	0.32	0.22	0.18	0.16	0.13

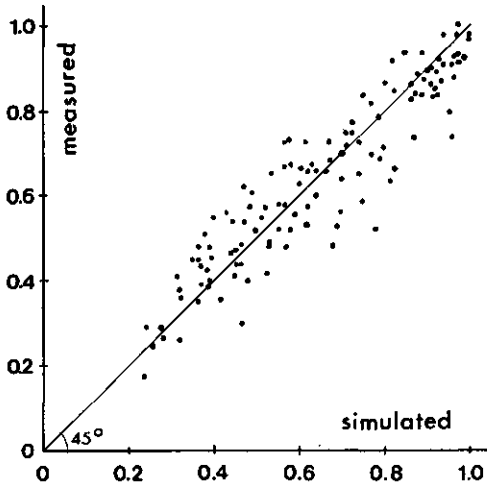


Fig. 4.3. Comparison of simulated and measured values of the proportion of diffuse radiation ( $f_d$ ). Dates as in Fig. 4.2.

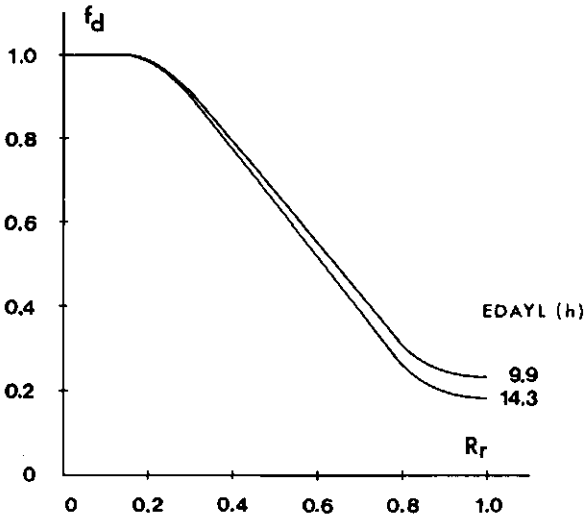


Fig. 4.4. Percentage of diffuse radiation ( $f_d$ ) in relation to relative daily radiation total ( $R_r$ ), for two effective daylengths. Effective daylength (EDAYL) is the time for which the sun height is above  $8^\circ$ .

of diffuse radiation (Table 4.1). For intermediate situations a linear interpolation between the data points of this table is used. This gives a reasonable correlation with the observed tendency in Fig. 4.2 (see Fig. 4.3). Table 4.1 has now, therefore, been incorporated in the models BACROS and PHOTON to replace the procedure that calculates the fraction of time that the sky is overcast. It should be noted that it is still assumed in BACROS that the clouds are evenly distributed over the day. The effect of daylength on  $f_d$  is shown in Fig. 4.4. The lines in this figure were calculated from Table 4.1 using an integration procedure.

#### 4.3 Assimilation-light response curves of single leaves

In general, the assimilation function of an individual leaf, as used in crop production models, is based on laboratory measurements. In former years it was thus concluded that the relation between absorbed radiant flux density and  $\text{CO}_2$  assimilation could be best equated by a rectangular hyperbola (De Wit, 1965). Later, Goudriaan and Van Laar (1978) stated that with this func-

tion the approach of the saturation level is too slow, and that a better fit can be obtained with the asymptotic exponential equation. However, making use of measured values of the light-saturated assimilation rate, PHOTON still underestimates the rate of gross  $\text{CO}_2$  assimilation for field-grown grass swards (unpublished measurements during spring 1983). This suggests that even with the asymptotic exponential curve the approach of the saturation level is still too slow. Support for this is provided by Marshall and Biscoe (1977). They found, using leaves of winter wheat, that the response of assimilation to irradiance for plants grown in controlled environments differs from that for field-grown plants. Whereas the measurements made on wheat plants grown in climate rooms could be best represented by a rectangular hyperbola, those made on plants grown outdoors were best described by a Blackman curve (Fig. 4.5).

This difference in the response of assimilation to irradiance suggests that the results of laboratory experiments cannot be extrapolated to the field. However, it is questionable whether this may be generalized, since the factors determining the shape of the assimilation-light response curve of a single leaf are still poorly understood (Goudriaan, pers. comm.). Few other detailed measurements of leaf assimilation-light response are available for gramineous plants grown in the field, but in nearly all cases they also show

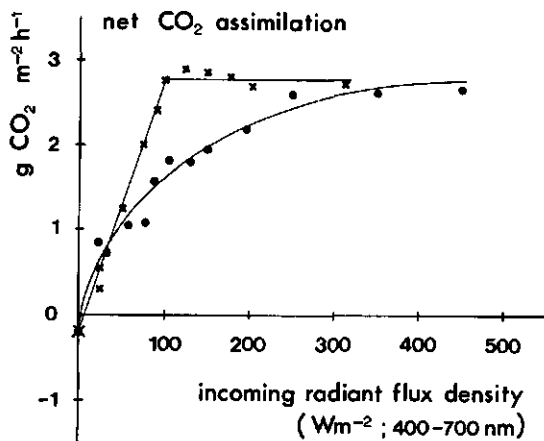


Fig. 4.5. Net assimilation-light response curves for a fully expanded flag leaf of winter wheat grown in the field (x) and in controlled climate room (•). From Marshall and Biscoe (1977).

a Blackman relationship (e.g. Kornher and Nyström, 1971; Azcón-Bieto et al., 1981). For the present study it is therefore assumed that the assimilation function of an individual leaf can be represented by the Blackman equation.

#### 4.4 Diffuse radiation and instantaneous rates of crop CO<sub>2</sub> assimilation

The impact of the proportion of diffuse radiation on the light response of field-grown swards was studied in experiments and by simulation. In this way it is possible also to evaluate the distribution of incoming diffuse and direct radiation over the leaves in the models BACROS and PHOTON.

Fig. 4.6 presents measured and simulated assimilation-light response data of

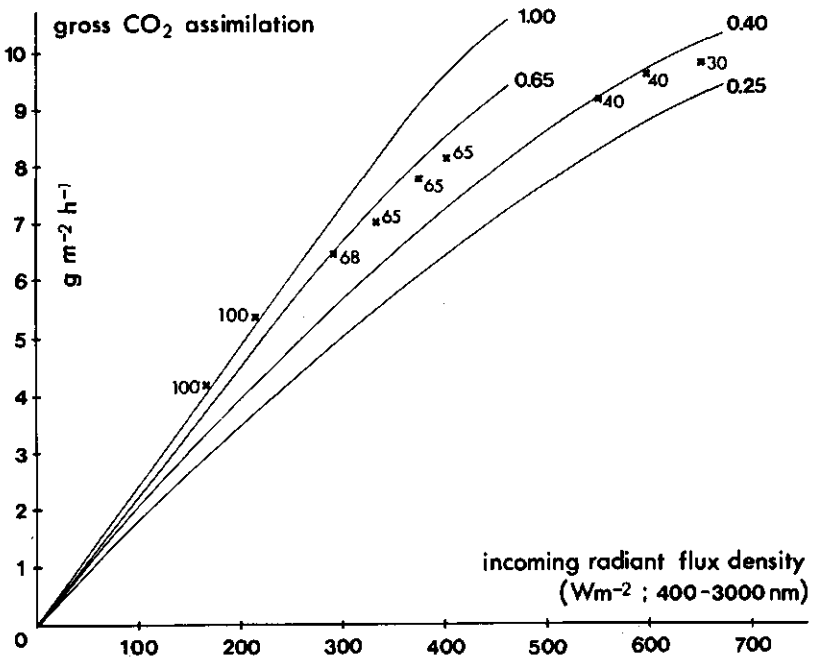


Fig. 4.6. Simulated (solid lines) and measured (crosses) rates of gross CO<sub>2</sub> assimilation in relation to the incoming radiant flux density, for different proportions of diffuse radiation. The proportion of diffuse radiation is expressed as a fraction for the simulation and as a percentage for the measurements. Wageningen, 5 May 1983; LAI = 4. Leaf characteristics used in the simulation: assimilation rate at light saturation: 5.0 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>; initial light-use efficiency: 1.53 x 10<sup>-5</sup> g CO<sub>2</sub> J<sup>-1</sup> (400-700 nm absorbed); Blackman curve.

a highly productive sward on 5 May 1983. This was a sunny day on which the proportion of diffuse radiation gradually increased during the afternoon. The sward characteristics are given in the legend of Fig. 4.6. The agreement between simulated and measured results is very good. This bears out the assumption that the section describing the distribution of incoming radiation in BACROS and PHOTON is essentially correct. Moreover, since measured rates of maximum gross assimilation are used, this also confirms the existence of a Blackman type relationship for the light response at leaf level. Using the asymptotic exponential equation, unrealistic high values of the leaf parameters are necessary to match the measured curves.

