ISSN 0308-3675

Merlewood Research and Development Paper
Number 67

RESPIRATION, LITTER NUTRIENTS, AND SOIL ORGANIC MATTER IN GRAZED AND UNGRAZED UPLAND LIMESTONE GRASSLAND.

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Research and Development 76/67
September 1976.

Introduction

The Moor House area of the northern Pennines (Conway, 1955; Eddy et al 1969) contains extensive areas of blanket bog in which isolated grassland swards occur. The underlying rocks are of the Yoredale series of the Carboniferous (limestone, sandstones and shales) and the soils are of low base status unless influenced by the weathering of the limestone (Johnson and Dunham, 1963).

The climate at Moor House (NGR 758328, altitude 560 m) was described by Manley (1943), who gave the following data based on 10-year averages: annual mean air temperature 5.3°C, mean air temperature of warmest month (July) 11.7°C, mean annual rainfall 1780 mm, mean annual snow cover 80 days. More recent Nature Conservancy records give similar values, the mean annual temperature of the air above a stand of Calluna vulgaris in 1969 was 5.43°C, that at 6 cm depth in peat below the Calluna was 5.44°C, and that at 6 cm depth in peat below Juncus squarrosus was 5.98°C (unpublished data). Manley (1942) also made observations on Great Dun Fell (834 m, NGR NY 711322, 4.8 km from Moor House) nearer to the site of the present investigations, where the climate was found to be more severe: annual mean air temperature 2.1°C, July mean air temperature 9.3°C. The present investigations were made inside and outside the exclosure on Knock Fell (NGR NY 717311, 4.5 km from Moor House, 1.3 km from Great Dun Fell).

In 1955, the Nature Conservancy established experimental sheep exclosures on the Moor House National Nature Reserve. Welch and Rawes (1964) described some effects on the vegetation of excluding sheep from these sites. At all sites, after 7 years, the bryophytes, lichens, and flowering plants other than grasses decreased, Nardus stricta and Juncus squarrosus declined markedly, but Deschampsia flexuosa increased notably. The number of species fell most (93 to 67) on Knock Fell, but the frequencies of Agrostis tenuis, D. caespitosa, Festuca rubra, and Achillea millefolium increased. The standing crops

after 7 years and after one season of exclosure were compared by harvesting in August 1962. The difference was least (18 g/m^2) at Little Dun Fell (the highest site), while on Knock Fell the difference was 95 g/m^2. This increase was produced mainly by the fine-leaved grasses. The effect of exclosure on the rare species of Pennine grasslands depends on their position in the succession. Some can exist only where grazing restricts their potential competitors, whereas others may be excluded by grazing.

The present studies were begun to determine if any measurable differences occurred in the respiration, organic matter content, chemical composition, and bulk density of the soil in grazed and ungrazed areas which could be attributed to the exclusion of sheep. Although the results are not conclusive, the data are worth documenting.

Site Description

The exclosure is sited on a level area below the summit of Knock Fell at an altitude of 747 m. The rock, which in places appears at the surface, is Carboniferous Limestone, overlain by a variable depth of material of mixed origin which we shall refer to as "head". In the area around the exclosure, peat, which is often eroded, lies on the head. In places, shallow mineral soils lie directly on the limestone.

Outside the exclosure, the vegetation varies from a closely-grazed Agrosto-Festucetum on the limestone, through a mixture of Agrostis, Festuca and Juncus squarrosus, to predominantly Juncus squarrosus on the peat.

The following profiles are examples of the soils at this site (sampled 23 October 1967):

Profile A

Vegetation: Closely-grazed turf dominated by Festuca-Agrostis, with Galium spp. and other small plants.

1 to 0 cm:	L/F layer.
0 to 15 cm:	Uniformally very dark greyish-brown (10 YR 3/2). At 10 to 15 cm depth, pH 6.2, loss on ignition (L.O.I.) 15.6%, moisture content 102.9% oven dry (O.D.) basis.
Underlying rock:	Carboniferous Limestone.

Profile B About 5 metres from Profile A

Vegetation:	Similar to that of Profile A.
5 to 4 cm:	L/F layer.
4 to 0 cm:	H layer (A_o), black (7.5 YR 2/0), pH 4.05, L.O.I. 51.43%, moisture content 245.8% (O.D. basis).
0 to 14 cm:	Uniformly dark yellowish-brown (10 YR 3.5/4). At 10 to 14 cm depth, pH 4.6 L.O.I. 5.45%, moisture content 52.8% (O.D. basis).
14 to 22 cm:	Dark greyish-brown (10 YR 4/2) with mottles of dark yellowish-brown (10 YR 4/4). At 15 to 20 cm depth, pH 4.9, L.O.I. 7.99%, moisture content 35.67% (O.D. basis).
Underlying rock:	Carboniferous Limestone.

Profile C Only H layer sampled. This type occurred distributed among areas of profile B type. The profile is similar and appears to be slightly wetter.

Vegetation:	Juncus squarrosus, acidophilous mosses (e.g. Polytrichum spp.).
H layer:	Black (7.5 YR 2/0). pH 3.4, L.O.I. 44.27%, moisture content 231.6%.

At 0 to 12 cm depth, silt and clay made up about 80% of A and 70% of B. Mineralogical analyses of the sand fraction indicated that profiles A and B differ only on minor points, being composite in origin and derived from the sandstones and shales of the area, as well as receiving a contribution from the underlying limestone (Dr. D. F. Ball, pers. comm.). To confine the present studies to a uniform soil type, an area similar to profile A about 5 m x 5 m, partly inside and partly outside the exclosure, was chosen for detailed study. In the classification of Avery (1973) this soil would be called a humic ranker, formerly it would have been classified as a rendzina. We assumed that the parts now inside and outside the exclosure were originally identical, and that any differences now observed are due to exclosure.

