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Ecophysiological aspects of herbage production in grazed and cut grassland

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Summary

Grasslands account for about 20% of the terrestrial CO_2 fluxes of the global carbon cycle and may therefore contribute to a global biotic carbon sequestration, reducing the rate of increase of atmospheric CO_2. At a fertilizer N input higher than 100 kg N ha^{-1} year^{-1} the annual gross crop CO_2 assimilation on loam and clay perennial ryegrass swards in the Netherlands is between 20 and 22 t C ha^{-1} under cutting or grazing management, irrespective of grazing system. The absence of an effect of N fertilization on crop CO_2 assimilation could be explained from a 'down-regulation' in the relationship between leaf N concentration and maximum leaf CO_2 assimilation rate from low to high N input levels. The main effect of low N was a marked reduction in leaf area development, reflected in lower herbage intake levels under grazing and a reduced light-use efficiency (LUE) under cutting with respect to the harvested yield. This reduction in LUE at decreasing N supply was associated with an increased allocation of assimilates to unharvested plant parts (roots and stubble). The latter phenomenon was also observed in a seminatural grassland ecosystem in Slovakia. In a study of short-term grassland ecosystem processes at the field scale (1 km length) in the Netherlands, a net CO_2 uptake was measured in spring whereas in the autumn a net emission occurred. After correction for soil and vegetation respiration, the relationship between short-wave irradiance and gross photosynthetic CO_2 flux was not different for the two parts of the growing season and was in accordance with measurements at much smaller spatial scales (1 or 2 m^2 of canopy).

Keywords: carbon balance, continuous grazing, CO_2 assimilation, cutting, grassland ecosystem, herbage production, nitrogen, perennial ryegrass, respiration, rotational grazing

Introduction

Grasslands play an important role in the cycling of CO_2. They account for about 20% of the terrestrial CO_2 fluxes of the global carbon cycle, and have a similar share in global soil organic carbon (Minami *et al.*, 1994). Grasslands may therefore contribute to a global biotic carbon sequestration, reducing the rate of increase of atmospheric CO_2. Figure 1 shows the annual carbon balance of mown perennial ryegrass swards at a fertilizer nitrogen (N) input range of 100 to 700 kg N ha^{-1} year^{-1} and ambient atmospheric CO_2 concentration (on average about 340 µmol mol^{-1}).

Figure 1. Annual carbon balance of mown perennial ryegrass swards at a fertilizer N range of 100 to 700 kg N ha^{-1} year^{-1}. Source: Pol-Van Dasselaar (1995).
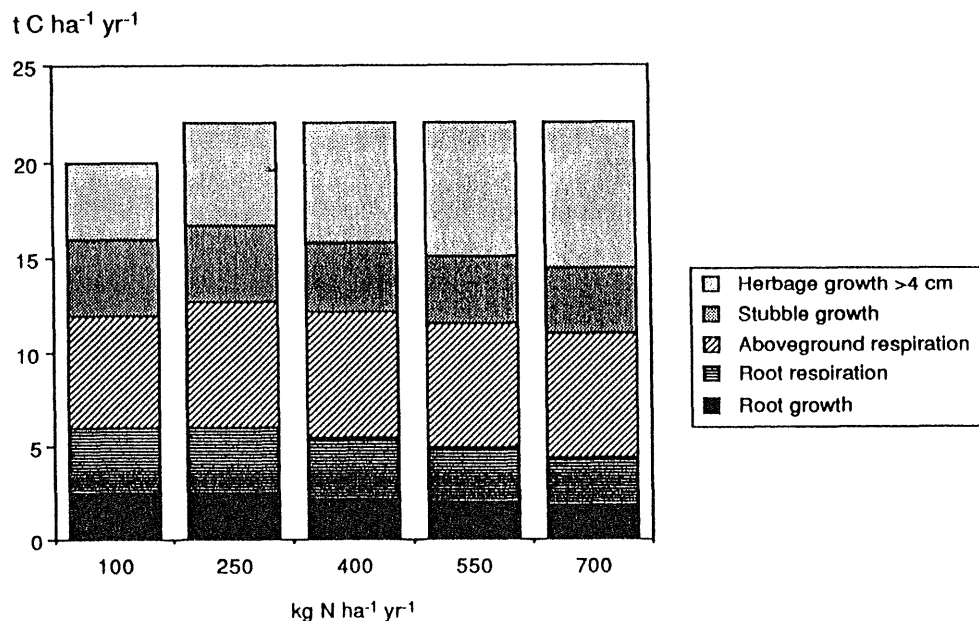
t C ha^{-1} yr^{-1}

kg N ha^{-1} yr^{-1}

Figure 1 is based on experimental results collected on loam and clay grassland soils in the Netherlands (Pol et al., 1995). The annual gross crop CO_2 assimilation of grass is, under good water supply, on average 22 t C ha^{-1} year^{-1} at fertilizer levels ranging from 250 to 700 kg N ha^{-1} year^{-1}. At a fertilizer level of 100 kg N ha^{-1} year^{-1} the annual gross crop CO_2 assimilation is about 10% lower. At increasing rates of N application a smaller part of the assimilated carbon is translocated to the roots and stubble, stimulating the production of harvestable herbage. The proportion of gross CO_2 uptake lost by shoot respiration equals about 30%, independent of rate of N application. The carbon balance of grazed grassland is more complex. Uptake of CO_2 may be restricted through sward damage caused by grazing animals, especially at high N input levels (Deenen, 1994). Besides, in undamaged grazed grassland the stubble production is higher than that in mown grassland due to higher tillering rates and more prostrate growth (Lantinga, unpublished measurements). The two grazing systems, continuous and rotational, differ, not only in the method 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 separated. But in spite of these differences, herbage intake may be similar under the two systems (Parsons et al., 1983b). In this paper three topics will be discussed: i) the backgrounds of herbage production under continuous and rotational grazing as influenced by the level of N supply, ii) the role of N in yield physiology of seminatural grassland ecosystems, and iii) CO_2 fluxes in grassland ecosystems at a regional level.