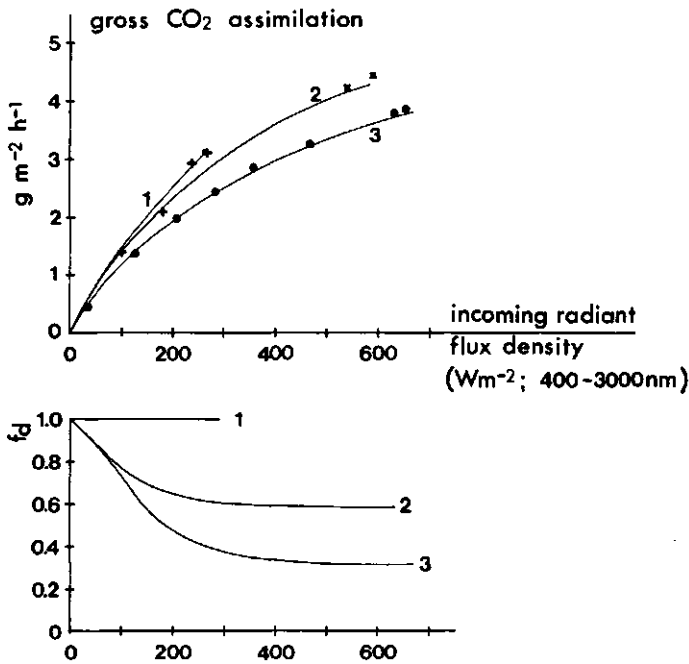


Fig. 4.7. Simulated (solid lines) and measured (data points) rates of gross CO<sub>2</sub> assimilation in relation to the incoming radiant flux density, for different patterns of the diffuse radiation fraction (lines 1, 2 and 3). Swifterbant, 14-16 August 1984; LAI = 2. Leaf characteristics used in the simulation; assimilation rate at light saturation: 2.4 g CO<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>; initial light-use efficiency: 0.85 x 10<sup>-5</sup> g CO<sub>2</sub> J<sup>-1</sup> (400-700 nm absorbed); Blackman curve.

In Fig. 4.7, some results are presented from an experiment carried out during August 1984. Here, the method of calculation was somewhat different from that which yielded Fig. 4.6. Three simulation runs were made, such that the three runs covered periods of measurements with similar fractions of diffuse radiation. Although the leaf characteristics were derived from trial runs, the very close agreement between simulated and measured results justifies again the description of the distribution of incoming diffuse and direct radiation over the leaves in BACROS and PHOTON, and the use of the Blackman curve.

From the results presented in Figs. 4.6 and 4.7 it will be clear that the impact of the proportion of diffuse radiation is considerable. At a given radiant flux density the  $\text{CO}_2$  assimilation rate of leaf canopies varies strongly, dependent on this proportion. Much care should be taken, therefore, in the interpretation of assimilation measurements carried out in natural environments.

#### 4.5 Diffuse radiation and daily total of gross $\text{CO}_2$ assimilation

The effect of the improved description of the diffuse radiation on the daily total of gross assimilation in BACROS and PHOTON has been studied for different times in the year. Since there are no essential differences throughout the year, results are given only for the 1<sup>st</sup> of July.

The simulation conditions were as follows:

- maximum rate of leaf gross assimilation:  $4.0 \text{ g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ ;
- initial light-use efficiency:  $1.11 \times 10^{-5} \text{ g CO}_2 \text{ J}^{-1}$  (PAR absorbed);
- LAI = 5;
- location: Wageningen (latitude  $52^\circ \text{ N}$ )

Fig. 4.8 shows the relationship between the daily total global radiation and the daily total of gross assimilation. It appears that: (a) up to a relative daily radiation total of 0.5 there is a proportional increase; and (b) above a relative daily radiation total of 0.6 the daily total of gross assimilation is virtually constant. Clearly, beyond a relative daily radiation total of 0.6, the effect of the increase in the amount of direct radiation on crop gross assimilation is offset by the (smaller) decrease in the amount of diffuse radiation (see Fig. 4.9). This response is quite different from the linear one predicted by the original versions of BACROS and PHOTON.



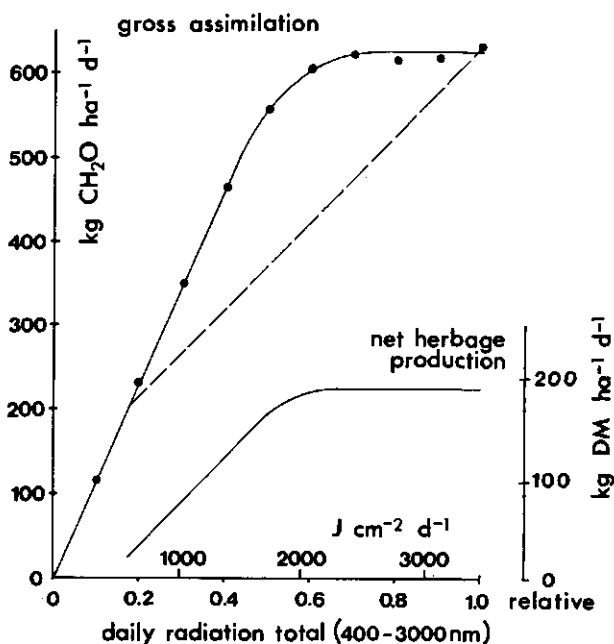


Fig. 4.8. Simulated relations of daily total gross assimilation and net herbage production to (relative) daily total of global radiation. Data from 1<sup>st</sup> of July. Simulation model PHOTON: ----- original version; ——— new version (Table 4.1).

To illustrate the consequences for the response of daily dry matter production to daily radiation total, a simple simulation model for herbage production was applied (Chapter 2). In the lower part of Fig. 4.7 the resulting relation is given; this closely approximates a Blackman curve. It may be concluded, therefore, that for a given day the response of crop production to daily radiation total is linear up to about 60% of its maximum value and that at higher daily radiation totals there is no further increase in the rate of crop production. This may explain the curvilinear relationship observed between total dry matter production of grass swards and total solar radiation over periods of a few days (Meijs, unpublished results).

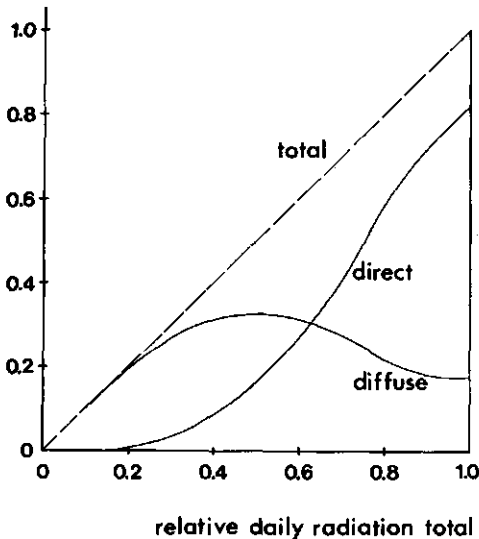


Fig. 4.9. Daily totals of diffuse and direct radiation, given as fractions of the maximum daily radiation total, in relation to the relative daily radiation total. Standard day: 1<sup>st</sup> of July.