Methods

Because of the small area available for sampling within the exclosure, only two cores 25 mm diameter and 10 cm long were collected inside at each sampling. Three similar cores were collected outside. Sampling was carried out at approximately monthly intervals from August 1966 to October 1967. Soil temperature was measured at 5 cm depth inside and outside at each sampling.

In the laboratory, the green vegetation was removed. The layer of dead plant remains, called the L/F layer, no attempt being made to subdivide it further, was separated from the soil, which was then cut to 7 cm length measuring from the mineral soil surface. This size of core was chosen

because it seemed likely that any changes in organic matter content in the absence of grazing would be apparent first in the L/F layer and the upper soil. Furthermore, initial studies showed that respiration, and therefore biological activity, declined with depth (Table 1).

The L/F layer and soil core were weighed into specially-designed respiration flasks (Howard, 1968). These and appropriate blank flasks were connected to Dixon respirometers (Dixon, 1952, p6). After overnight equilibration, oxygen uptake was measured at field temperature, except where this fell below 2.8°C when, for practical reasons, respiration was measured at 2.8°C. The respirometer temperature was then increased to 10°C, and respiration was measured after overnight equilibration. All respiration measurements were corrected to 0°C and 760 mm (NTP). The colour of each core was then checked against a Munsell chart to ensure they were profile A type, the cores were divided into 0 to 3.5 cm and 3.5 to 7 cm lengths, and the soil and L/F material was oven-dried at 105°C (OD), weighed, and ground for analysis.

Analyses were as follows:

a) Soils: loss on ignition at 550°C (L.O.I.), organic carbon and hydrogen (dry combustion), total nitrogen (Kjeldahl). C, H, N data are only available for samples collected between April and October 1967.

b) L/F layers: organic carbon and hydrogen. Where sufficient material was available, loss-on-ignition was measured and total phosphorus, calcium and potassium, were determined on the perchloric/nitric/sulphuric acid digest of the oven-dry material. Potassium was determined by flame emission spectroscopy, calcium by atomic absorption spectroscopy, and phosphorus by the molybdenum blue method in a Technicon Auto-analyzer.

Results and Discussion

Computer plots of the data for bulk density, loss-on-ignition, total L/F layer material and chemical analyses, suggested that during the period of the observations there were no significant trends with time in the variables measured. This lack of detectable seasonal trends may be due to the small number of samples collected at each sampling or it may be a real feature of this type of upland grassland. Frankland et al (1963) found that the large spatial variability in woodland soils obscured possible monthly differences in spite of the intensive sampling procedure followed, and a similar result was obtained by Ball and Williams (1968) for two upland grassland sites in North Wales. For present purposes, it is possible to consider all the values of a variable for the grazed cores as a single sample from one population, and those for ungrazed cores as a single sample from another population. We therefore set up the null hypothesis that there was no difference between the samples from grazed and ungrazed plots for any of the variables measured. Results of chemical analyses of the L/F layer are given in Table 2, and of chemical analyses and bulk densities of soil in Table 3. Variances of the data of Tables 2, and 3 were compared using the F test and the means were then compared by the appropriate method (Bailey, 1959). Differences within soil cores are shown in Table 3 and between soil cores in Table 4.

The quantities and chemical analyses of L/F layer material of grazed and ungrazed plots were not significantly different (Table 2). This is rather interesting considering the much greater amount of standing crop inside the exclosure (Welch and Rawes, 1964). However, the reason may lie, at least partly, in the fact that much of the dead plant material in the ungrazed plot is associated with the vegetation away from the soil surface, and is not present in our cores. We shall return to this point later.

In both grazed and ungrazed areas, bulk density was greater in the soil at 3.5 to 7 cm depth than at 0 to 3.5 cm depth (Table 3). This is no doubt due, at least partly, to the greater percentage of organic matter in the 0 to 3.5 cm depth in both grazed and ungrazed soils. In the 3.5 to 7 cm depth, bulk density was greater in the grazed soil (Table 4). This difference is interesting, as it cannot be due to the percentage of organic matter, which is not significantly different between soils at this depth. However, the total amount of organic matter at 3.5 to 7 cm depth was greater in the grazed soil. Hence, although the proportions of mineral soil/organic matter were not different, both the bulk density and the total amount of organic matter in the 3.5 to 7 cm cores were greater in the grazed soil, suggesting that the soil is more compact. This is consistent with the view that this effect is caused by sheep trampling. The fact that the effect is not observed in the 0 to 3.5 cm soil may be explained by the resilience of the grass root mat, which transfers the weight of the sheep to the lower soil without itself being permanently compressed. A similar effect was found by Keen and Cashen (1932) and by Robinson and Alderfer (1952).

The organic matter content (L.O.I. in grams) was uniformly distributed in the 0 to 7 cm cores, those from the grazed area having more organic matter than those from the ungrazed area. The difference between the mean values for the 0 to 7 cm depth was 605 g/m^2. This difference could be caused by (a) trampling of sheep increasing the rate at which dead plant remains are incorporated into the soil, (b) incorporation of sheep faeces into the soil, (c) a combination of (a) and (b). The nitrogen content of the 0 to 3.5 cm soil cores was greater ($p < 0.001$) and the C/N lower ($p < 0.01$) in the grazed area, which is consistent with (b) and (c), since incorporation of little-decomposed plant remains would presumably increase the C/N ratio. Our results do not enable us to assess the relative importance of (b) and (c); for this more detailed studies would be necessary.

C/N was greater in both 0 to 3.5 cm and 3.5 to 7 cm layers of soil from the ungrazed area than in the corresponding layers from the grazed area. This was the only chemical difference between grazed and ungrazed plots at 3.5 to 7 cm depth.

In both grazed and ungrazed areas, total N, organic C and C/H are greater in the 0 to 3.5 cm layer than in the 3.5 to 7 cm layer, and the soil shows no significant difference between the two layers with respect to C/N.