Productivity of grassland under continuous and rotational grazing as influenced by fertilizer N supply

Historical overview

Grazing is the most important method of utilization of grassland. Zero-grazing, i.e. feeding of mown grass to housed cattle, or summer-feeding, i.e. feeding of ensiled grass to housed cattle during the growing season, is used only to a limited extent as the extra costs in comparison with grazing exceed the benefits resulting from the higher grassland yield per unit area. The harvested yield under grazing is always lower than under a cutting regime due to more stubble production, grazing losses (senescence of uneaten grass for instance around dung patches) and sward damage (urine scorching and poaching). Grazing can be performed in many different ways. 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 herbage quality, a high herbage allowance is needed. 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 18th century, as noted by Johnstone *et al.* (1944). They quoted the writings of James Anderson (1797), who described certain types of grazing practice, 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 the trials by 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 was somewhat dubious, as there were differences in the level and pattern of nitrogen fertilization. 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 the case of rotational grazing nitrogen was applied more regularly (at the start of each regrowth period). It is now known that there need to be no problems with nitrogen application in the presence of cattle (Hood, 1974). In the 1950s and 1960s rotational grazing became more and more common practice in the Netherlands. The main reasons for this rapid expansion were the introduction of cheap fertilizer and methods of fencing, and improved information to the farmers. In other countries continuous grazing was still the most important grazing system and was studied in experiments. For instance, McMeekan & Walshe (1963) concluded from experiments with dairy cows under New Zealand conditions that stocking rate was a more important factor in determining the efficiency of pasture utilization than the grazing method. These results stimulated Hood (1974) to start experiments with continuous grazing in the UK, at high rates of nitrogen fertilizer and high stocking rates. He found at an average stocking rate of 4 cows ha^{-1} and a fertilizer rate of 500 kg N ha^{-1}year^{-1} no difference in milk production per head between the two grazing systems. This result gave a new impetus to the discussion on grazing systems and in countries like Germany, Belgium and the Netherlands, similar trials were started in the late 1970s. In general, the results of experiments with 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 & Lantinga, 1985).

Physiological studies

In all of the above trials, only data on animal production were obtained. No detailed measurements on herbage production were made since this is difficult and laborious, especially under continuous grazing. In the early 1980s, Parsons *et al.* (1983 a,b) and Lantinga (1985; Table 1) studied the physiology of grass growth under grazing by making use of measurements of CO_2 assimilation and respiration with crop enclosures. This method provides more insight into the process of herbage production in grazed swards.

Table 1. Total crop gross CO_2 assimilation (CO_2 uptake) and herbage intake under continuous and rotational grazing with steers at two nitrogen levels during the grazing season of 1981. Relative figures within brackets. Location: permanent perennial ryegrass sward on river clay in Wageningen. Source: Lantinga (1985).

GRAZING SYSTEM	FERTILIZATION	CO2	HERBAGE	PROPORTION
		UPTAKE (A)	INTAKE (B)	INGESTED
	(kg N ha⁻¹)	(t C ha⁻¹)	(t C ha⁻¹)	(b/a * 100)
Continuous	115	20.2 (93)	3.7 (69)	18.3
	430	19.8 (91)	5.4 (100)	27.3
Rotational	120	20.6 (95)	3.8 (70)	18.4
	500	21.6 (100)	5.4 (100)	25.0

It can be seen in Table 1 that at high nitrogen the cumulative gross CO_2 assimilation over the grazing season was 9% higher under rotational compared to continuous grazing, whereas there was no difference in animal production. The higher efficiency of utilization of assimilates under continuous grazing at high N was attributed to lower grazing losses (less rejected grass and lower topping losses) and lower costs for aboveground maintenance respiration (less biomass). The level of nitrogen application had no clear effect on total gross CO_2 assimilation (Table 1). Since the average LAI was not different among the four treatments (around 3), it could be concluded that gross CO_2 assimilation per unit leaf area was not depressed at low N. This is also shown in Figure 2, where crop gross assimilation rates at 500 W m⁻² (400-3000 nm) at high N are plotted against those for low N at the same LAI and measured in the same part of the season. The absence of an effect of N fertilization on leaf CO_2 assimilation can be explained from a "down-regulation" in the relationship between leaf N concentration and CO_2 assimilation rate from low to high N input levels (Figure 3). Probably, at high N fertilization a higher proportion of leaf N is not present in active Rubisco but in the form of inactive Rubisco, amino acids, amides and inorganic N. The main effect of low N was a marked reduction in the rate of leaf area development. This was reflected in longer regrowth periods under rotational grazing and lower stocking densities under continuous grazing at low N, resulting in lower herbage intake levels per ha. The lower proportion of assimilated carbon ingested at low N was accompanied by a higher allocation of carbon to the stubble and especially the roots. This is in accordance with the results presented in Figure 4, where the relationship between leaf N content and light-use efficiency (LUE) is presented at three yield levels above a 4-cm stubble. At optimal N supply, LUE was about 2 g DM MJ⁻¹ PAR. At suboptimal N supply, LUE decreased, but due to 'dilution' of plant N in an increasing plant mass (Wilson & Lemaire, 1992) the relationship between leaf N

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content and LUE was less steep at higher herbage masses. Since there was no decrease in the rate of leaf CO_2 assimilation, the reduction in LUE at decreasing N supply levels could be explained only by an increased allocation of assimilates to unharvested plant parts (roots and stubble). According to Belanger *et al.* (1994) especially root respiration and exudation do increase in the case of N deficiency.

Figure 2. *Relationship between crop gross assimilation at 500 W m^2 (400-3000 nm) in high and low N grazed swards measured at the same LAI and in the same part of the season. Source: Lantinga (1985).*
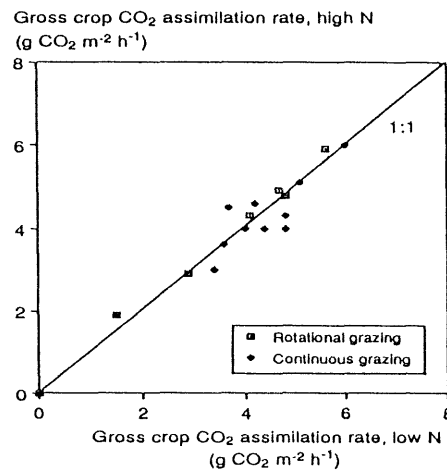
Gross crop CO_2 assimilation rate, high N
(g CO_2 m^{-2} h^{-1})

Gross crop CO_2 assimilation rate, low N
(g CO_2 m^{-2} h^{-1})