#### 4.6 Conclusions

- The influence of the proportion of diffuse radiation on the rate of crop CO<sub>2</sub> assimilation is considerable.
- The modelling of the distribution of incoming diffuse and direct radiation over the leaves of a canopy in the models BACROS and PHOTON is adequate.
- Over a wide range of relative daily radiation totals (actual/maximum daily total of radiation) the average proportion of the diffuse component in the incoming radiation is much higher than is assumed in BACROS and PHOTON.
- For leaves of field-grown grass the relation between absorbed radiant flux density and the rate of CO<sub>2</sub> assimilation can be best represented by a Blackman curve.
- With an improved description of the proportion of diffuse radiation the relation between daily total radiation and daily total gross assimilation (and dry matter production) is approximately a Blackman curve with the intersection at a relative daily radiation total of 0.6.

## 5 Final remarks

### 5.1 Simulation of productivity of grass swards under grazing

This dissertation presents models for simulation of the production of grass swards under continuous and rotational grazing with cattle. The grass sward was considered in this study as a leaf canopy. Morphogenetic processes, such as tiller dynamics, were not taken into account. This simplified approach is acceptable, since in the swards considered there are no significant changes in tiller density: under intensive continuous grazing with cattle, the high tiller density shows little variation with time (Arosteguy et al., 1983), whereas the rotational grazing periods are so short that tiller number can hardly change (except through extreme trampling, which was not considered in this study).

The production models presented were based on observed relations between sward  $\text{CO}_2$  assimilation, respiration and herbage intake. For continuous grazing at high nitrogen fertilization rates (about  $450 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ ) it was found that, irrespective of season, 25% of the gross assimilation minus the maintenance respiration (expressed in terms of  $\text{CH}_2\text{O}$ ) of the above-ground biomass was harvested as animal intake (expressed as dry matter). This observation was the basis for a dynamic model for calculation of the net herbage production. The constancy of the carbon allocation pattern throughout the grazing season is due to the suppression of stem elongation by the grazing animals. This is different from rotational grazing, where the production rate in the harvestable sward layer is stimulated by stem elongation during May and early June.

To estimate herbage production during a rotational grazing period, a new formula was developed (Chapter 2), which can be seen as an improved version of Linehan's formula. For both formulae, the undisturbed production of the sward during the grazing period is needed. Currently, this production is normally measured directly in a fenced part of the area to be grazed. However, this is inaccurate because the grazing period is often so short (3 or 4 days) that the difference between the yields are too small. Another method is needed, therefore, to determine this undisturbed production.

For this purpose, measured production rates of swards with an initial herbage mass close to the recommended grazing stage for rotational grazing

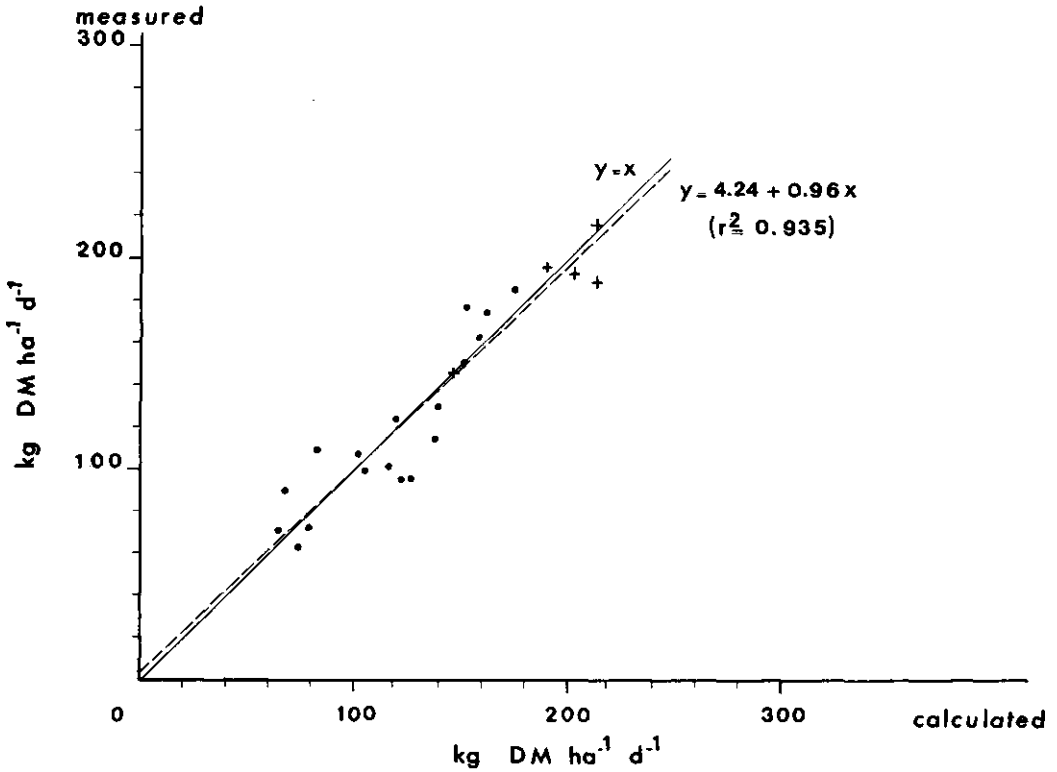


Fig. 5.1. Comparison of calculated and measured undisturbed herbage production of grass swards during the grazing stage of a rotational grazing system. For calculation procedure: see text.  
+ : period between early May and early June; • : growing season from early June onwards.

(1700 kg DM ha<sup>-1</sup> above 4 cm) were compared with simulated production rates under continuous grazing, obtained using the model presented in Chapter 3 (Figs. 3.5 and 3.6). The data were collected by Meijs (unpublished) under conditions with an optimal supply of water and nutrients. The growth periods were 7 or 8 days.

The comparison revealed that the herbage production of a sward in the grazing stage for rotational grazing was, on average, twice or 2.5 times the production level under continuous grazing (Fig. 5.1). The higher value was found for the period early May-early June and was a result of stem elongation.

undisturbed herbage  
production

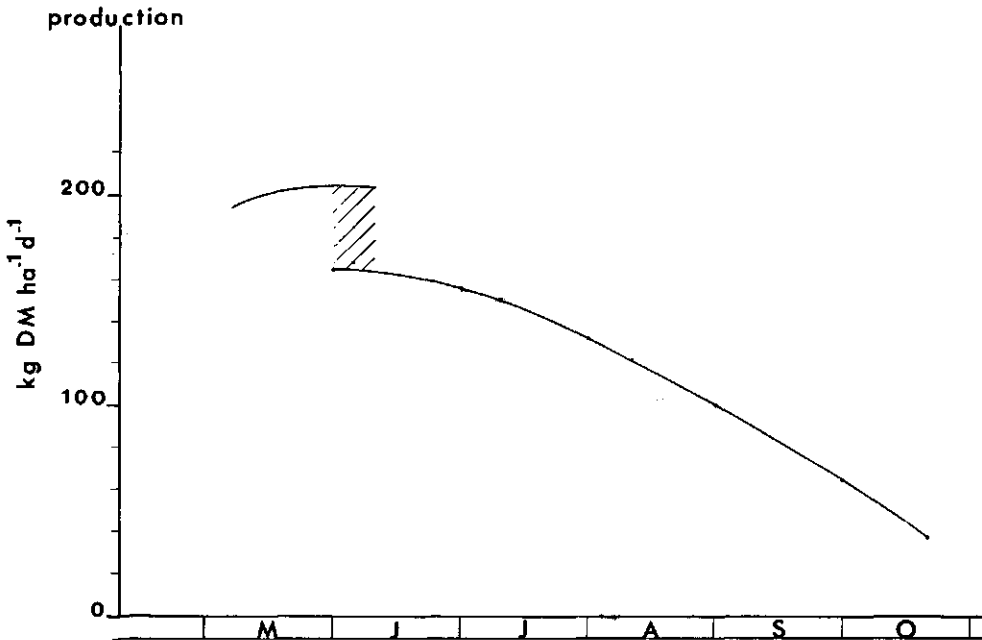


Fig. 5.2. Average seasonal pattern of the undisturbed herbage production at the onset of a rotational grazing period, with an optimal supply of water and nutrients.