It is clear then, that there is no evidence of organic matter accumulation in the L/F layer or in the 0 to 7 cm soil after exclosure; indeed, in the latter the organic matter content is lower. This is contrary to the conclusion of Welch and Rawes (1964) that organic matter had accumulated in the L/F layer of the ungrazed area which they studied. Their conclusion was made on the basis of the ash content of the litter layer in spite of the fact that the total weights of the stubble-litter layers from the grazed and ungrazed plots were not significantly different. The results of the present study suggest that in the absence of grazing much of the dead grass is supported by the vegetation and does not fall to the soil surface. This agrees with the observation made earlier that no seasonal trend was detected in the quantity of L/F material during the period of sampling. Welch and Rawes (1964) found that in the Knock Fell exclosure after seven years without grazing, the dead material in the upper herbage (58.4 g/m^2) accounted for 26.8% of the total (217.8 g/m^2). It seems likely that a significant amount of decomposition of the dead vegetation may take place among the standing crop. Allen (pers. comm.) found that grass litter decomposing in hair nets among the standing crop inside the exclosure lost 40 to 55% of its dry weight (according to species) in one year and up to 75% in three years.

Therefore, when grassland ecosystems are being compared as in this study, it is not sufficient to look only to the soil and litter layer for accumulation of dead plant remains, the standing vegetation should also be included.

Field temperatures are shown in Fig. 1. Respiration results are given on an oven-dry basis, at 10°C (Fig. 2 L/F layer; Fig. 4, 0 to 7 cm soil core), and at a temperature as close as possible to that prevailing at the time of sampling (Fig. 3, L/F layer; Fig 5, 0 to 7 cm soil). The equipment available at the time did not allow respiration to be measured at 2.8°C, although, during the winter, the field temperature often fell below this value. The results were also calculated on an organic matter basis and, for the soil, on a volume basis. The respiration of the L/F layer was also calculated on an area basis.

Respiration was clearly related to temperature (Figs. 3 and 5). At 10°C, respiration was significantly correlated with moisture content: grazed L/F $R = 0.947$, $p < 0.001$; ungrazed L/F $R = 0.644$, $p < 0.05$; grazed soil $R = 0.629$, $p < 0.05$; ungrazed soil $R = 0.465$, NS. The greater correlation coefficient in both L/F and soil from grazed as opposed to ungrazed areas is interesting, and suggests a microbial population with different moisture response characteristics.

The overall moisture, field temperature, and respiration during the period of the observations were each examined by a paired t test of the mean value for each sampling of grazed and ungrazed areas. Moisture and temperature showed no significant difference, and neither did respiration on whatever basis it was expressed except for respiration per gram LOI at 10°C, which was greater in the ungrazed soil ($p < 0.05$). This suggests that there may be some biological difference, associated with the organic matter, which only becomes evident at higher temperatures. At low temperatures, respiration is low and thus any differences are likely to be small.

The paired t test detects overall differences, but only if these are mostly in the same direction. It is possible for differences of opposite sign to cancel out, and this could be important, for example, if, in the first half of the observations, the differences were all in one direction, while in the second half they were all in the opposite direction (e.g. Fig.4). Examination of Figs. 1-5 shows that differences between grazed and ungrazed areas do occur at certain times. Thus, Fig. 1 shows that in August 1967 the temperature in the grazed plot at 5 cm depth was 3.7 deg C greater than that in the ungrazed plot, presumably due to differences in the insulating properties of the vegetation cover. Fig. 3 shows that in August 1966 respiration in the grazed L/F layer was greater than that of the ungrazed, but the positions were reversed in August 1967. There is no obvious reason for this. Again, there is no obvious reason for the occasional differences in respiration of the L/F layer at 10°C (Fig. 2) and in the 0 to 7 cm soil cores (Fig. 4), they do not appear to be caused by differences in moisture content. The respiration of the 0 to 7 cm soil cores shows occasional differences (Fig.5) particularly at temperatures $\geq$ 10°C, but they are not consistent.

Conclusions

The results of this investigation show certain differences between the grazed and ungrazed soils, which, although small in absolute terms, are statistically significant:

1. N content was greater, and C/N lower, in 0 to 3.5 cm soil from the grazed area.

2. Organic matter content of 0 to 3.5 cm soil was greater in the grazed area in both percentage and absolute terms.

3. Bulk density of soil at 3.5 to 7 cm was greater in the grazed area.

4. O_2/g LOI at 10°C was greater in the ungrazed soil.

1 and 2 can be attributed to incorporation of sheep faeces into the soil. The higher N content of the grazed soil is likely to improve the productivity of the grass sward. The small difference in bulk density (3) may have little influence on other properties, but if the compaction increases with time, other effects may become apparent. Published results indicate that compaction sometimes increases, sometimes decreases, plant growth. The contradictory effects probably stem from differences in the amount of compaction in relation to aeration and moisture. Where moisture is limiting, and aeration adequate, a certain amount of compaction may be beneficial by increasing moisture content per unit volume of soil. Beyond that point, the soil may become so dense that aeration and movement of moisture are restricted (Lull, 1959).

The difference in O_2/g LOI (4) at first appears anomalous, one might expect that the higher N content of the soil in the grazed area would lead to a higher level of microbial activity and thus a greater oxygen uptake than in the ungrazed area. However, our result is consistent with the conclusions drawn from (1) and (2), as Floate (1970) found that, on average, only $\frac{1}{3}$ as much CO_2 was evolved from sheep faeces as from the grass from which these were derived. Our results are consistent in suggesting that in the grazed area the soil organic matter is strongly influenced by sheep faeces, while that in the ungrazed plot is likely to be derived from dead plant material.