Figure 3. *Relationship between leaf nitrogen concentration and maximum net leaf CO_2 assimilation rate as influenced by level of N supply (low N: 0 and 250 kg N ha^{-1} year^{-1}; high N: 400 kg N ha^{-1} year^{-1}). Source: Ruttenberg (1989).*

Maximum net leaf CO_2 assimilation rate
(mg CO_2 m^{-2} s^{-1})

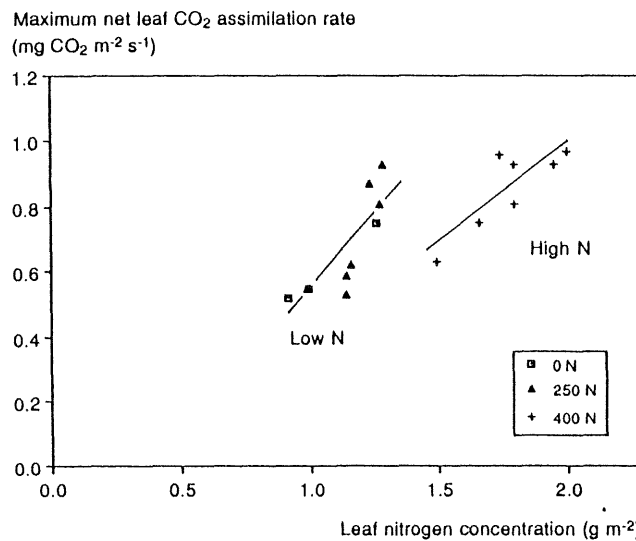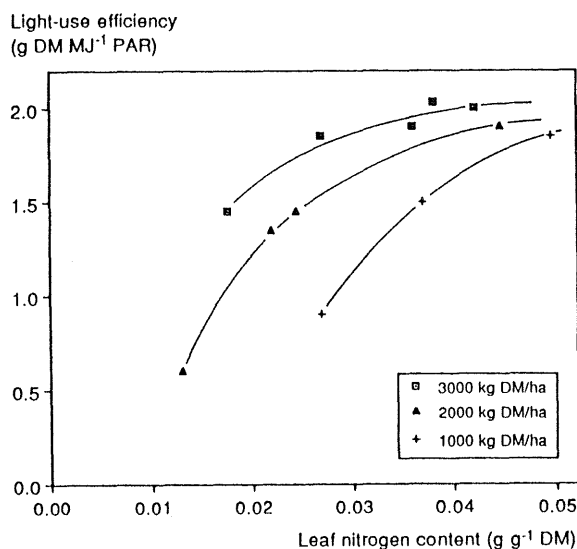Leaf nitrogen concentration (g m^{-2})

Figure 4. Relationship between leaf nitrogen content and light-use efficiency at three levels of herbage yield above a 4-cm stubble. Source: Van den Broek (1989).

The role of nitrogen in yield physiology of seminatural grassland ecosystems: an example from Slovakia

There is considerable information about the influence of nitrogen on dry matter production but little concerning yield physiology of grassland in Slovakia. Therefore some ecophysiological aspects of the influence of nitrogen (0, 150 and 300 kg N ha^{-1} year^{-1}) and cutting intensity (three or five times per year) were studied during the period 1976-1988 in the central part of Slovakia near Banska Bystrica (Gáborčik & Krajčovič, 1992). The location was a seminatural grassland characterized by an *Anthoxantho-Agrostietum* assocation with cocksfoot (*Dactylis glomerata* L.) as the main species. Amongst others, the following growth parameters were investigated: average crop growth rate (CGR), LAI at harvest and average net assimilation rate (NAR). Under both cutting regimes application of N influenced growth parameters in the following order: CGR > LAI > NAR (Table 2). The small difference in NAR between the two fertilized treatments is in accordance with results from perennial ryegrass swards in the Netherlands discussed previously. The distribution of assimilates between shoot and root was also influenced by N fertilization. Whereas the average root biomass in the control treatment (N0) was 1.05 kg DM m[-2], it decreased to 0.82 and 0.76 kg DM m[-2] in N150 and N300 treatments, respectively. However, application of N enhanced the proportion of living roots from 49% to 61 and 74%, respectively. Also, the structure of the sward aboveground was influenced by N. In the N0 treatment the highest amount of dry matter was found in the lowest sward layer (0-10 cm). In the fertilized treatments, most of the dry matter had been accumulated in the sward layer 10-25 cm. This confirms the stimulating effect of N on harvestable herbage yield at the expense of stubble growth.

Table 2. Growth parameters of a seminatural grassland ecosystem in Slovakia as influenced by N supply and cutting frequency. 3-C and 5-C denote cutting 3 or 5 times per year, respectively. Source: Gáborčík & Krajčovič, 1992.

N SUPPLY	CGR		LAI		NAR	
(kg N ha^{-1} year^{-1})	(g DM m^{-2}d^{-1})		(m^2 leaf m^{-2} soil)		(g DM m^{-2} leaf d^{-1})	
	3-C	5-C	3-C	5-C	3-C	5-C
0	1.90	1.05	1.28	0.45	2.82	2.44
150	6.43	3.86	2.87	1.37	4.71	4.27
300	7.19	4.55	3.53	1.66	4.92	4.44

