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The effect of nitrogen fertilization upon the herbage production of tall fescue swards continuously grazed with sheep. 1. Herbage growth dynamics

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Abstract

The effect of level of nitrogen application upon the dynamics of herbage growth in a continuously grazed sward of tall fescue was investigated during two successive years. In order to obtain a large range of sward structural conditions, the experiments were carried out with two contrasting cultivars: cv. Clarine and cv. Barcel, and, in Year 2, with two different sward heights or leaf area indices (LAIs). During each of five experimental periods (2–3 weeks), swards received either optimum (N2) or deficient (N1) N applications, were maintained at their target LAI, and leaf growth was measured on labelled tillers. With continuously defoliated tillers, N-shortage had only a small effect on the leaf elongation rate compared with tillers protected by cages. The leaf production per tiller was only slightly reduced by N shortage, and it was mainly by the means of a reduction in tiller density that the N deficiency resulted in reduced herbage growth per hectare. These results indicate that, in continuously grazed swards, in contrast with results previously found in intermittently defoliated swards, leaf elongation is not the only important component of difference in herbage growth and that the promotion of tillering rate is an additional pathway for N response in such management regimes.

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Introduction

Herbage production in continuously grazed perennial ryegrass-dominated pastures has been analysed in detail by several authors (Bircham, 1981; Hodgson *et al.*, 1981; Grant *et al.*, 1983; Parsons *et al.*, 1983a;b; Lantinga, 1985). These studies were carried out in relatively similar ecological conditions: oceanic climate, with ample nitrogen application allowing the plants to express their growth potential. However, there is a lack of information about the response of other species such as tall fescue to such management regimes despite its importance in many other temperate countries around the world with more continental or Mediterranean climates.

Economic constraints, and the need to preserve the environment, have led farmers to reduce nitrogen inputs in grazing systems and to develop more extensive forms of management. Under these conditions it is important to know if continuously grazed systems can remain efficient even with low N inputs.

Considerable work has been done on the effect of N fertilization on both herbage and animal production in rotational grazing systems (Arnold and Holmes, 1958; Campling *et al.*, 1958; Holmes, 1968; Leaver, 1985), but the mechanisms involved in the increases of productivity were not clearly analysed. Thus, it was difficult to explain the large variability in response to N fertilizer from 5 kg DM kg^{-1} N (Peel and Matkin, 1984) to 15 kg DM kg^{-1} N (Holmes, 1968). Lantinga (1985) found that under continuous or rotational grazing at low and high N input there was no difference in seasonal crop CO_2 assimilation but a large difference in herbage production and herbage intake owing to an effect of N fertilizer on the partitioning of assimilates. More recent results of Gastal and Lemaire (1988) and Belanger *et al.* (1992) permit an ecophysiological explanation for the mechanisms involved in the effect of nitrogen deficiency on herbage growth under an intermittent defoliation regime. These authors analysed simultaneously the effect of N deficiency on morphogenic and on photosynthetic processes. They concluded that the major effect of N deficiency can be explained by a reduction in the leaf expansion rate and consequently by a reduction in the quantity of photosynthetically active radiation (PAR) absorbed by the sward, and also by a reduction in the proportion of assimilate allocated to shoot growth (Belanger *et al.*, 1992). Only 20% of the total effect of N deficiency on herbage growth could be directly attributed to the reduction in the leaf photosynthetic capacity. These results led to the hypothesis that in a continuously grazed sward, where the LAI is kept constant, the major part of the N effect should disappear.

In order to verify such a hypothesis, an experiment was carried out during two successive years on swards of two morphologically contrasting genotypes of tall fescue at two levels of N fertilizer application. The swards were continuously grazed by sheep and were maintained at similar heights or LAIs by a 'put and take' technique. Therefore, it was possible to investigate a large range of sward structure conditions by the combination of genotypes and sward height for testing the stability of the effect of N fertilizer on herbage growth. The use of the technique of lamina turnover measurement allowed the estimation of growth, senescence and intake fluxes from labelled tillers during different periods of the year.