In this type of study, we are observing the product of a series of interactions, but we do not know the precise nature of the interactions involved. A simple diagrammatic representation of the organic matter transfers can be constructed (Fig. 6). Sheep may contribute to soil organic matter directly by faeces, and indirectly by influencing the rate of transfer of plant material to the litter and soil. Sheep may also influence the rate of plant production. However, the experimental testing of even such a simple model would require a large amount of work.

ACKNOWLEDGEMENTS

We are grateful to the Merlewood Chemical Section for the chemical analyses.

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Table 1

Respiration with depth for one soil core. Other cores showed a similar decrease of respiration with depth.

Soil Depth (cm) 25 mm diam. core	$\mu 10_2/h/g$ OD uptake
0-2	54.40
2.5-4.5	29.00
5-7	11.60
7-9	7.73
20-22.5	0.70

Table 2. Chemical analyses of L/F layer (OD basis).

	Mean ± standard error			
	grazed		ungrazed	
total N percent	1.13 ± 0.03	(19)	1.11 ± 0.03	(16)
organic C percent	27.57 ± 1.29	(19)	26.02 ± 1.30	(17)
total H percent	3.85 ± 0.16	(19)	3.64 ± 0.17	(17)
C/H	7.15 ± 0.08	(19)	7.13 ± 0.08	(17)
C/N	24.35 ± 0.90	(19)	22.84 ± 0.82	(16)
total K percent	0.51 ± 0.02	(13)	0.47 ± 0.02	(14)
total Ca percent	0.34 ± 0.03	(13)	0.34 ± 0.02	(14)
total P percent	0.119 ± 0.004	(13)	0.114 ± 0.004	(14)
total L/F layer material g/m^2	886.86 ± 81.99	(40)	1043.57 ± 94.73	(34)

None of the differences between means of grazed and ungrazed samples was significant at the 5% level.

No. in sample shown in brackets.

Table 3. Soil bulk density, organic matter content, and chemical analyses (OD basis). Figures in brackets indicate number in sample. Significance levels are for within - core comparison.

		Mean ± standard error			
		0 to 3.5 cm		3.5 to 7 cm	
Grazed	bulk density g/cc	0.517 ± 0.014	(30)	0.670 ± 0.010***	(30)
	LOI percent	21.41 ± 0.35***	(34)	16.59 ± 0.22	(34)
	LOI g/core	1.936 ± 0.030	(26)	1.914 ± 0.030	(26)
	total N percent	0.80 ± 0.02***	(17)	0.63 ± 0.02	(17)
	organic C percent	9.66 ± 0.45***	(10)	7.23 ± 0.30	(10)
	total H percent	1.41 ± 0.04**	(10)	1.21 ± 0.03	(10)
	C/H	6.83 ± 0.17***	(10)	5.96 ± 0.13	(10)
	C/N	11.56 ± 0.21	(10)	11.44 ± 0.12	(10)
Ungrazed	bulk density g/cc	0.518 ± 0.014	(25)	0.615 ± 0.014***	(25)
	LOI percent	19.83 ± 0.29***	(28)	16.76 ± 0.30	(28)
	LOI g/core	1.766 ± 0.091	(20)	1.773 ± 0.043	(20)
	total N percent	0.74 ± 0.02***	(16)	0.63 ± 0.02	(16)
	organic C percent	9.23 ± 0.23***	(10)	7.65 ± 0.24	(10)
	total H percent	1.33 ± 0.04	(10)	1.26 ± 0.03	(10)
	C/H	6.96 ± 0.09***	(10)	6.07 ± 0.12	(10)
	C/N	12.49 ± 0.19	(10)	11.95 ± 0.18	(10)

Table 4. Summary of differences between soil cores.

core depth		Mean ± standard error grazed	ungrazed
0 to 3.5 cm	bulk density g/cc	0.517 ± 0.014	0.518 ± 0.014
	LOI percent OD	21.41 ± 0.35**	19.83 ± 0.29
	LOI g/core	1.936 ± 0.030**	1.766± 0.091
	N percent OD	0.80 ± 0.02*	0.74 ± 0.02
	C percent OD	9.66 ± 0.45	9.23 ± 0.23
	H percent OD	1.41 ± 0.04	1.33 ± 0.04
	C/H	6.83 ± 0.17	6.96 ± 0.09
	C/N	11.56 ± 0.21	12.49 ± 0.19**
3.5 to 7 cm	bulk density g/cc	0.670 ± 0.010**	0.615± 0.014
	LOI percent OD	16.59 ± 0.22	16.76 ± 0.30
	LOI g/core	1.914 ± 0.030**	1.773± 0.043
	N percent OD	0.63 ± 0.02	0.63 ± 0.02
	C percent OD	7.23 ± 0.30	7.65 ± 0.24
	H percent OD	1.21 ± 0.03	1.26 ± 0.03
	C/H	5.96 ± 0.13	6.07 ± 0.12
	C/N	11.44 ± 0.12	11.95 ± 0.18*
0 to 7 cm	bulk density g/cc	0.595 ± 0.010** (40)	0.568± 0.010 (32)
	LOI g/core	3.829 ± 0.053*** (28)	3.532± 0.062 (21)