This implies that the undisturbed herbage production of grass swards in the grazing stage for rotational grazing may be simply derived from Figs. 3.5 and 3.6, using the appropriate multiplication factor. This procedure is labour-saving and preferable to field measurements, in situations with short grazing periods, with non-limiting moisture and nutrients.

In Chapter 3 the average seasonal pattern of net herbage production under continuous grazing was also computed (Fig. 3.8). A similar pattern can be found for the undisturbed herbage production of swards at the onset of a rotational grazing period, by multiplying the line in Fig. 3.8 by 2 or 2.5, as mentioned above. This gives the relation presented in Fig. 5.2 (a transition zone was included for early June to allow for a gradual change in the production pattern).

## 5.2 Grazing losses

Grazing losses are defined as the fraction of herbage production that is not consumed by the animals on the pasture (Meijs et al., 1982). The standards for grazing losses under the different grazing management systems applied in the Netherlands (Anon., 1984) are often no more than guesses. For these, it is assumed that all grazing residues are removed by topping, and that the amount of topped grass represents the grazing loss. In modern grassland management, however, topping after each grazing period is rarely performed, as the rotational grazing system normally involves alternation between one or two grazing cycles (without topping) and a silage cut. In this way, grazing residues remaining after the last grazing are removed by the silage cut. Calculations of grazing losses based on amounts of topped grass are meaningless in these cases. Under continuous grazing, the herbage production necessary for the calculation cannot be measured at all.

A new method is needed, therefore, to determine the efficiency of utilization of the production capacity of grass swards under different management systems. This can be done by comparing the total amount of harvested dry matter (herbage intake plus silage grass) with the total dry matter production under a certain cutting regime. The total production under this cutting regime is then considered as a measure of the production capacity of the grass sward.

For this purpose the sward should be cut whenever the weight of dry matter above 4 cm exceeds  $2000 \text{ kg ha}^{-1}$ . The harvesting regime is then roughly analogous to a common rotational grazing system in which grazing is prevented below a sward height of 4 cm, to maintain individual intake.

The utilization efficiency is then calculated as the total amount of dry matter harvested by the cattle and as silage, divided by the production capacity established in this way. Such an approach is applicable in any grassland management system.

Preliminary calculations have shown that under intensive rotational or continuous grazing -without taking silage cuts- the utilization efficiency defined in this way is between 80 and 85%, provided that the individual animal intake is not restricted. The utilization efficiency is not increased because of:

- (a) higher losses due to plant death under grazing in comparison with mowing;

- (b) the existence of areas of unpalatable grass surrounding dung patches. Maintenance of the quality and nutritive value of the sward requires topping of this grass, at least once during the grazing season in early summer. It should be noted that recent research on continuous grazing (Lantinga, unpublished) has shown that at increasing levels of nitrogen fertilization the amount of rejected grass around dung patches decreases markedly. This may be because at high nitrogen fertilization rates, *all* of the herbage is relatively unpalatable;
- (c) damage to the sward, due to urine-scorching, dung patches, tiller pulling and trampling;
- (d) lower assimilation rate per unit leaf area during grazing than during regrowth. For a given LAI, the assimilation rate is generally highest in regrowing swards and lowest in rotationally grazed swards; continuously grazed swards show an intermediate value (Chapter 1; King et al., 1984). This is caused by differences in average leaf age, and thus also assimilatory capacity. In the context of rotational grazing, this observation may imply that to maximize production the grazing period should be made as short as possible.

However, the utilization efficiency may be considerable lower than 80 to 85%. Under rotational grazing, this can occur if the grass offered to the cattle is too long. High grazing residues are then inevitable, whereas tiller density and, later on, botanical composition may be adversely affected. With silage-making, heavy cuts and long field periods reduce sward quality and dry matter production. In continuous grazing systems, a suboptimal stocking density not only affects the utilization efficiency directly, but also leads to an increase of the area of rejected grass around dung patches.

### 5.3 Management considerations of continuous and rotational grazing

In Chapter 1 it is concluded that there are no differences in productivity between continuous and rotational grazing. There are, however, clear indications that intensive continuous grazing (high fertilization level, mean sward height kept at about 7 cm) is the best way to maintain a high sward quality in the long term. Counts of tiller density in pastures continuously grazed by cattle show that the normal density is about 200 tillers of good grass species

per dm<sup>2</sup> throughout the year (Lantinga, unpublished measurements). Parsons et al. (1983a) report that by continuous hard grazing with sheep, this number may even reach 650 tillers per dm<sup>2</sup>. Tiller densities of 200 per dm<sup>2</sup> or more act as a natural barrier for the invasion of unwanted plant species. Moreover, it has been observed (Neuteboom, pers. comm.) that under continuous grazing, unwanted couch grass (*Elymus repens*) cannot withstand the frequent defoliation, whereas perennial ryegrass (*Lolium perenne*) thrives. Continuous grazing may therefore be a useful method of suppressing couch grass and promoting perennial ryegrass. For this reason, continuously-grazed pastures may need less frequent reseeding than rotationally-grazed pastures, where the tiller density is normally below 100 per dm<sup>2</sup>.

Another advantage of continuous grazing is that during periods of water stress, grass production remains at a fairly high level, as a result of the high tiller density (Chapter 3). To utilize this production it is necessary, however, to lower the mean sward height to about 6 cm. There is then no need for irrigation to maintain production at a reasonable level during periods with little rainfall.

Continuous grazing is a system with relatively low costs and labour input, but some management skill is required to maintain the sward height at the optimum level, especially in late spring when the tillers express their potential for stem elongation. However, with rotational grazing this is also a critical period, in which it is difficult to offer herbage of a constant high feeding quality to the cattle. To ensure this, the sward height at the onset of grazing should not be greater than about 18 cm. At greater sward heights, the feeding quality decreases. Concentrate supplementation might then need to be increased to maintain milk production.

Maintenance of an optimal mean sward height in a continuously grazed pasture, throughout the grazing season, guarantees a constant supply of high quality herbage for the grazing cattle; this results in regular lactation curves. Recent research (Lantinga, unpublished results) has shown that under optimal conditions of continuous grazing the herbage consumed provides sufficient energy to support maintenance plus a daily production of 25-30 kg milk (4% fat) during the period April-June.

In the trials described in Chapter 1 the optimum sward height was maintained by adjusting the stocking rate in the paddocks (the so-called 'put and take' method). In practice, however, such management is much more difficult



because there are no parking paddocks for the cows. However, fluctuations in herbage production may also be countered by taking silage cuts if there is excess grass, or by feeding concentrates and/or additional roughage during periods of grass shortage.

In Chapter 3, the seasonal pattern of net herbage production under continuous grazing is considered. To manage the continuous grazing system, the average seasonal pattern of potential stocking density, as presented in Fig. 3.8, can be used. From this pattern it follows that 5 to 6 dairy cows can be stocked on each ha during May and June. It is necessary, however, to begin grazing already in April, as soon as the sward height has reached a level of 7 to 8 cm. Since the production rate of the sward at that time is lower than that in May and June, a larger area is required. To allow for this lower production rate, the grazing activities of the stock may also be restricted to the day-time during a number of days in April. The grassland area that is not needed for grazing can be reserved for the production of silage grass. During May and June, two silage cuts can be taken from this area.