This paper is concerned with an analysis of the effect of N fertilizer on herbage growth dynamics in interaction with the differences in sward structure resulting from combinations of cultivars and sward heights. A second paper will deal with the effect of N upon herbage intake and efficiency of herbage utilization.

Materials and methods

General conditions of the experiments

The experiments were carried out during 1987 and 1988 at INRA Station d'Ecophysiologie, Lusignan (46°26′ N; 0°7′ E). The weather conditions during these 2 years were relatively similar to average conditions for the site. The potentially large water deficit in summer was totally overcome by irrigation in order to maintain herbage growth over the season. The pastures were established on a loam soil of pH 6·4, sufficiently fertilized with P and K.

Swards of tall fescue (*Festuca arundinacea* Schreb.) were sown in April 1986 and were grazed uniformly by sheep during autumn in order to obtain a pasture well adapted to grazing at the beginning of spring 1987. The grazing animals were castrated sheep of the Texel breed of about 80 kg live weight.

Treatments and experimental design

Two levels of N fertilization were applied over the two successive years in order to generate two contrasting levels of N nutrition—N1, 40 kg ha^{-1}, and N2, 90 kg ha^{-1}—applied as ammonium nitrate every 45 days during the growing season. These correspond to annual N inputs of 160 and 360 kg ha^{-1}.

Two varieties of tall fescue were sown: cv. Clarine, characterized by a low tiller density and large tillers, and cv. Barcel, with a higher tiller density but smaller tillers. These two cultivars have similar heading dates.

During 1987 the four N × variety treatments were replicated in two randomized blocks in paddocks of 600 m^2 and were maintained at uniform LAI of approximately 2. During 1988, the two blocks were maintained at two different LAIs: 3 (H) or 2 (L).

Pasture management and experimental periods

During the growing season the number of sheep per paddock was adjusted frequently in order to maintain a given sward height corresponding to the expected LAI. During periods of 2 or 3 weeks, measurements were made on labelled tillers (see below). Two periods of measurements were made during 1987—P1, 15 June to 6 July, and P2, 2–19 October—and three other periods during 1988—P3, 5–18 April; P4, 6–20 June; P5, 5–22 September. During each period, eighty sward-height measurements were made every 2 days in each paddock with an HFRO sward stick. At the beginning and the end of each period, eight turves of 750 cm^2 were removed from each paddock. On each turf, four measurements of sward height were made and the herbage was cut at soil level with a scalpel for determination of living biomass, dead biomass, tiller density and LAI. The LAI was estimated by the measurement of the lamina/pseudostem ratio and the specific leaf weight by electronic planimeter on a subsample. This procedure was repeated at the middle and at the end of each period. Therefore, for each period and each treatment, it was possible to establish a relationship between sward height (H) and LAI and to use it for maintaining all treatments at an equal and constant LAI. Between successive periods the swards were maintained at constant height by eye estimation.

Herbage growth measurements

The leaf tissue growth was measured on individual tillers labelled in each paddock at the beginning of each experimental period. This method was adapted from those described by Bircham (1981), Davies (1981) and Arosteguy (1982). The tillers were labelled with coloured plastic telephone wire at soil level and were grouped in series of eight (in 1987) or nine (in 1988) tillers regularly spaced along a 2-m transect. In each paddock eight transects were randomly allocated, i.e. sixty-four labelled tillers in 1987 or seventy-two in 1988. On each tiller, the length of each leaf was recorded twice a week. The mature leaves were identified by presence of the ligule. The leaf elongation rate (LER) was calculated only on elongating leaves that were not grazed during the measurement interval. Making a mark at the leaf tips allowed us identification of the occurrence of any defoliation. The LER was calculated for each measurement interval and expressed in mm tiller^{-1} d^{-1} and was converted to growth rate (mg organic matter [OM] tiller^{-1} d^{-1}) using the weight of OM per unit of leaf length estimated from 150 tillers removed from the sward at the beginning and end of each period. Estimation of the tiller density was made at the same time on the turves used for LAI measurements (see above). Leaf growth rate in terms of kg OM ha^{-1} was calculated by multiplying the growth rate per tiller by the average tiller density.