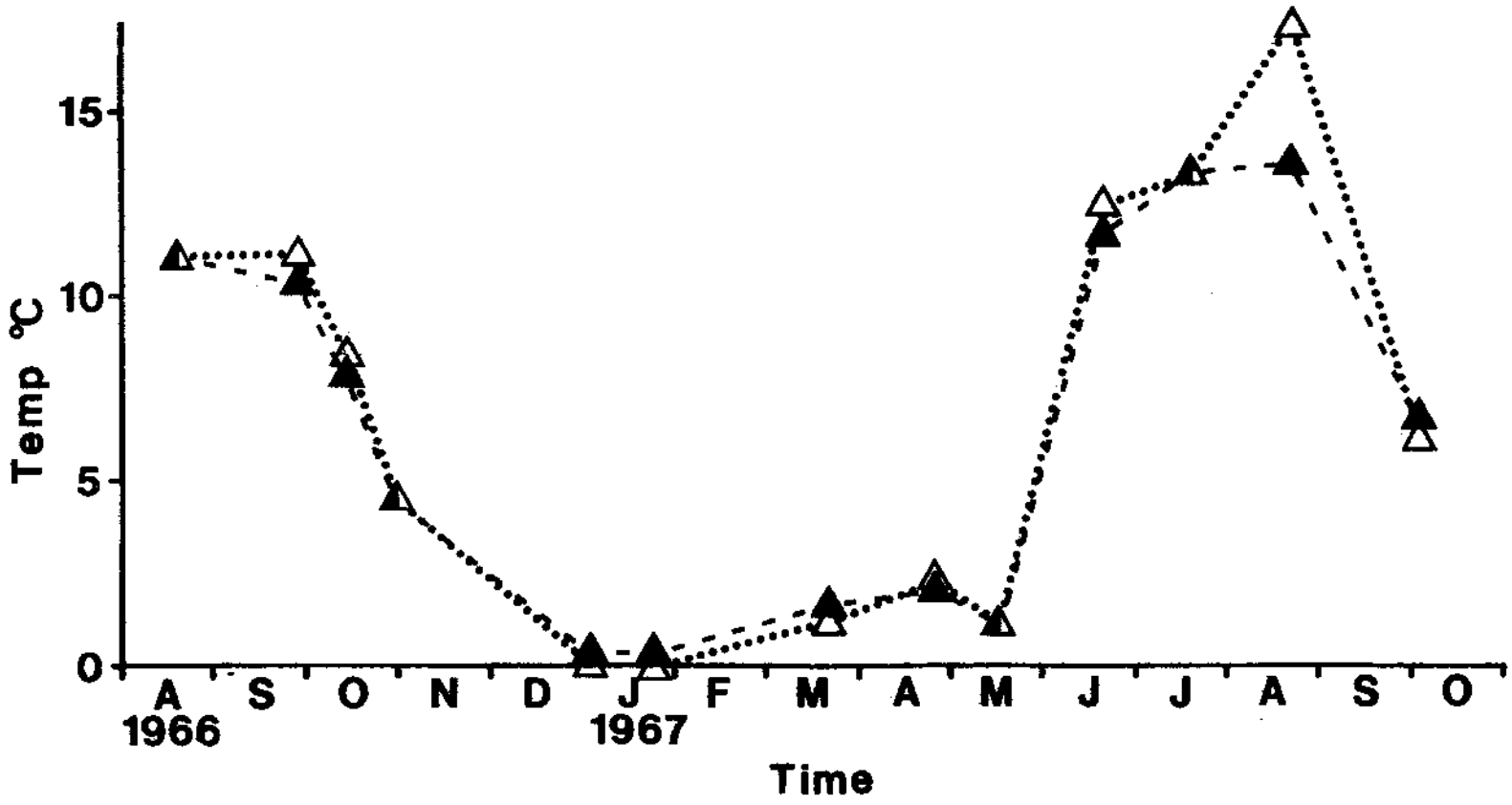

Fig. 1. Soil temperature at 5 cm depth △·····△ grazed, ▲- - -▲ ungrazed

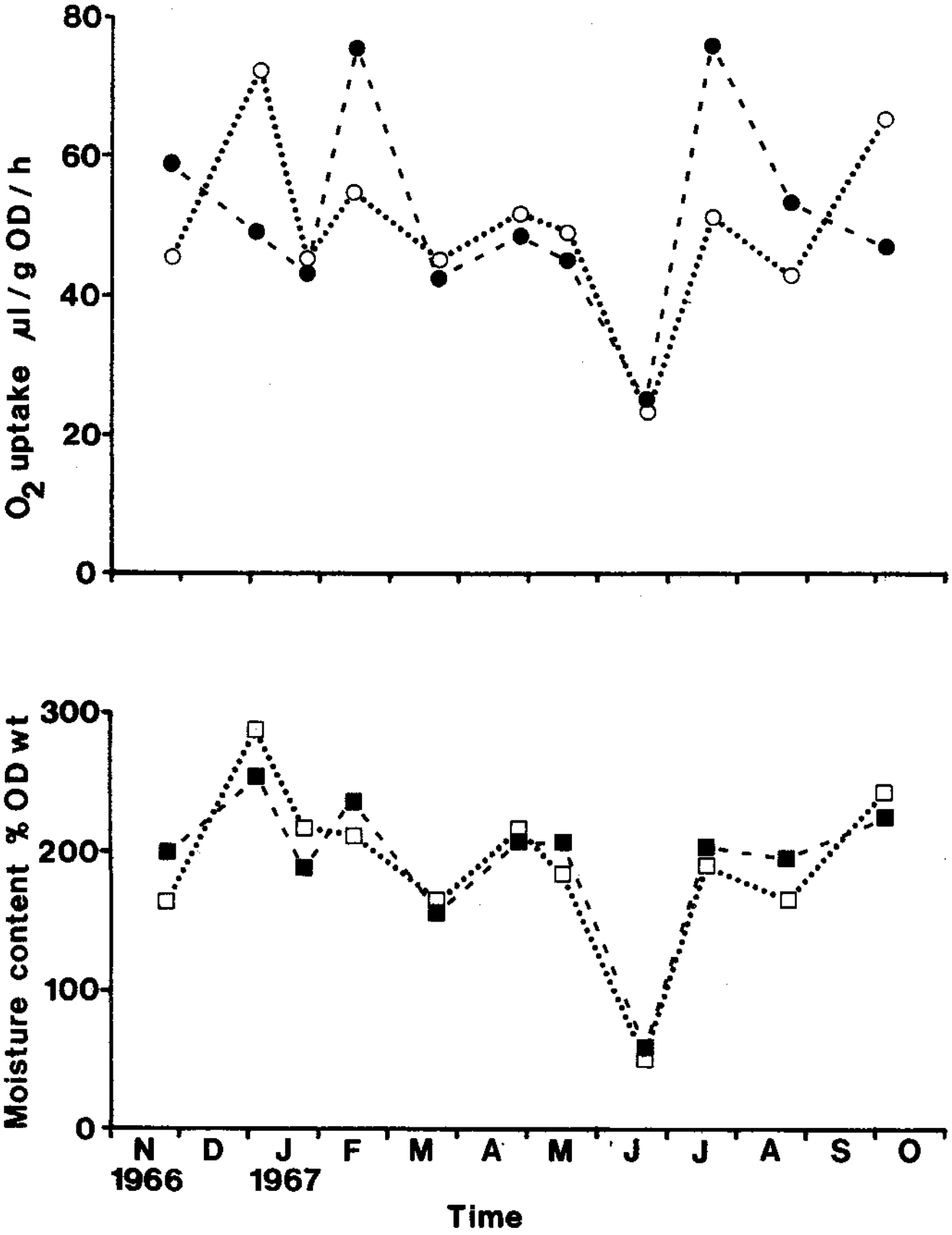

Fig. 2 L/F layer, mean O_2 uptake at 10°C, ○·····○ grazed, ●- - - -● ungrazed, mean