According to Fig. 3.8, the carrying capacity of the continuously grazed sward decreases gradually from mid-June until the end of the grazing season. This implies that the grazed area must be increased, starting at about the end of June. Clearly, the number of readjustments depends on the actual pattern of herbage production, but it can be seen in Fig. 3.8 that about twice the area is needed for grazing during the last part of the grazing season as in the period May-June. However, it is also possible, of course, to feed more concentrates and/or additional roughage during the latter part of the grazing season.

It will be clear that the continuous grazing system can be applied in various forms. For instance, after one or two silage cuts, the whole silage aftermath can be used for grazing, while the area that has so far been continuously grazed is partly enclosed for silage. This may be a wise decision, from the viewpoint of sward quality, because of the positive effects of grazing on botanical composition and tiller density. After two silage cuts, the sward quality may have deteriorated severely.

However, whatever decision is taken, it must always be aimed at maintaining an optimum sward height in the grazed area throughout the grazing season, i.e. a mean height of 7 to 8 cm if the moisture supply is sufficient and about 6 cm during periods of water stress.

## Summary

In the Netherlands, rotational grazing, with grazing periods of 2 to 5 days, is the most common grazing system at present. In contrast with other countries of North-western Europe, the continuous grazing system is used here only to a limited extent. However, the results of numerous comparative trials at high nitrogen fertilization levels and high stocking rates, carried out in the 1970's, suggest that there is no significant difference in animal production between the two grazing systems.

Experiments were carried out to determine the physiological and environmental limits to herbage production under continuous and rotational grazing. This was done by measuring the seasonal patterns and seasonal totals of sward  $\text{CO}_2$  assimilation and animal production. The experiments were carried out on heavy clay soils at two nitrogen fertilization levels (125 and about 450  $\text{kg N ha}^{-1} \text{ yr}^{-1}$ ). With 450  $\text{kg N ha}^{-1} \text{ yr}^{-1}$ , cumulative gross assimilation over the grazing season was 9% higher with rotational than with continuous grazing, but there was no difference in animal production. The higher efficiency of utilization of gross assimilation products under continuous grazing was due to lower topping losses and lower costs of above-ground maintenance respiration. Under both grazing systems, gross  $\text{CO}_2$  assimilation per unit leaf area was not depressed at all at 125  $\text{kg N ha}^{-1} \text{ yr}^{-1}$ , but there was a marked reduction of the rate of leaf area development in the second half of the grazing season. The absence of any effect in the first half of the grazing season was due probably to a residual effect of previously applied nitrogen. This effect can be considerable on heavy clay soils.

The herbage intake under rotational grazing is often estimated using Linehan's formula, which takes into account the herbage production during grazing. This formula was evaluated by means of dynamic simulation, with measured assimilation-light response curves as the main input. It emerged that in some practical situations of rotational grazing, the herbage production during the grazing period is significantly underestimated using Linehan's formula. This is mainly because Linehan's formula assumes exponential growth of the sward at all stages of growth. Since this is not correct for a sward in the absence of grazing, a new comprehensive formula is derived, using the assumption that the sward is in the linear growth phase at the start of grazing. Comparisons with the simulation output show that this new

formula for estimating herbage intake is valid for all situations of rotational grazing.

To manage the continuous grazing system successfully, information is needed about the seasonal changes in production capacity with this grazing system. An experiment with dairy cows revealed that throughout the grazing season a constant proportion (equal to 0.25 at the high nitrogen level) of the carbohydrate pool, derived from gross assimilation minus above-ground maintenance respiration, was ingested by the grazing cattle. This observation formed the basis for a dynamic model to compute the net herbage production under continuous grazing throughout the grazing season, using data on radiation and temperature. It appears that, although there is a gradual decline from spring to autumn, the highest production rates occur in June. The average seasonal pattern of net herbage production, predicted by the model using average weather data, can be used for management purposes of the continuous grazing system. It is then possible to adjust stocking density during the grazing season, to achieve the maximum pasture output without adversely affecting the botanical composition and tiller density of the sward. Although the limited time available for this study made it impossible to examine effects of rotational and continuous grazing on the long term, there are good indications that continuous grazing is preferable in this respect. Moreover, the continuous grazing system seems better able to withstand periods with low rainfall, owing to the higher tiller density. During prolonged periods of water stress, however, the mean sward height must be lowered to about 6 cm, instead of the normal optimum level of 7 to 8 cm. It was observed on the clay soils that there is then actually no need for irrigation to achieve high pasture outputs. This is due partly to the unchanged carbon allocation pattern during periods of water stress.

The simulated production rates under continuous grazing were compared with measured production rates of grass swards with an initial herbage mass close to the recommended grazing stage for rotational grazing (1700 kg DM ha<sup>-1</sup> above 4 cm), in order to develop a simple method for estimating the undisturbed herbage production rate at the onset of a rotational grazing period. The herbage production of a sward in the grazing stage for rotational grazing was, on average, 2 or 2.5 times the production level under continuous grazing. The higher value was found for the period early May-early

June and was a result of stem elongation. This observation may serve as a simple method for estimation of the undisturbed production rate.

A new procedure was developed to deal with grazing losses. Here, the utilization efficiency is calculated by comparing the total amount of harvested dry matter (herbage intake plus silage grass) with the total production under a certain cutting regime. This approach is applicable in any grassland management situation.

The  $\text{CO}_2$  assimilation of a leaf canopy is strongly dependent on the ratio between diffuse and direct radiation. This produces much of the scattering often observed in field measurements on the assimilation-light response of crop surfaces. It is shown that the crop production models PHOTON and BACROS, developed at the Department of Theoretical Production Ecology of the Wageningen Agricultural University, treat the distribution of diffuse and direct radiation over the leaves of a canopy correctly, but that the proportion of the diffuse component is significantly underestimated over a wide range of radiation levels. Radiation measurements were used to improve the section in these models describing the separation between diffuse and direct radiation. Literature survey showed that the leaf assimilation-light response in field-grown grass swards can be best calculated using a Blackman curve, rather than the frequently used asymptotic exponential curve. With these improvements, the relation between daily total radiation and daily total gross assimilation (and dry matter production) is shown to approximate to a Blackman curve, with the intersection at 60% of the maximum radiation total on that day, i.e. that under a perfectly clear sky.

## Samenvatting

In Nederland is tegenwoordig omweiden, met beweidingssystemen van 2 tot 5 dagen, het meest gangbare beweidingssysteem. In tegenstelling tot andere landen in Noordwest-Europa, wordt standweiden hier slechts op beperkte schaal toegepast. Resultaten van vergelijkende proeven, uitgevoerd in de zeventiger jaren bij hoge stikstofgiften en hoge veebezettingen, wijzen echter op een gelijke dierlijke produktie bij de twee beweidingssystemen.

Er werden proeven uitgevoerd om de gewasfysiologische beperkingen voor grasproduktie onder stand- en omweiden vast te stellen. Dit werd gedaan door het seizoensverloop en de seizoenstotalen van  $\text{CO}_2$ -assimilatie en dierlijke produktie te meten. De proeven werden uitgevoerd op zware kleigronden bij twee niveaus van stikstofbemesting (125 en ongeveer  $450 \text{ kg N ha}^{-1} \text{ jr}^{-1}$ ). Bij  $450 \text{ kg N ha}^{-1} \text{ jr}^{-1}$  was de bruto assimilatie over het weideseizoen onder omweiden 9% hoger in vergelijking met standweiden, maar er was geen verschil in dierlijke produktie. De hogere benuttings-efficiëntie van de assimilaten onder standweiden was het gevolg van lagere verliezen door bloten en lagere kosten voor onderhoudsademhaling. Onder beide beweidingssystemen was er geen invloed van de stikstofbemesting op de  $\text{CO}_2$ -assimilatie per eenheid bladoppervlakte. Bij de gift van  $125 \text{ kg N ha}^{-1} \text{ jr}^{-1}$  trad echter wel een duidelijke vertraging in de snelheid van bladontwikkeling gedurende de tweede helft van het weideseizoen op. De afwezigheid van enig stikstof-effect in de eerste helft van het weideseizoen was mogelijk te wijten aan een nawerkingseffect van eerder gegeven stikstof. Deze nawerking kan aanzienlijk zijn op zware kleigronden.