During the periods P2, P3 and P4, thirty additional tillers per paddock were labelled and protected from animals by cages in order to compare the short-term response of LER to N fertilizer treatments between defoliated and non-defoliated tillers.

Statistical analysis

For each period, analysis of variance was made for the different variables: sward state variables (tiller density, sward height, LAI, biomass) and growth rate variables (LER, mm d^{-1}; growth per tiller, mg OM d^{-1}; growth per hectare, kg OM d^{-1}). These variables were recorded several times during each period: twice for state variables and five or six times for growth variables. Thus the analysis of variance was made on elementary data and it was possible to introduce a time factor in the model. For the two periods of 1987, the experimental design permitted calculation of a block effect, and the main factors N and genotype and their interaction were directly tested using the residual mean square. During 1988, in absence of replication, the main factors N, genotype and LAI were tested using their interaction with time. The different first-order interactions: N × genotype, N × LAI and genotype × LAI were tested with their corresponding second-order interaction with time. The probability corresponding with each calculated F is indicated in the table to allow a better estimation of the statistical significance of the data.

Results

Sward characteristics during the experimental periods

Nitrogen content in herbage. The differences in N content in herbage between the two N fertilizer treatments reflect the severity of the nitrogen deficiency created by the N treatment. The differences in %N between N2 (optimum) and N1 (deficient) varied between 0·5 and 1 (Table 1).

Herbage mass. There were no differences in herbage mass between N and variety treatments (Table 2). The LAI treatment imposed in 1988 generated significant differences in herbage mass.

Tiller density. During 1987, tiller density remained low, about 3000 tillers m^{-2}. It increased during winter 1987–88 to about 6500 tillers m^{-2} during P3 (spring) and stabilized in summer and autumn (Table 3). The analysis of variance indicates that the effects of N and variety were significant for all periods: high N application increased tiller density by 22% from 4686 to 5712 tillers m^{-2}, and Barcel had about 20% more tillers than Clarine. The difference in LAI during 1988 did not affect the tiller density except in period P4.

Sward height and leaf area index. The sward height was statistically significant between N

Table 1. Nitrogen content (g N 100 g DM^{-1}) of living biomass for each treatment during the five periods (average of two determinations)

		1987		1988				
		P1	P2	P3	P4	P5	Mean P1–P5	Mean P3–P5
Clarine N1	L	3·1	2·9	2·6	2·6	2·7	2·78	2·63
	H			2·4	2·5	2·6		2·50
Clarine N2	L	3·7	3·4	3·0	3·5	3·6	3·44	3·37
	H			3·0	3·4	3·4		3·27
Barcel N1	L	2·8	2·9	2·5	2·6	3·1	2·78	2·73
	H			2·6	2·7	2·9		2·73
Barcel N2	L	3·8	3·5	3·0	3·4	3·8	3·50	3·44
	H			3·1	3·4	3·6		3·37
s.e.		0·29	0·15	0·23	0·18	0·17		

L denotes swards maintained at low LAI and H at high LAI.
N2, N1 denote low and high N application rates.

treatments only for periods P3, P4 and P5 (Table 4). The effect of variety was highly significant for all periods, and the effect of LAI was highly significant for the three periods of 1988 when different LAI treatments were introduced. In terms of LAI (Table 5), significant differences attributable to variety disappeared after P1, and the difference in LAI between treatments during 1988, which averaged 2·4 *vs* 1·6, indicated a satisfactory achievement of two sward conditions. The effect of N was significant only for the period P3, and appeared only in the case of H swards.