CO$_2$ fluxes in grassland ecosystems

Short-term relationships between the environment and plant physiological processes, such as photosynthesis and respiration, underlie long-term plant growth. However, in general, a substantial discrepancy exists between the spatial scales when it comes to studying plant performance at both temporal scales. Research on photosynthesis and respiration is usually confined to a spatial maximum of approximately 1 or 2 m^2 of canopy, whereas research on growth is pursued on all spatial scales. At field scale the heterogeneity in space in soil and plant characteristics is largely unknown in quantitative terms, different between different fields, and sizeable. To study short-term grassland ecosystem processes at the field scale without the need to explicitly consider field heterogeneity and its consequences for plant response, the Netherlands Energy Research Foundation (ECN) applied the Aerodynamic Gradient Technique in Dutch pasture land near Cabauw (Hensen *et al.*, 1995). The site is composed of a characteristic succession of strips of pasture land - intensively managed for dairy farming, mixed rotational grazing and cutting, and predominantly *Lolium perenne* L. - and waterways. The soil consists of a 0.5-0.8 m thick layer of alluvial clay on a massive peat layer. The groundwater Table was high (at approximately 1 m depth), but varied in time and space. From the measurements instantaneous mass (CO$_2$ and H$_2$O) and energy exchange were calculated for a large area, in the order of 1 km length. A measured fetch always simultaneously comprised pasture land at different stages of regrowth, and, therefore, did not have an unequivocal leaf area or homogeneous canopy characteristics. A consequence of the applied technique is that it does not explicitly distinguish between aboveground and belowground processes contributing to the mass exchange. Figure 5 shows the average diurnal patterns of the ecosystem CO$_2$ exchange for two contrasting months, April and August 1993, for vegetation and soil organic matter together. During night-time an upward CO$_2$ flux of 0.2-0.4 mg m^{-2} s^{-1} was observed. During day-time a maximum downward CO$_2$ flux of 0.7 mg m^{-2} s^{-1} was observed at noon in April, and of 0.4 mg m^{-2} s^{-1} before noon in August. The ecosystem CO$_2$ flux is the net result of often contrasting effects of environmental conditions on CO$_2$ fluxes in the ecosystem components. In April 1993 there was an average daily net CO$_2$ uptake by the ecosystem of 5.25 g CO$_2$ m^{-2} d^{-1}, whereas in August 1993 there was a net CO$_2$ emission of 5.11 g CO$_2$ m^{-2} d^{-1}. It is obvious that during day-time the radiation level plays an important role in the ecosystem CO$_2$ flux. Figure 6 suggests a convergence of [CO$_2$]$_{atm}$ in the lower part of the boundary layer to 345-350 µmol mol^{-1} at increasing short-wave irradiance (global radiation). The triangular relationship reflects both a reduced atmospheric mixing at low irradiance due

to occurrence of an atmospheric inversion layer, and an increasing net CO_2 assimilation and therefore depletion of atmospheric CO_2 at increasing irradiance.

Figure 5. Average diurnal patterns of ecosystem CO_2 flux in pasture land near Cabauw, the Netherlands, for April and August 1993 (source data: ECN).
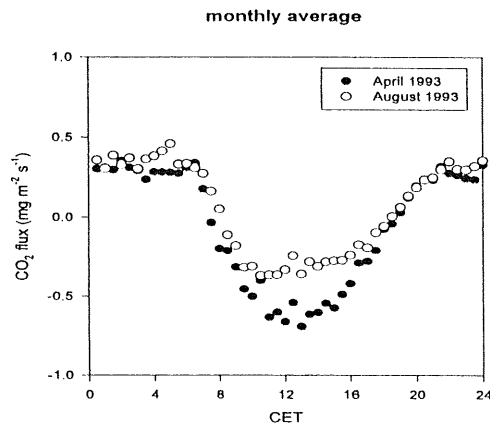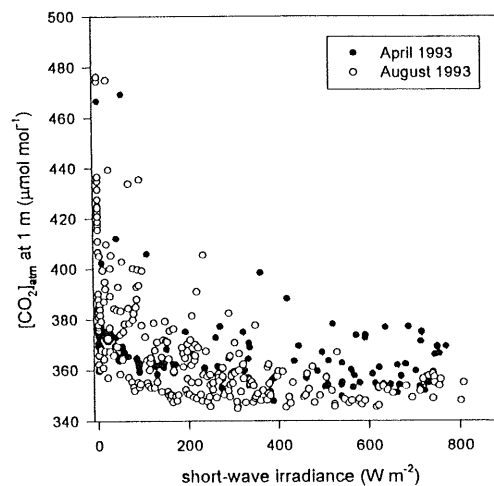

Figure 6. Atmospheric $[CO_2]$ at 1 m height (half-hourly average) as a function of short-wave irradiance (global radiation) in pasture land near Cabauw, the Netherlands, during April and August 1993 (source data: ECN and KNMI).

The relationship between short-wave irradiance (I_s) and ecosystem CO_2 flux (F_c), shown in Figure 7, can be regressed by either a hyperbolic or an exponential curve (r^2 approximately 0.75 in all cases), in accordance with relationships found at smaller spatial scales. Comparison of April and August 1993 shows a higher upward CO_2 flux at zero irradiance and lower asymptotic CO_2 flux value in August, e.g. $F_{c.\ April} = 1.44 \times I_s$

$/(252+I_s)+0.30$ and $F_{c,\ August}=-1.32xI_s/(224+I_s)+0.42$. This difference might partly be due to different contributions by the soil organic matter component during both months. Since the night-time ecosystem CO_2 flux is determined by respiration of both vegetation and soil organic matter, those values can be used to approximate day-time ecosystem respiration as a function of temperature. When subtracting this calculated ecosystem respiration from the measured day-time ecosystem CO_2 flux, an approximation of the (gross) photosynthetic CO_2 flux is the result.

Figure 7. Ecosystem CO_2 flux (measured half-hourly averages) and derived photosynthetic CO_2 flux (half-hourly averages) as a function of short-wave irradiance (global radiation) in pasture land near Cabauw, the Netherlands, during April and August 1993 (source data: ECN and KNMI).
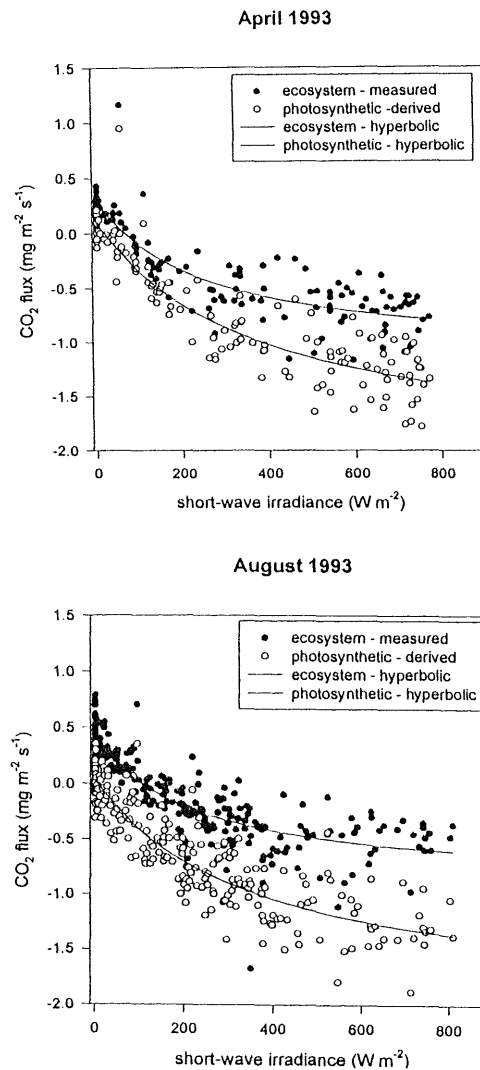
April 1993