moisture content, □·····□ grazed, ■- - - -■ ungrazed

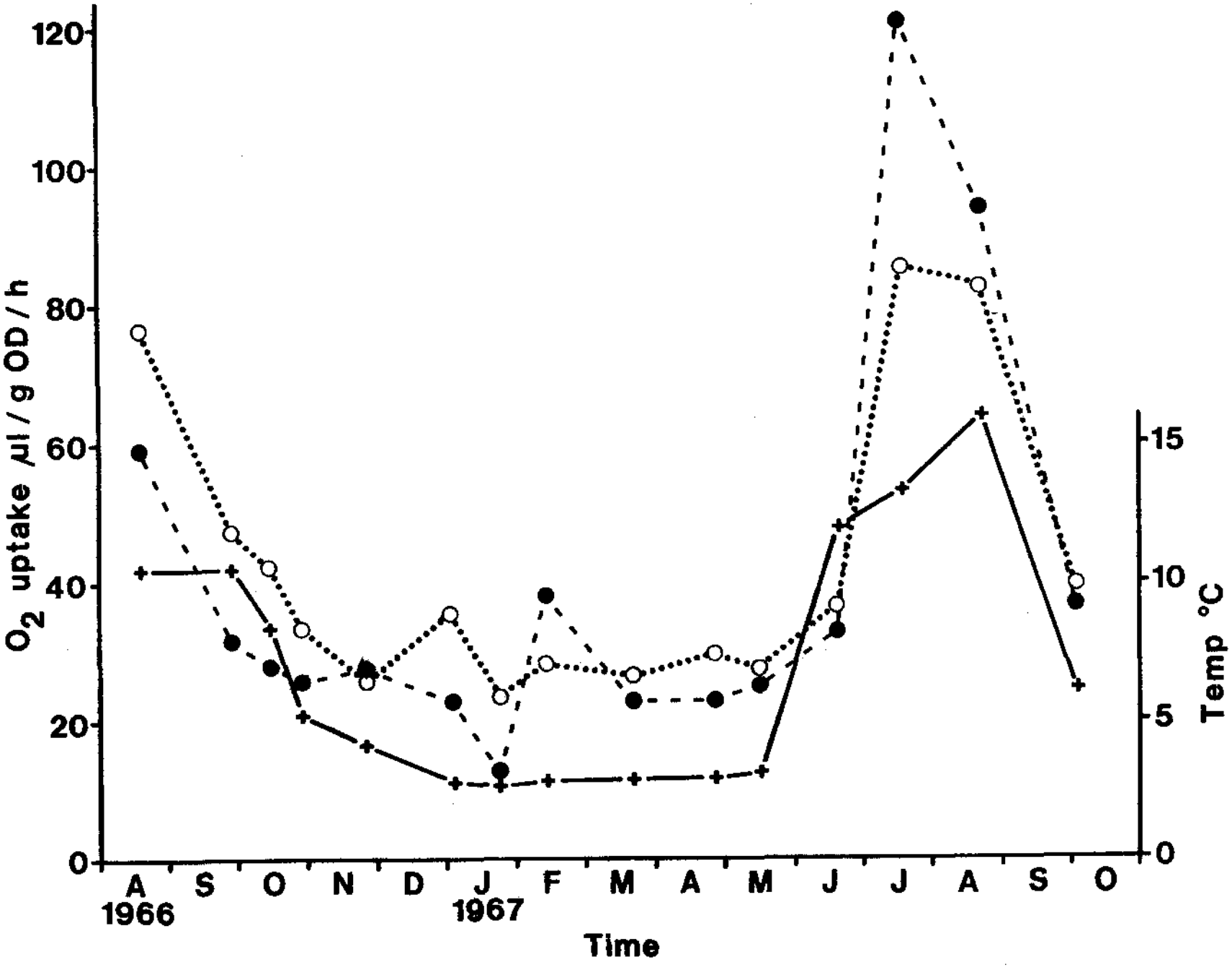

Fig. 3 L/F layer, mean O_2 uptake at field temperature, ○·····○ grazed, ●- - - -● ungrazed, +——+ respirometer bath temperature