The relationship between sward height (Ht) and LAI was calculated for each period and each N × variety treatment. The effect of variety was significant for all periods and reflected the morphological differences of the two genotypes as illustrated in Figure 1:

$$\text{Clarine: LAI} = 0{\cdot}41 + 0{\cdot}15\ (\pm 0{\cdot}007) \times \text{Ht} \quad (1)$$

$$\text{Barcel: LAI} = 0{\cdot}37 + 0{\cdot}18\ (\pm 0{\cdot}010) \times \text{Ht} \quad (2)$$

To obtain the same LAI for the two varieties, it was necessary to have a greater sward height with Clarine than with Barcel. This condition was not entirely respected during the first period when the LAI of Clarine was 1·5 *vs* 1·8 for Barcel. This difference occurred because the LAI × H relationships were not yet clearly established so that the difference of about 0·7 cm in sward height between the two genotypes (Table 4) was insufficient to generate similar LAIs. This small difference was corrected successfully in the subsequent periods.

The effect of N application on sward structure appeared to be less than that of genotype:

$$\text{N1: LAI} = 0{\cdot}46 + 0{\cdot}15\ (\pm 0{\cdot}007) \times \text{Ht} \quad (3)$$

$$\text{N2: LAI} = 0{\cdot}41 + 0{\cdot}17\ (\pm 0{\cdot}009) \times \text{Ht} \quad (4)$$

Table 2. Herbage mass (kg OM ha^{-1}) for each treatment during the five periods (average of two determinations)

		1987		1988				
		P1	P2	P3	P4	P5	Mean P1–P5	Mean P3–P5
Clarine N1	L	1090	1462	1619	1525	1331	1405	1492
	H			1747	1719	1779		1748
Clarine N2	L	1127	1366	1441	1376	1440	1350	1419
	H			2045	1785	1715		1848
Barcel N1	L	1218	1336	1387	1345	1095	1280	1276
	H			1753	1657	1637		1682
Barcel N2	L	1128	1604	1485	1327	1049	1319	1287
	H			2071	1765	1533		1790
s.e.		129·4	197·4	141·3	97·3	301·2		
Probability attributable to each treatment								
Nitrogen		0·55	0·37	0·09	0·97	0·83		
Variety		0·18	0·43	0·31	0·14	0·07		
LAI				0·03	0·0002	0·0026		

L denotes swards maintained at low LAI and H at high LAI.
N2, N1 denote low and high N application rates.

Table 3. Tiller density per m² in sward for each treatment during the five periods (average of two determinations)

		1987		1988				
		P1	P2	P3	P4	P5	Mean P1–P5	Mean P3–P5
Clarine N1	L	2538	2670	5540	4473	4820	4008	4944
	H			5267	4293	4553		4704
Clarine N2	L	2839	3128	6170	6320	5467	4785	5986
	H			6353	5160	4807		5440
Barcel N1	L	3202	3550	6460	4860	5220	4658	5513
	H			6126	4873	5127		5375
Barcel N2	L	3671	4229	7773	7060	5940	5735	6924
	H			8413	6093	6173		6893
s.e.		314·1	262·9	547·1	488·4	510·1		
Probability attributable to each treatment								
Nitrogen		0·0032	0·0002	0·002	0·0005	0·033		
Variety		0·0001	0·0001	0·0018	0·03	0·028		
LAI				0·86	0·05	0·47		

L denotes swards maintained at low LAI and H at high LAI.
N2, N1 denote low and high N application rates.

The two N treatments progressively became different over the different periods as a consequence of the increase in tiller density.

Leaf elongation rate (LER) on individual tillers

The analysis of variance indicated that neither the interactions N × variety nor N × LAI were significant in any period. The LAI × variety interaction was significant only during period P5 (Table 6). It was therefore justifiable to analyse directly the main effect of the three factors. The effect of N was highly significant except in autumn 1987 (period P2) possibly because of low temperatures. Apart from this period, the LER of N2 swards was 15–28% higher than that of N1 swards. The effect of genotype was significant only during 1987. The higher LER of Barcel during the period P1 was the consequence of its higher LAI. The effect of LAI on LER was significant only for the two last periods. H swards had 20% greater LER than L swards.