De grasopname onder omweiden wordt vaak geschat met behulp van de formule van Linehan, waarin rekening wordt gehouden met de grasproduktie tijdens beweiding. Deze formule werd getoetst met een simulatiemodel, waarin gemeten assimilatie-licht responscurven waren ingevoerd. Hieruit bleek dat in sommige situaties de grasproduktie tijdens de beweidingperiode aanmerkelijk wordt onderschat met de formule van Linehan. Dit is een gevolg van de aanname door Linehan dat altijd exponentiële groei optreedt. Aangezien dit niet juist is voor een gesloten grasgewas, is een nieuwe formule afgeleid, uitgaande van lineaire groei bij aanvang van de beweiding. Vergelijkingen met de simulatieuitkomsten tonen aan dat de nieuwe formule een goede schatting van de grasopname voor alle situaties van omweiden geeft.

Voor een goede uitvoering van het standweidesysteem moeten seizoensveranderingen in het produktieniveau bekend zijn. In een experiment met melk-koeien werd gevonden dat over het gehele weideseizoen, een constante fractie (0.25 bij het hoge stikstofniveau) van de koolhydraten, afkomstig van bruto assimilatie verminderd met bovengrondse onderhoudsademhaling, werd opgenomen door de weidende dieren. Deze waarneming vormde de basis voor een dynamisch model voor berekening van het seizoensverloop van de netto grasproduktie onder standweiden. De benodigde weersgegevens zijn de dagelijkse straling en de gemiddelde dagelijkse temperatuur. Hoewel de capaciteit voor  $\text{CO}_2$ -assimilatie geleidelijk afneemt van voorjaar naar najaar, blijkt dat gemiddeld de hoogste produkties optreden in Juni. In deze maand is de straling gemiddeld het hoogst. Het berekende gemiddelde seizoensverloop van de netto grasproduktie kan als leidraad dienen voor aanpassing van de veedichtheid gedurende het weideseizoen.

Hoewel lange-termijn effecten van stand- en omweiden op zodekwaliteit niet bestudeerd konden worden, zijn er goede aanwijzingen dat in dit opzicht standweiden de voorkeur verdient. Bovendien blijft onder standweiden de produktie gedurende perioden met vochttekorten langer op peil; dit als gevolg van de hogere spruitdichtheid. De gemiddelde gewashoogte moet dan wel worden teruggebracht van het normale optimale niveau van 7 tot 8 cm naar ongeveer 6 cm. Op de kleigronden werd geconstateerd dat er dan in feite geen behoefte aan berekening is om relatief hoge produkties te behalen. Dit is gedeeltelijk een gevolg van de waargenomen ongevoeligheid van de koolstof-distributie voor veranderingen in de vochtvoorziening.

De gesimuleerde produktiesnelheden onder standweiden zijn vergeleken met gemeten produktiesnelheden in percelen met grasopbrengsten rondom het aanbevolen beweidingsstadium voor omweiden (1700 kg droge stof per ha boven 4 cm) om een eenvoudige schattingsmethode te ontwikkelen voor de ongestoorde grasproduktie gedurende een omweidingsperiode. Deze moet worden ingevoerd in de formule voor berekening van de (gestoorde) grasproduktie tijdens beweiding. De grasproduktie in het omweidingsstadium bleek gemiddeld 2 of 2,5 keer zo hoog te zijn dan het produktieniveau onder standweiden. De hogere waarde werd gevonden voor de periode begin Mei - begin Juni en was het gevolg van stengelstrekking. Onder intensief standweiden wordt stengelstrekking onderdrukt door de grazende dieren. De

gevonden correlaties kunnen dienen als schatting van de ongestoorde produktie gedurende een omweidingsperiode.

Een nieuwe methode voor bepaling van beweidingsverliezen wordt beschreven. Hier wordt de efficiëntie van benutting van de produktie-capaciteit berekend door de totale hoeveelheid geoogst gras (grasopname en gemaaid kuilgras) te vergelijken met de totale produktie onder een bepaald maai-regime. Deze methode is toepasbaar bij elke graslandgebruikswijze.

De  $\text{CO}_2$ -assimilatie van een gewas bij een bepaalde stralingsdichtheid is sterk afhankelijk van de verhouding tussen diffuse en directe straling. Dit brengt een groot deel van de spreiding teweeg, welke vaak wordt waargenomen bij metingen in het veld. Bij de vakgroep Theoretische Teeltkunde van de Landbouwhogeschool te Wageningen zijn de modellen PHOTON en BACROS ontwikkeld voor simulatie van gewasproduktie. Er wordt aangetoond dat in deze modellen de invallende straling op een juiste wijze over de bladeren van het gewas wordt verdeeld, maar dat de fractie diffuus licht in bijna alle situaties aanzienlijk wordt onderschat. Stralingsmetingen werden gebruikt om in deze modellen de sectie te verbeteren waarin een opsplitsing wordt gemaakt in direct en diffuus licht. Uit de literatuur bleek dat de assimilatie-licht responscurve van grasbladeren in het veld beter kan worden weergegeven met een Blackman curve dan met de vaak gebruikte asymptotisch exponentiële curve. Met deze verbeteringen blijkt het verband tussen dagelijkse totale straling en dagelijkse totale bruto assimilatie (en droge stofproduktie) vrijwel een Blackman curve te zijn met het snijpunt bij ongeveer 60% van de maximale stralingssom, dat is het dagtotaal onder een zeer heldere hemel.