August 1993

Figure 7 also shows the derived photosynthetic CO_2 flux. It appears that the hyperbolic relationship between short-wave irradiance and CO_2 flux is retained. In both months, the calculated average crop gross CO_2 assimilation at 500 W m^{-2} was about 1.2 g CO_2 m^{-2} s^{-1}. This would correspond with an average LAI of about 2.5 (Lantinga, 1985). From these data it could be concluded that, even at this large spatial scale and with the specific spatial heterogeneity in this pasture land, clear relationships existed between basic environmental variables on the one hand and ecosystem CO_2 fluxes on the other hand, similar to processes at smaller spatial scales. Both the involvement of other environmental variables as shown above and spatial heterogeneity in vegetation and soil organic matter components are likely to explain the remaining variance. However, statistical regression analysis is bound to include only a limited part of these factors, and is, therefore, to be supplemented by more detailed mechanistic modelling.

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Summary

Grasslands account for about 20% of the terrestrial CO_2 fluxes of the global carbon cycle and may therefore contribute to a global biotic carbon sequestration, reducing the rate of increase of atmospheric CO_2. At a fertilizer N input higher than 100 kg N ha^{-1} year^{-1} the annual gross crop CO_2 assimilation on loam and clay perennial ryegrass swards in the Netherlands is between 20 and 22 t C ha^{-1} under cutting or grazing management, irrespective of grazing system. The absence of an effect of N fertilization on crop CO_2 assimilation could be explained from a 'down-regulation' in the relationship between leaf N concentration and maximum leaf CO_2 assimilation rate from low to high N input levels. The main effect of low N was a marked reduction in leaf area development, reflected in lower herbage intake levels under grazing and a reduced light-use efficiency (LUE) under cutting with respect to the harvested yield. This reduction in LUE at decreasing N supply was associated with an increased allocation of assimilates to unharvested plant parts (roots and stubble). The latter phenomenon was also observed in a seminatural grassland ecosystem in Slovakia. In a study of short-term grassland ecosystem processes at the field scale (1 km length) in the Netherlands, a net CO_2 uptake was measured in spring whereas in the autumn a net emission occurred. After correction for soil and vegetation respiration, the relationship between short-wave irradiance and gross photosynthetic CO_2 flux was not different for the two parts of the growing season and was in accordance with measurements at much smaller spatial scales (1 or 2 m^2 of canopy).

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Introduction

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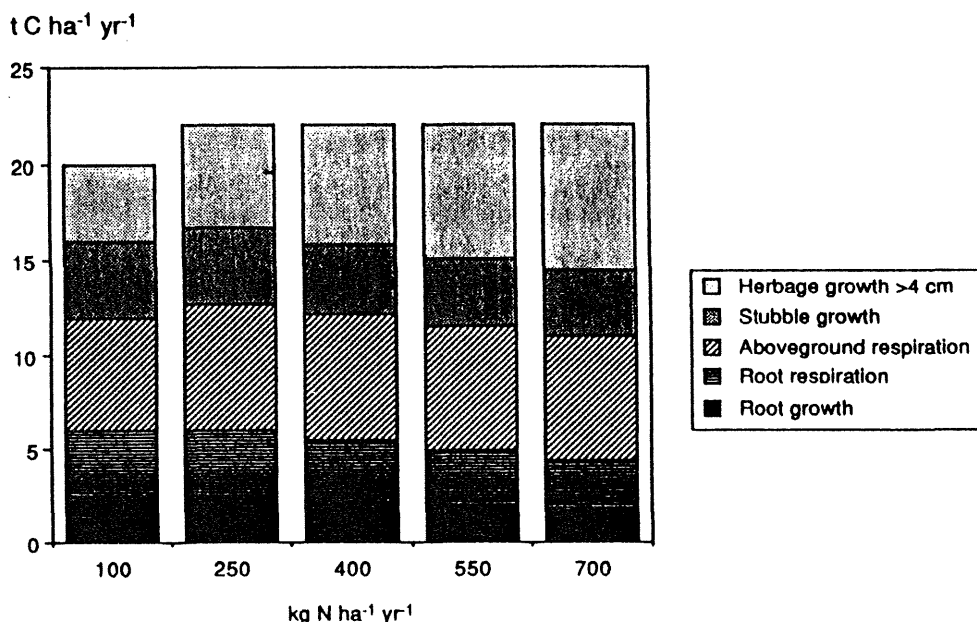lizer N range of 100 to 700 kg N ha⁻¹ year⁻¹. Source: Pol-Van Dasselaar (1995).

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Productivity of grassland under continuous and rotational grazing as influenced by fertilizer N supply

Historical overview

Grazing is the most important method of utilization of grassland. Zero-grazing, i.e. feeding of mown grass to housed cattle, or summer-feeding, i.e. feeding of ensiled grass to housed cattle during the growing season, is used only to a limited extent as the extra costs in comparison with grazing exceed the benefits resulting from the higher grassland yield per unit area. The harvested yield under grazing is always lower than under a cutting regime due to more stubble production, grazing losses (senescence of uneaten grass for instance around dung patches) and sward damage (urine scorching and poaching). Grazing can be performed in many different ways. 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 herbage quality, a high herbage allowance is needed. 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 18th century, as noted by Johnstone *et al.* (1944). They quoted the writings of James Anderson (1797), who described certain types of grazing practice, 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 the trials by 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 was somewhat dubious, as there were differences in the level and pattern of nitrogen fertilization. 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 the case of rotational grazing nitrogen was applied more regularly (at the start of each regrowth period). It is now known that there need to be no problems with nitrogen application in the presence of cattle (Hood, 1974). In the 1950s and 1960s rotational grazing became more and more common practice in the Netherlands. The main reasons for this rapid expansion were the introduction of cheap fertilizer and methods of fencing, and improved information to the farmers. In other countries continuous grazing was still the most important grazing system and was studied in experiments. For instance, McMeekan & Walshe (1963) concluded from experiments with dairy cows under New Zealand conditions that stocking rate was a more important factor in determining the efficiency of pasture utilization than the grazing method. These results stimulated Hood (1974) to start experiments with continuous grazing in the UK, at high rates of nitrogen fertilizer and high stocking rates. He found at an average stocking rate of 4 cows ha⁻¹ and a fertilizer rate of 500 kg N ha⁻¹year⁻¹ no difference in milk production per head between the two grazing systems. This result gave a new impetus to the discussion on grazing systems and in countries like Germany, Belgium and the Netherlands, similar trials were started in the late 1970s. In general, the results of experiments with 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 & Lantinga, 1985).