The mean LER of protected tillers remained higher than that of grazed tillers in all periods and the effect of N fertilizer was amplified by grazing exclusion (Table 7). The dynamics of leaf growth on tillers after caging is shown in Figure 2. Grazed tillers did not exhibit any response to N fertilizer, but the LER of protected tillers progressively increased, the effect of N fertilizer appearing after about 10 days.

Table 4. Sward height (cm) for each treatment during the five periods (average of 8–10 determinations)

		1987		1988				
		P1	P2	P3	P4	P5	Mean P1–P5	Mean P3–P5
Clarine N1	L	13·3	10·5	9·7	9·1	7·9	10·1	8·9
	H			12·9	12·1	11·3		12·1
Clarine N2	L	13·1	10·7	9·5	9·7	7·5	10·1	8·9
	H			13·1	11·9	10·3		11·8
Barcel N1	L	12·2	9·1	8·5	8·7	7·7	9·2	8·3
	H			10·7	11·2	10·2		10·7
Barcel N2	L	12·8	8·7	9·2	8·6	7·3	9·3	8·4
	H			11·4	10·9	9·6		10·6
s.e.		0·95	0·54	0·56	0·56	0·65		
Probability attributable to each treatment								
Nitrogen		0·51	0·48	0·051	0·055	0·0005		
Variety		0·006	0·0001	0·0001	0·0001	0·0006		
LAI				0·0001	0·0001	0·0001		

L denotes swards maintained at low LAI and H at high LAI.
N2, N1 denote low and high N application rates.

Table 5. Leaf area index of sward for each treatment during the five periods (average of two determinations)

		1987		1988				
		P1	P2	P3	P4	P5	Mean P1–P5	Mean P3–P5
Clarine N1	L	1·4	2·4	1·7	1·8	1·4	1·7	1·6
	H			2·1	2·2	2·4		2·2
Clarine N2	L	1·6	2·4	1·7	1·7	1·6	1·8	1·7
	H			2·6	2·2	2·6		2·5
Barcel N1	L	1·9	2·3	1·6	1·8	1·4	1·8	1·6
	H			2·3	2·4	2·3		2·3
Barcel N2	L	1·7	2·6	1·7	1·8	1·4	1·8	1·6
	H			2·8	2·6	2·7		2·7
s.e.		0·34	0·24	0·15	0·22	0·62		
Probability attributable to each treatment								
Nitrogen		0·84	0·15	0·0014	0·83	0·61		
Variety		0·028	0·33	0·47	0·086	0·83		
LAI				0·0001	0·0008	0·011		

L denotes swards maintained at low LAI and H at high LAI.
N2, N1 denote low and high N application rates.

Herbage growth

In order to estimate herbage growth per unit area, the data on LER were combined with data on leaf width, specific leaf weight and tiller density. Leaf width was not affected by N treatment and was significantly different between the two genotypes for all periods: 5·65 and 5·04 mm for Clarine and Barcel respectively (data not shown). The specific leaf weight did not differ between the two varieties, but varied with N treatment: 4·9 and 4·6 mg cm^{-2} for N1 and N2 respectively. The differences between treatments in tiller density are presented in Table 3.

The analysis of variance of herbage growth showed that the interactions between N and LAI or between variety and LAI were rarely significant except during period P5 (Table 8). Even during this period the magnitude of the interaction was small in comparison with the effects of N fertilizer and/or variety. Thus the level of LAI of the sward had little effect on the response of herbage growth to either N fertilizer application or to variety. The interaction between N fertilizer and variety was only significant for the first two periods in 1987. During these periods the response of Clarine to high N application was less than for Barcel; Clarine showed an increase of 16% and 7% for P1 and P2 respectively compared with 24% and 18% for Barcel. During 1988, the two varieties showed a similar increase of 30% in herbage growth in response to high N application (Table 8). Barcel had a significantly higher herbage growth than Clarine during the first experimental period, but this difference disappeared in the following periods when similar LAIs were maintained between varieties.