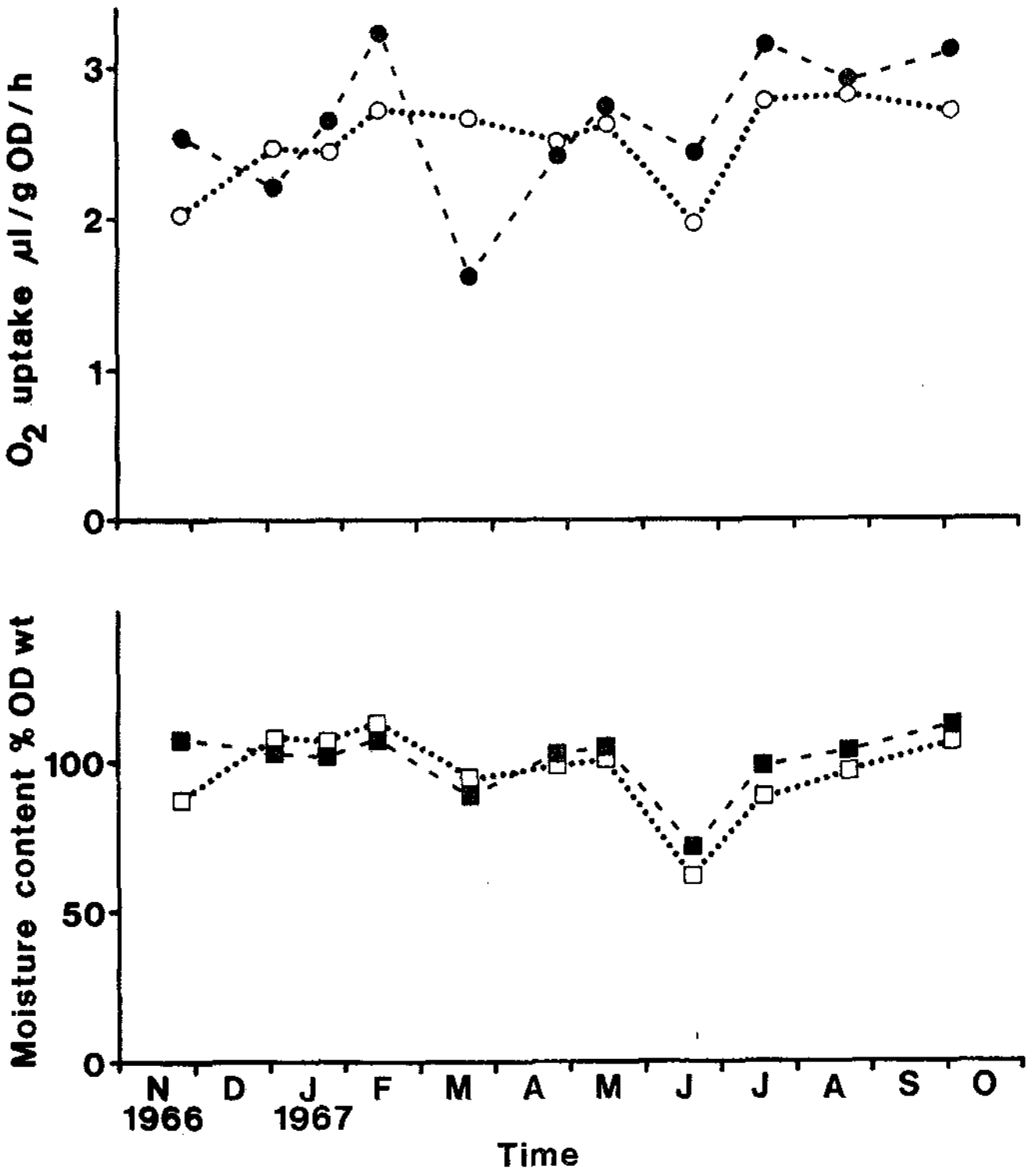

Fig. 4 0 to 7 cm soil cores, mean O_2 uptake at 10°C, ○·····○ grazed, ●- - - -● ungrazed, mean moisture content, □·····□ grazed, ■- - - -■ ungrazed