Physiological studies

In all of the above trials, only data on animal production were obtained. No detailed measurements on herbage production were made since this is difficult and laborious, especially under continuous grazing. In the early 1980s, Parsons *et al.* (1983 a,b) and Lantinga (1985; Table 1) studied the physiology of grass growth under grazing by making use of measurements of CO_2 assimilation and respiration with crop enclosures. This method provides more insight into the process of herbage production in grazed swards.

Table 1. *Total crop gross CO_2 assimilation (CO_2 uptake) and herbage intake under continuous and rotational grazing with steers at two nitrogen levels during the grazing season of 1981. Relative figures within brackets. Location: permanent perennial ryegrass sward on river clay in Wageningen. Source: Lantinga (1985).*

GRAZING SYSTEM	FERTILIZATION	CO2 UPTAKE (A)	HERBAGE INTAKE (B)	PROPORTION INGESTED
	(kg N ha⁻¹)	(t C ha⁻¹)	(t C ha⁻¹)	(b/a * 100)
Continuous	115	20.2 (93)	3.7 (69)	18.3
	430	19.8 (91)	5.4 (100)	27.3
Rotational	120	20.6 (95)	3.8 (70)	18.4
	500	21.6 (100)	5.4 (100)	25.0

It can be seen in Table 1 that at high nitrogen the cumulative gross CO_2 assimilation over the grazing season was 9% higher under rotational compared to continuous grazing, whereas there was no difference in animal production. The higher efficiency of utilization of assimilates under continuous grazing at high N was attributed to lower grazing losses (less rejected grass and lower topping losses) and lower costs for aboveground maintenance respiration (less biomass). The level of nitrogen application had no clear effect on total gross CO_2 assimilation (Table 1). Since the average LAI was not different among the four treatments (around 3), it could be concluded that gross CO_2 assimilation per unit leaf area was not depressed at low N. This is also shown in Figure 2, where crop gross assimilation rates at 500 W m⁻² (400-3000 nm) at high N are plotted against those for low N at the same LAI and measured in the same part of the season. The absence of an effect of N fertilization on leaf CO_2 assimilation can be explained from a "down-regulation" in the relationship between leaf N concentration and CO_2 assimilation rate from low to high N input levels (Figure 3). Probably, at high N fertilization a higher proportion of leaf N is not present in active Rubisco but in the form of inactive Rubisco, amino acids, amides and inorganic N. The main effect of low N was a marked reduction in the rate of leaf area development. This was reflected in longer regrowth periods under rotational grazing and lower stocking densities under continuous grazing at low N, resulting in lower herbage intake levels per ha. The lower proportion of assimilated carbon ingested at low N was accompanied by a higher allocation of carbon to the stubble and especially the roots. This is in accordance with the results presented in Figure 4, where the relationship between leaf N content and light-use efficiency (LUE) is presented at three yield levels above a 4-cm stubble. At optimal N supply, LUE was about 2 g DM MJ⁻¹ PAR. At suboptimal N supply, LUE decreased, but due to 'dilution' of plant N in an increasing plant mass (Wilson & Lemaire, 1992) the relationship between leaf N

content and LUE was less steep at higher herbage masses. Since there was no decrease in the rate of leaf CO_2 assimilation, the reduction in LUE at decreasing N supply levels could be explained only by an increased allocation of assimilates to unharvested plant parts (roots and stubble). According to Belanger *et al.* (1994) especially root respiration and exudation do increase in the case of N deficiency.

Figure 2. Relationship between crop gross assimilation at 500 W m² (400-3000 nm) in high and low N grazed swards measured at the same LAI and in the same part of the season. Source: Lantinga (1985).
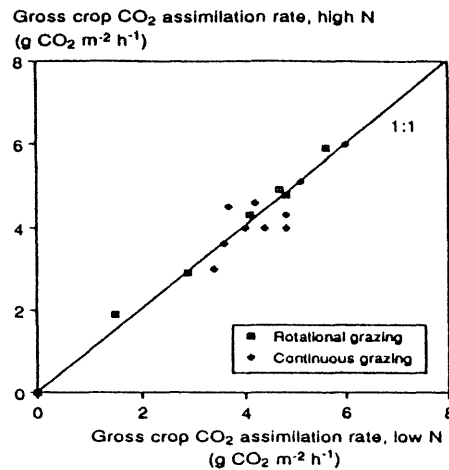