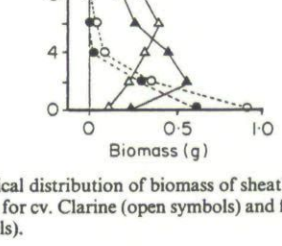

Figure 1. Vertical distribution of biomass of sheath (●, ○) and lamina (▲, △) for cv. Clarine (open symbols) and for cv. Barcel (closed symbols).

Discussion

Leaf elongation rate on individual tillers

It was possible to analyse the relationship between LER and mean air temperature for each measurement interval (3 or 4 days) within each period. Two different regressions for each N treatment have been calculated:

$$\text{N1: LER} = 3{\cdot}51 + 0{\cdot}290 \times \text{T} \quad r = 0{\cdot}47 \quad (5)$$

$$\text{N2: LER} = 0{\cdot}96 + 0{\cdot}583 \times \text{T} \quad r = 0{\cdot}61 \quad (6)$$

The data points are very dispersed (Figure 3), indicating a great variability in the response of LER to temperature. Relationships have been

Table 6. Leaf elongation rate (mm d^{-1}) on labelled tillers for each treatment during the five periods (average of 5–7 determinations)

		1987		1988				
		P1	P2	P3	P4	P5	Mean P1–P5	Mean P3–P5
Clarine N1	L	10·22	7·88	6·96	6·55	5·75	7·47	6·42
	H			6·79	7·80	7·96		7·52
Clarine N2	L	13·69	7·68	8·04	7·55	7·42	8·88	7·67
	H			8·72	10·82	9·41		9·65
Barcel N1	L	11·25	6·76	6·92	5·73	6·07	7·35	6·24
	H			7·09	7·74	7·43		7·42
Barcel N2	L	16·12	7·42	8·15	7·39	7·54	9·32	7·69
	H			7·81	9·85	8·61		8·76
s.e.		1·466	0·768	0·592	0·608	0·361		
Probability attributable to each treatment								
Nitrogen		0·0001	0·3500	0·0080	0·0020	0·0007		
Variety		0·0005	0·0103	0·5700	0·1000	0·1300		
Nitrogen/variety		0·1100	0·0870	0·3000	0·7800	0·3700		
LAI				0·7000	0·0013	0·0005		
LAI/nitrogen				0·7100	0·0600	0·3300		
LAI/variety				0·4700	0·9600	0·0200		

L denotes swards maintained at low LAI and H at high LAI.
N2, N1 denote low and high N application rates.

calculated between LER and T for tall fescue and other grass species in both controlled and field conditions under cutting regimes (Peacock, 1975; Thomas and Norris, 1977; Lemaire, 1985; Woodward and Friend, 1988). These authors have distinguished different responses of LER to temperature according to the physiological stage of tillers, i.e. vegetative or reproductive. For tall fescue, with non-limiting N, Gastal *et al.* (1992) proposed Gompertz equations for a range of temperature from 0 to 25°C. The comparison of our data at high N, in each situation, vegetative or reproductive, with these equations showed a great reduction of LER at a given temperature under continuous grazing compared with infrequent cutting. This reduction in LER was greater in spring: from 30 to 10 mm d^{-1}. The progressive death of reproductive tillers in spring due to removal of apices and the continual appearance of unvernalized and vegetative tillers in continuously grazed swards could be the major cause of the reduction in potential LER in comparison with undefoliated swards mainly composed of reproductive tillers. However, the reduction in LER in continuously grazed swards in comparison with infrequently defoliated sward persisted even when the sward returned to the vegetative stage in summer and autumn. Comparison of the data for the summers 1987 and 1988 (Figure 3b) shows a large difference in LER for a given temperature. The tiller density doubled from summer 1987 (P1) to summer 1988 (P4) for swards maintained at equivalent height or LAI (Table 4), and as a consequence the leaf area per tiller or the leaf length per tiller was greater during P1 (284 mm $tiller^{-1}$) than during P4 (213 mm $tiller^{-1}$).