## References

- Alberda, T. and L. Sibma (1968). Dry matter production and light interception of crop surfaces. III. Actual herbage production in different years as compared with potential values. *Journal of British Grassland Society* 23: 206-215.
- Anonymous (1984). *Handboek voor de rundveehouderij*. Proefstation voor de Rundveehouderij, Lelystad.
- Arosteguy, J.C., J. Hodgson, W.G. Souter and G.T. Barthram (1983). Herbage growth and utilisation on swards grazed by cattle and sheep. In: *Efficient Grassland Farming* (Ed. A.J. Corral), pp. 155-158. Proceedings of the 9th General Meeting of the European Grassland Federation. The British Grassland Society, Hurley.
- Azcón-Bieto, J., G.D. Farquhar and A. Caballero (1981). Effects of temperature, oxygen concentration, leaf age and seasonal variations on the CO<sub>2</sub> compensation point of *Lolium perenne* L. *Planta* 152: 497-504.
- Azcón-Bieto, J. and C.B. Osmond (1983). Relationship between photosynthesis and respiration. The effect of carbohydrate status on the rate of CO<sub>2</sub> production by respiration in darkened and illuminated wheat leaves. *Plant Physiology* 71: 574-581.
- Behaeghe, T.J. (1979). *De seizoenvariatie in de grasgroei*. Rijksuniversiteit Gent, 272 pp.
- Bircham, J.S. and J. Hodgson (1983). The influence of sward condition on rates of herbage growth and senescence in mixed swards under continuous stocking management. *Grass and Forage Science* 38: 323-331.
- Brougham, R.W. (1956). Effect of intensity of defoliation on regrowth of pasture. *Australian Journal of agricultural Research* 7: 377-387.
- Burg, P.F.J. van, M.L. 't Hart and H. Thomas (1980). Nitrogen and grassland - past and present situation in the Netherlands. In: *Proceedings International Symposium of the European Grassland Federation on 'The role of nitrogen in intensive grassland production'* (Eds. W.H. Prins and G.H. Arnold), pp. 15-33. Pudoc, Wageningen.
- Corral, A.J. (1984). Grass growth and seasonal pattern of production under varying climatic conditions. Proceedings of the 10th General Meeting of the European Grassland Federation (Eds. H. Riley and A.O. Skjelvåg), Ås: 36-45.
- Davies, A. (1981). Tissue turnover in the sward. In: *Sward measurement Handbook* (Eds. J. Hodgson, R.D. Baker, A. Davies, A.S. Laidlaw, J.D. Leaver), pp. 179-208. The British Grassland Society, Hurley.
- Deinum, B. (1976). Photosynthesis and sink size: an explanation for the low productivity of grass swards in autumn. *Netherlands Journal of Agricultural Science* 24: 238-246.
- Deinum, B., M.L. 't Hart and E. Lantinga (1983). Photosynthesis of grass swards under rotational and continuous grazing. In: *Proceedings of the XIV International Grassland Congress* (Eds. J.A. Smith and V.W. Hays), Lexington: 407-410.
- Ernst, P., Y.L.P. Le Du and L. Carlier (1980). Animal and sward production under rotational and continuous grazing management - a critical appraisal. *Proceedings International Symposium of the European Grassland Federation on 'The role of nitrogen in intensive grassland production'* (Eds. W.H. Prins and G.H. Arnold), pp. 119-126. Pudoc, Wageningen.
- Frame, J. (1981). Herbage mass. In: *Sward measurement Handbook* (Eds. J. Hodgson, R.D. Baker, A. Davies, A.S. Laidlaw, J.D. Leaver), pp. 39-69. The British Grassland Society, Hurley.



- Frankena, H.J. (1936). Hoe moeten wij weiden? Officieel Orgaan van den Algemeenen Nederlandschen Zuivelbond 10 en 11: 1-12.
- Gales, K. (1979). Effect of water supply on partitioning of dry matter between roots and shoots in *Lolium perenne*. Journal of Applied Ecology 16: 863-877.
- Goudriaan, J. (1977). Crop micrometeorology: a simulation study. Simulation Monographs Series. Pudoc, Wageningen, 249 pp.
- Goudriaan, J. and H.H. van Laar (1978). Calculation of daily totals of the gross CO<sub>2</sub> assimilation of leaf canopies. Netherlands Journal of Agricultural Science 26: 373-382.
- Goudriaan, J., H.H. van Laar, H. van Keulen and W. Louwerse (1984). Simulation of the effect of increased atmospheric CO<sub>2</sub> on assimilation and transpiration of a closed crop canopy. Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin, Math.-Nat. R. XXXIII 4: 352-356.
- Grant, S.A., G.T. Barthram and L. Torvell (1981). Components of regrowth in grazed and cut *Lolium perenne* swards. Grass and Forage Science 36: 155-168.
- Grant, S.A., G.T. Barthram, L. Torvell, J. King and H.K. Smith (1983). Sward management, lamina turnover and tiller population density in continuously stocked *Lolium perenne*-dominated swards. Grass and Forage Science 38: 333-344.
- Hansen, G.K. (1978). Utilization of photosynthates for growth, respiration, and storage in tops and roots of *Lolium multiflorum*. Physiologia Plantarum 42: 5-13.
- Hodgson, J., J.S. Bircham, Sheila A. Grant and J. King (1981). The influence of cutting and grazing management on herbage growth and utilisation. In: Plant Physiology and herbage production (Ed. C.E. Wright), Occasional Symposium no. 13, Nottingham, pp. 51-62. The British Grassland Society, Hurley.
- Hood, A.E.M. (1974). Intensive set-stocking of dairy cows. Journal of British Grassland Society 29: 63-67.
- Iwasaki, M. (1972). Comparison of some simplified methods for measuring the forage consumed by grazing animals. Bulletin National Grassland Research Institute 1: 31-37.
- Jackson, D.K. (1974). Some aspects of production and persistency in relation to height of defoliation of *Lolium perenne* (var. S.23). In: Proceedings of the XII International Grassland Congress (Eds. V.G. Iglovikov and A.P. Movsissyants), Moscow; Vol. III, Part 1: 202-214.
- Johnstone-Wallace, D.B. and K. Kennedy (1944). Grazing management practices and their relationship to the behaviour and grazing habits of cattle. Journal of Agricultural Science 34: 190-197.
- Jones, M.B., E.L. Leafe, W. Stiles and B. Collett (1978). Pattern of respiration of a perennial ryegrass crop in the field. Annals of Botany 42: 693-703.
- Jones, M.B., E.L. Leafe and W. Stiles (1980). Water stress in field-grown perennial ryegrass. I. Its effect on growth, canopy photosynthesis and transpiration, Annals of applied Biology 96: 87-101.
- Keulen, H. van (1976). A calculation method for potential rice production. Contributions, Central Research Institute for Agriculture, Bogor, Indonesia, No. 21, 26 pp.
- Keulen, H. van (1982). Crop production under semi-arid conditions, as determined by moisture availability. In: Simulation of plant growth and crop production (Eds. F.W.T. Penning de Vries and H.H. van Laar), pp. 159-174. Simulation Monographs Series. Pudoc, Wageningen.

- King, J., E.M. Sim and S.A. Grant (1984). Photosynthetic rate and carbon balance of grazed ryegrass pastures. *Grass and Forage Science*, 39: 81-92.
- Kornher, A. and S. Nyström (1971). Über Bestimmungen der Produktion und Produktivität von Futterpflanzenbeständen nach einem Photosynthesemodell-Photosynthesemessungen und Modellberechnungen im Vergleich mit experimentellen Zuwachsbestimmungen. *Acta Agriculturae Scandinavica* 21: 267-283.
- Laeven-Kloosterman, A.F. and J. Overvest (1983). Graslandgebruikssystemen en arbeidsopbrengst. Gebundelde Verslagen nr. 24. Nederlandse Vereniging voor weide- en voederbouw, pp. 1-8
- Leafe, E.L., W. Stiles, A.J. Parsons and B. Collett (1979). The growth of the grass sward under grazing. Annual Report GRI Hurley 1978: 50.
- Linehan, P.A., J. Lowe and R.H. Stewart (1947). The output of pasture and its measurement. Part II. *Journal of British Grassland Society* 2: 145-168.
- Luten, W. and H. Schlepers (1981). Standweiden. *Bedrijfsontwikkeling* 3: 251-257.
- Marshall, B. and P.V. Biscoe (1977). A mobile apparatus for measuring leaf photosynthesis in the field. *Journal of Experimental Botany* 28: 1008-1017.
- McCree, K.J. (1982). Maintenance requirements of white clover at high and low growth rates. *Crop Science* 22: 345-351.
- Meijs, J.A.C. (1981). Herbage intake by grazing dairy cows. *Agricultural Research Reports* 909. Pudoc, Wageningen, 264 pp.
- Meijs, J.A.C. (1983). The influence of concentrate supplementation on herbage intake by grazing dairy cows. 2. Report of the experiment on herbage intake in 1982. Rapport I.V.V.O. Lelystad no. 149.
- Meijs, J.A.C., J.W.F. Hijink, P. Ernst and H. Schlepers (1982). Beweidingsverliezen (Grazing losses). Rapport nr. 145. Instituut voor Veevoedingsonderzoek, Lelystad.
- McMeekan, C.P. and M.J. Walshe (1963). The inter-relationship of grazing method and stocking rate in the efficiency of pasture utilization by dairy cattle. *Journal of Agricultural Science* 61: 147-163.
- Monteith, J.L. (1965). Light distribution and photosynthesis in field crops. *Annals of Botany* 29: 17-37.
- Monteith, J.L. (1977). Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society of London B* 281: 277-294.
- Moser, L.E., J.J. Volenec and C.J. Nelson (1982). Respiration, carbohydrate content and leaf growth of tall fescue. *Crop Science* 22: 781-786.
- Overgaard Mogensen, V. (1977). Field measurements of dark respiration rates of roots and aerial parts in Italian ryegrass and barley. *Journal of applied Ecology* 14: 243-252.
- Parsons, A.J., E.J. Leafe, W. Stiles and B. Collett (1981). The growth of a grass sward under grazing. Annual Report GRI Hurley 1980: 37-40.
- Parsons, A.J. and M.J. Robson (1981). Seasonal changes in the physiology of S24 perennial ryegrass (*Lolium perenne* L.). 3. Partition of assimilates between root and shoot during the transition from vegetative to reproductive growth. *Annals of Botany* 48: 733-744.
- Parsons, A.J. and M.J. Robson (1982). Seasonal changes in the physiology of S24 perennial ryegrass (*Lolium perenne* L.). 4. Comparison of the carbon balance of the reproductive crop in spring and the vegetative crop in autumn. *Annals of Botany* 50: 167-177.
- Parsons, A.J. E.L. Leafe, B. Collett and W. Stiles (1983a). The physiology of grass production under grazing. 1. Characteristics of leaf and canopy photosynthesis of continuously-grazed swards. *Journal of Applied Ecology*, 20: 117-126.