Figure 3. Relationship between leaf nitrogen concentration and maximum net leaf CO_2 assimilation rate as influenced by level of N supply (low N: 0 and 250 kg N ha⁻¹ year⁻¹; high N: 400 kg N ha⁻¹ year⁻¹). Source: Rultenberg (1989).
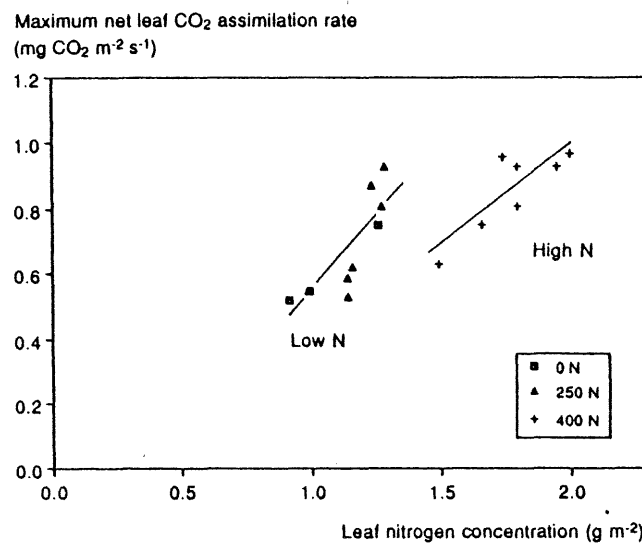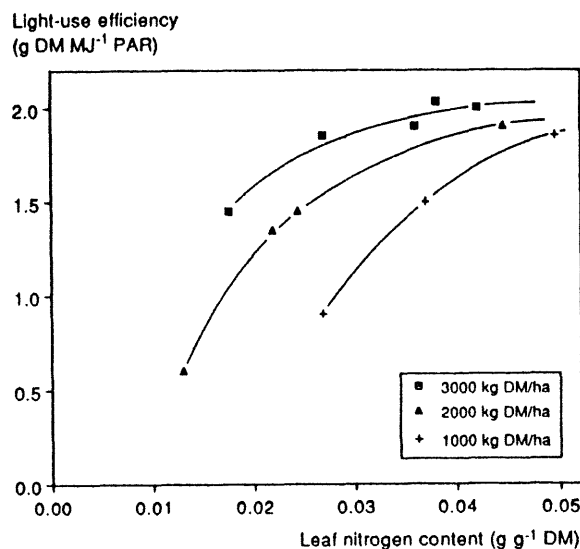
Figure 4. Relationship between leaf nitrogen content and light-use efficiency at three levels of herbage yield above a 4-cm stubble. Source: Van den Broek (1989).

The role of nitrogen in yield physiology of seminatural grassland ecosystems: an example from Slovakia

There is considerable information about the influence of nitrogen on dry matter production but little concerning yield physiology of grassland in Slovakia. Therefore some ecophysiological aspects of the influence of nitrogen (0, 150 and 300 kg N ha^{-1} year^{-1}) and cutting intensity (three or five times per year) were studied during the period 1976-1988 in the central part of Slovakia near Banska Bystrica (Gáborčik & Krajčovič, 1992). The location was a seminatural grassland characterized by an *Anthoxantho-Agrostietum* assocation with cocksfoot (*Dactylis glomerata* L.) as the main species. Amongst others, the following growth parameters were investigated: average crop growth rate (CGR), LAI at harvest and average net assimilation rate (NAR). Under both cutting regimes application of N influenced growth parameters in the following order: CGR > LAI > NAR (Table 2). The small difference in NAR between the two fertilized treatments is in accordance with results from perennial ryegrass swards in the Netherlands discussed previously. The distribution of assimilates between shoot and root was also influenced by N fertilization. Whereas the average root biomass in the control treatment (N0) was 1.05 kg DM m[-2], it decreased to 0.82 and 0.76 kg DM m[-2] in N150 and N300 treatments, respectively. However, application of N enhanced the proportion of living roots from 49% to 61 and 74%, respectively. Also, the structure of the sward aboveground was influenced by N. In the N0 treatment the highest amount of dry matter was found in the lowest sward layer (0-10 cm). In the fertilized treatments, most of the dry matter had been accumulated in the sward layer 10-25 cm. This confirms the stimulating effect of N on harvestable herbage yield at the expense of stubble growth.

Table 2. Growth parameters of a seminatural grassland ecosystem in Slovakia as influenced by N supply and cutting frequency. 3-C and 5-C denote cutting 3 or 5 times per year, respectively. Source: Gáborčík & Krajčovič, 1992.

N SUPPLY (kg N ha⁻¹ year⁻¹)	CGR (g DM m⁻²d⁻¹)		LAI (m² leaf m⁻² soil)		NAR (g DM m⁻² leaf d⁻¹)	
	3-C	5-C	3-C	5-C	3-C	5-C
0	1.90	1.05	1.28	0.45	2.82	2.44
150	6.43	3.86	2.87	1.37	4.71	4.27
300	7.19	4.55	3.53	1.66	4.92	4.44

CO$_2$ fluxes in grassland ecosystems

Short-term relationships between the environment and plant physiological processes, such as photosynthesis and respiration, underlie long-term plant growth. However, in general, a substantial discrepancy exists between the spatial scales when it comes to studying plant performance at both temporal scales. Research on photosynthesis and respiration is usually confined to a spatial maximum of approximately 1 or 2 m² of canopy, whereas research on growth is pursued on all spatial scales. At field scale the heterogeneity in space in soil and plant characteristics is largely unknown in quantitative terms, different between different fields, and sizeable. To study short-term grassland ecosystem processes at the field scale without the need to explicitly consider field heterogeneity and its consequences for plant response, the Netherlands Energy Research Foundation (ECN) applied the Aerodynamic Gradient Technique in Dutch pasture land near Cabauw (Hensen et al., 1995). The site is composed of a characteristic succession of strips of pasture land - intensively managed for dairy farming, mixed rotational grazing and cutting, and predominantly *Lolium perenne* L. - and waterways. The soil consists of a 0.5-0.8 m thick layer of alluvial clay on a massive peat layer. The groundwater Table was high (at approximately 1 m depth), but varied in time and space. From the measurements instantaneous mass (CO$_2$ and H$_2$O) and energy exchange were calculated for a large area, in the order of 1 km length. A measured fetch always simultaneously comprised pasture land at different stages of regrowth, and, therefore, did not have an unequivocal leaf area or homogeneous canopy characteristics. A consequence of the applied technique is that it does not explicitly distinguish between aboveground and belowground processes contributing to the mass exchange. Figure 5 shows the average diurnal patterns of the ecosystem CO$_2$ exchange for two contrasting months, April and August 1993, for vegetation and soil organic matter together. During night-time an upward CO$_2$ flux of 0.2-0.4 mg m⁻² s⁻¹ was observed. During day-time a maximum downward CO$_2$ flux of 0.7 mg m⁻² s⁻¹ was observed at noon in April, and of 0.4 mg m⁻² s⁻¹ before noon in August. The ecosystem CO$_2$ flux is the net result of often contrasting effects of environmental conditions on CO$_2$ fluxes in the ecosystem components. In April 1993 there was an average daily net CO$_2$ uptake by the ecosystem of 5.25 g CO$_2$ m⁻² d⁻¹, whereas in August 1993 there was a net CO$_2$ emission of 5.11 g CO$_2$ m⁻² d⁻¹. It is obvious that during day-time the radiation level plays an important role in the ecosystem CO$_2$ flux. Figure 6 suggests a convergence of [CO$_2$]$_{atm}$ in the lower part of the boundary layer to 345-350 µmol mol⁻¹ at increasing short-wave irradiance (global radiation). The triangular relationship reflects both a reduced atmospheric mixing at low irradiance due

to occurrence of an atmospheric inversion layer, and an increasing net CO_2 assimilation and therefore depletion of atmospheric CO_2 at increasing irradiance.