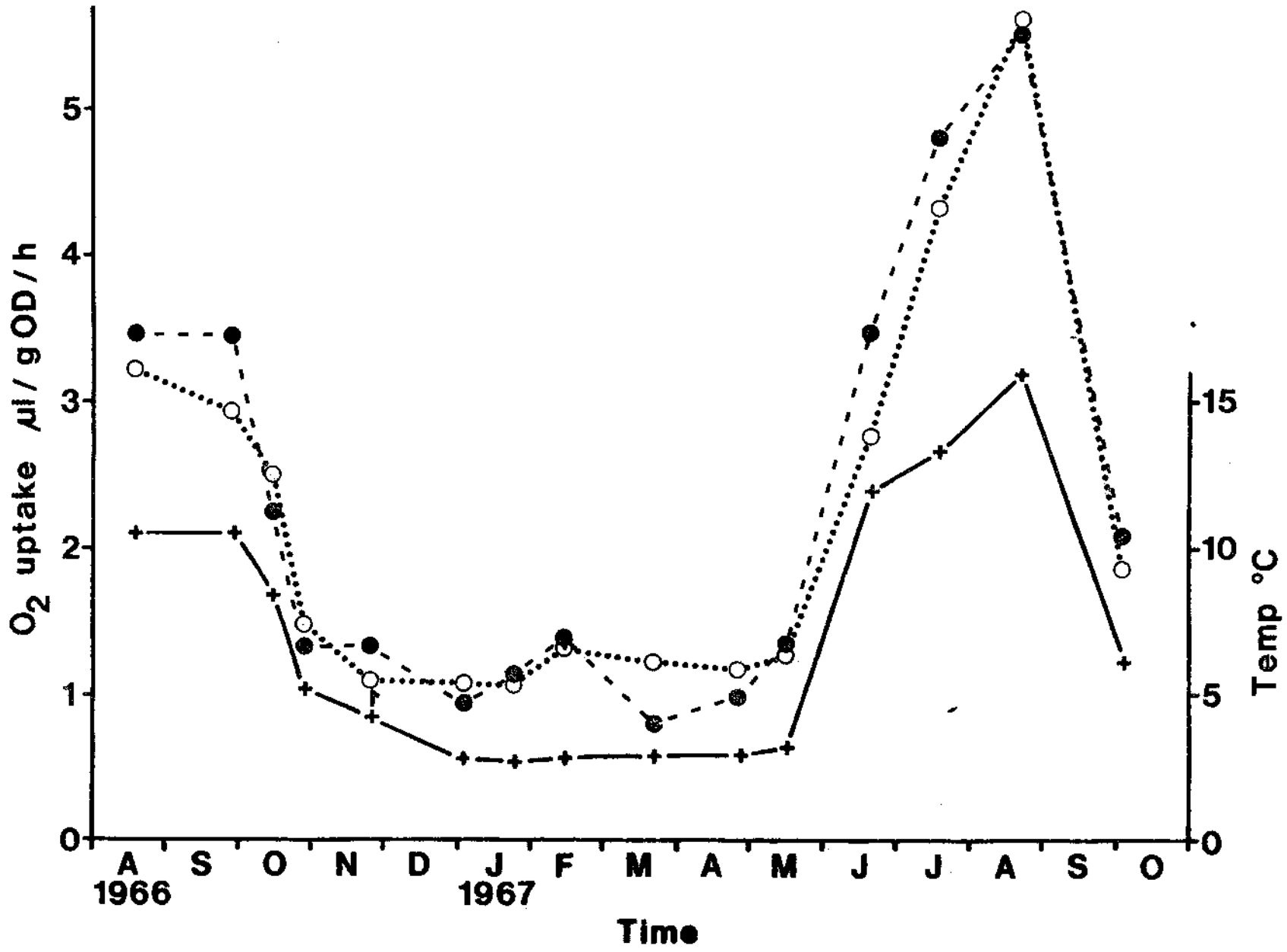

Fig. 5 0 to 7 cm soil cores, mean O_2 uptake at field temperature, ○·····○ grazed, ●- - -● ungrazed, +——+ respirometer bath temperature

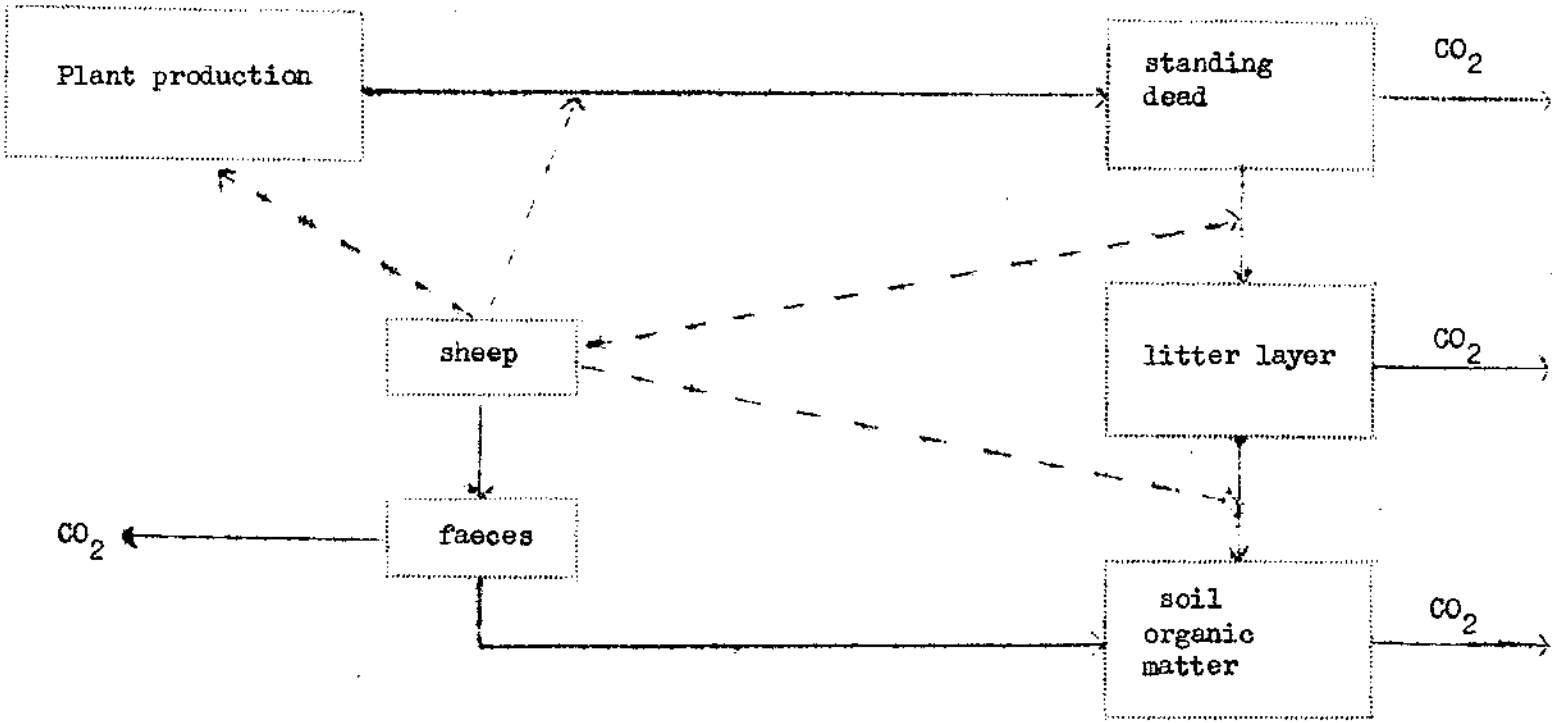

Figure 6. A simplified representation of organic matter transfers in the grazed area. Continuous lines are carbon transfers, broken lines indicate possible influences on rates.