- Parsons, A.J., E.L. Leafe, B. Collett, P.D. Penning and J. Lewis (1983b). The physiology of grass production under grazing. II. Photosynthesis, crop growth and animal intake of continuously-grazed swards. *Journal of Applied Ecology* 20: 127-139.
- Parsons, A.J., E.L. Leafe and P.D. Penning (1983c). Crop physiological limitation to production under continuous and rotational grazing. *Proceedings of the 9th General Meeting of the European Grassland Federation* (Ed. A.J. Corral), pp. 145-148.
- Peacock, J.M. (1976). Temperature and leaf growth in four grass species. *Journal of Applied Ecology* 13: 225-232.
- Penning de Vries, F.W.T. (1983). Modelling of growth and production. In: *Encyclopedia of Plant Physiology New Series Vol. 12D; Physiological Plant Ecology IV* (Eds. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler), pp. 118-150. Springer-Verlag Berlin Heidelberg 1983.
- Penning de Vries, F.W.T. and H.H. van Laar (1982). Simulation of growth processes and the model BACROS. In: *Simulation of plant growth and crop production*. (Eds. F.W.T. Penning de Vries and H.H. van Laar), pp. 114-135. Pudoc, Wageningen.
- Prins, W.H. (1983). Limits to nitrogen fertilizer on grassland. Doctoral Thesis Wageningen. Veenstra, Groningen, (x)+44 pp.
- Redmann, R.E. and Z.M. Abouguendia (1978). Partitioning of respiration from soil, litter and plants in a mixed-grassland ecosystem. *Oecologia* (Berl.) 36: 69-79.
- Robson, M.J. and A.J. Parsons (1978). Nitrogen deficiency in small closed communities of S24 ryegrass. I. Photosynthesis, respiration, dry matter production and partition. *Annals of Botany* 42: 1185-1197.
- Ryle, G.J.A. and C.E. Powell (1975). Defoliation and regrowth in the graminaceous plant: the role of current assimilate. *Annals of Botany* 39: 297-310.
- Schlepers, H., M.L. 't Hart, S. Boer Iwema, A. de Jong and J.H. Neuteboom (1982). Vergelijking van de onderzoeksresultaten van drie jaar omweiden - standweiden (1978-1980) op de Ir. A.P. Minderhoudhoeve te Swifterbant. Mededeling no. 66, Vakgroep Landbouwplantenteelt en Graslandkunde, Landbouwhogeschool Wageningen.
- Sheehy, J.E., J.M. Cobby and G.J.A. Ryle (1979). The growth of perennial ryegrass: a model. *Annals of Botany* 43: 335-354.
- Sheehy, J.E., J.M. Cobby and G.J.A. Ryle (1980). The use of a model to investigate the influence of some environmental factors on the growth of perennial ryegrass. *Annals of Botany* 46: 343-365.
- Stigter, C.J. and V.M.M. Musabilha (1982). The conservative ratio of photosynthetically active to total radiation in the tropics. *Journal of Applied Ecology* 19: 853-858.
- St-Pierre, J.C. and M.J. Wright (1972). Distribution of <sup>14</sup>C Photosynthates in Timothy during the vegetative stage of growth. *Crop Science* 12: 191-194.
- Spiertz, J.H.J. and J. Ellen (1978). Effects of nitrogen on crop development and grain growth of winter wheat in relation to assimilation and utilization of assimilates and nutrients. *Netherlands Journal of agricultural Science* 26: 210-231.
- Wardlaw, I.F. (1969). The effect of water stress on translocation in relation to photosynthesis and growth. II. Effect during leaf development in *Lolium temulentum* L. *Australian Journal of Biological Science*, 22: 1-16.
- Wilman, D. and A.A. Mohamed (1981). Response to nitrogen application and interval between harvests in five grasses. 2. Leaf development. *Fertilizer Research* 2: 3-20.

- Wilman, D. and P.T. Wright (1983). Some effects of applied nitrogen on the growth and chemical composition of temperate grasses. *Herbage Abstracts* 53: 387-393.
- Wilson, J.R. (1975). Comparative response to nitrogen deficiency of a tropical and temperate grass in the interrelation between photosynthesis, growth, and the accumulation of non-structural carbohydrate. *Netherlands Journal of agricultural Science* 23: 104-112.
- Wit, C.T. de (1965). Photosynthesis of leaf canopies. *Agricultural Research Reports* no. 663. Pudoc, Wageningen, 57 pp.
- Wit, C.T. de et al. (1978). Simulation of assimilation, respiration and transpiration of crops. *Simulation Monographs Series*. Pudoc, Wageningen, 148 pp.
- Wit, C.T. de, H.H. van Laar and H. van Keulen (1979). Physiological potential of crop production. In: *Plant Breeding Perspectives* (Eds. J.Sneep and A.J.T. Hendriksen), pp.47-82. Pudoc, Wageningen.
- Wolledge, J. and E.L. Leafe (1976). Single leaf and canopy photosynthesis in a ryegrass sward. *Annals of Botany* 40: 773-783.
- Zemmelink, G. (1980). Effect of selective consumption on voluntary intake and digestibility of tropical forages. *Agricultural Research Reports* 896. Pudoc, Wageningen, 100 pp.

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### Curriculum vitae

Egbert Anne Lantinga werd geboren op 23 juni 1956 te Middelburg. Na het behalen van het diploma Atheneum-B aan het Goese Lyceum te Goes in 1974, begon hij in september van datzelfde jaar met een studie aan de Landbouwhogeschool te Wageningen. In maart 1981 studeerde hij met lof af in de richting Landbouwplantenteelt met als hoofdvakken de Leer van het Grasland en de Theoretische Teeltkunde en als keuzevakken de Meteorologie en Klimatologie en de Veevoeding. Van april 1981 tot juli 1984 deed hij met subsidie van de Nederlandse organisatie voor zuiver-wetenschappelijk onderzoek (Z.W.O.) onderzoek naar de produktiviteit van grasland onder beweiding. Dit onderzoek werd als gastmedewerker van de Landbouwhogeschool bij de vakgroepen Landbouwplantenteelt en Graslandkunde en Theoretische Teeltkunde uitgevoerd. Vanaf 1 juli 1984 is hij als wetenschappelijk medewerker werkzaam bij de vakgroep Landbouwplantenteelt en Graslandkunde.