Figure 5. Average diurnal patterns of ecosystem CO_2 flux in pasture land near Cabauw, the Netherlands, for April and August 1993 (source data: ECN).
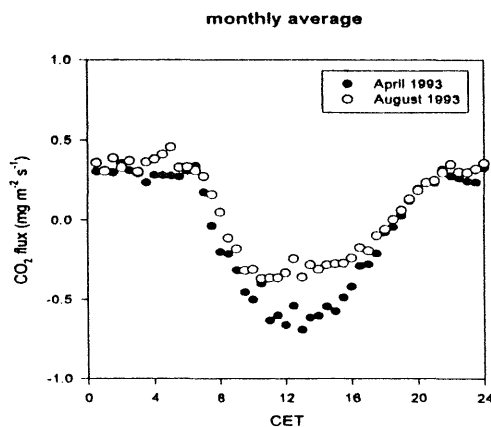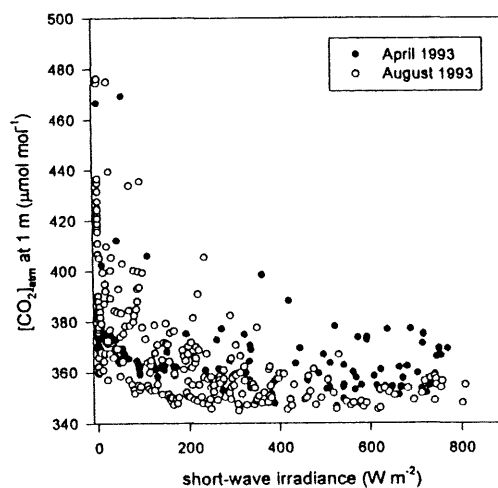

Figure 6. Atmospheric $[CO_2]$ at 1 m height (half-hourly average) as a function of short-wave irradiance (global radiation) in pasture land near Cabauw, the Netherlands, during April and August 1993 (source data: ECN and KNMI).

The relationship between short-wave irradiance (I_s) and ecosystem CO_2 flux (F_c), shown in Figure 7, can be regressed by either a hyperbolic or an exponential curve (r^2 approximately 0.75 in all cases), in accordance with relationships found at smaller spatial scales. Comparison of April and August 1993 shows a higher upward CO_2 flux at zero irradiance and lower asymptotic CO_2 flux value in August, e.g. $F_{c. April}=1.44xI_s$

$/(252+I_s)+0.30$ and $F_{c, August}=-1.32xI_s/(224+I_s)+0.42$. This difference might partly be due to different contributions by the soil organic matter component during both months. Since the night-time ecosystem CO_2 flux is determined by respiration of both vegetation and soil organic matter, those values can be used to approximate day-time ecosystem respiration as a function of temperature. When subtracting this calculated ecosystem respiration from the measured day-time ecosystem CO_2 flux, an approximation of the (gross) photosynthetic CO_2 flux is the result.

Figure 7. Ecosystem CO_2 flux (measured half-hourly averages) and derived photosynthetic CO_2 flux (half-hourly averages) as a function of short-wave irradiance (global radiation) in pasture land near Cabauw, the Netherlands, during April and August 1993 (source data: ECN and KNMI).
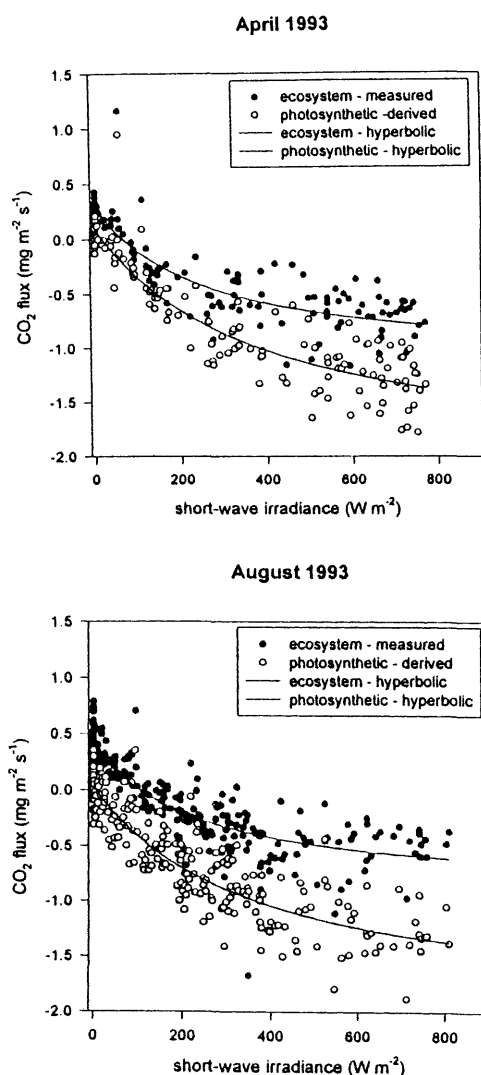
April 1993

August 1993

Figure 7 also shows the derived photosynthetic CO_2 flux. It appears that the hyperbolic relationship between short-wave irradiance and CO_2 flux is retained. In both months, the calculated average crop gross CO_2 assimilation at 500 W m^{-2} was about 1.2 g CO_2 m^{-2} s^{-1}. This would correspond with an average LAI of about 2.5 (Lantinga, 1985). From these data it could be concluded that, even at this large spatial scale and with the specific spatial heterogeneity in this pasture land, clear relationships existed between basic environmental variables on the one hand and ecosystem CO_2 fluxes on the other hand, similar to processes at smaller spatial scales. Both the involvement of other environmental variables as shown above and spatial heterogeneity in vegetation and soil organic matter components are likely to explain the remaining variance. However, statistical regression analysis is bound to include only a limited part of these factors, and is, therefore, to be supplemented by more detailed mechanistic modelling.

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