Different authors have reported an effect of tiller size (in terms of weight or in terms of leaf area) on LER (Thomas, 1977; Nelson and Sleeper, 1981; Arosteguy, 1982; Grant *et al.*, 1989). This effect of tiller size on LER can be more precisely analysed by a comparison of the leaf

Table 7. Comparison of nitrogen effect on LER on grazed or protected tillers (mm $tiller^{-1}$ d^{-1})

	Grazed tillers				Protected tillers			
	N1	N2	Mean	N2/N1	N1	N2	Mean	N2/N1
P2	7·3	7·6	7·4	1·03	9·0	10·8	9·9	1·20
P3	6·9	8·2	7·6	1·18	8·0	9·6	8·8	1·20
P4	7·0	8·9	7·9	1·28	8·5	12·5	10·5	1·47
Mean	7·1	8·2	7·6	1·16	8·5	11·0	9·7	1·29

N1 = low N application rate.
N2 = high N application rate.

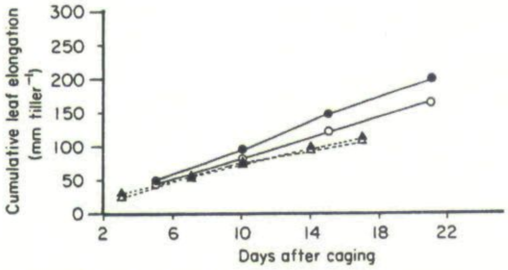

Figure 2. Cumulated leaf elongation of grazed (▲, △) or caged (●, ○) tillers during autumn 1987 for high N (closed symbols) and for low N (open symbols).

elongation of individual tillers protected or not from grazing. Relationships between LER and the total green leaf length of individual tillers (Lg) were observed on protected tillers ($r = 0{\cdot}61^{***}$), while on grazed tillers the correlation was not significant ($r = 0{\cdot}10$, NS). As pointed out by Grant *et al.* (1989), defoliation is more frequent on bigger tillers, and this is the reason why the correlation between LER and Lg becomes less in grazed situations. Thus, the LER could be related more to the average leaf length of the tiller during a certain period preceding the measurement than to its instantaneous leaf length. Our data did not allow estimates of this 'average Lg' on individual tillers and, in order to avoid the variability induced by recent defoliations at individual tiller level, we calculated the mean LER for each tiller class of 5 cm of L. The regressions obtained for grazed and protected tillers were very similar and the slopes did not differ (Figure 4):

$$\text{Grazed: LER} = 3{\cdot}66 + 0{\cdot}0088 \times \text{LG} \quad r = 0{\cdot}84 \quad (9)$$

$$\text{Protected: LER} = 4{\cdot}47 + 0{\cdot}0093 \times \text{Lg} \quad r = 0{\cdot}91 \quad (10)$$

In terms of these equations, the specific effect of the grazing animals on LER appears to be restricted to the small difference in the intercept values, though protected tillers will have an increasingly larger Lg than grazed tillers and will therefore grow faster. Grant *et al.* (1989) showed that comparison of LER between grazed and ungrazed tiller introduces an element of bias as tillers are not grazed at random, the tallest tillers (with larger Lg) being defoliated more frequently than the smaller ones. As indicated in the Materials and methods section, the LER of grazed tillers was determined only on the tillers whose elongating leaves were not grazed during the measurement period. The mean defoliation interval for this category of leaf was about 17 days (Mazzanti and Lemaire, 1994), thus for an average measurement period of 3·5 days only 20% of labelled tillers were lost from the LER determination and therefore the bias could be considered as relatively small.

The reduction in the LER of tillers maintained at low mean leaf area by continuous grazing could explain the relatively low response of LER to N fertilizer compared with that obtained under infrequent defoliation (Gastal and Lemaire, 1988). In swards of higher tiller density at high N maintained at similar LAI, the leaf area per tiller was smaller than in low-N swards. This phenomenon could partly counterbalance the effect of N

Table 8. Herbage growth (kg OM ha^{-1} d^{-1}) for each treatment during the five periods (average of 5–7 determinations)

		1987		1988				
		P1	P2	P3	P4	P5	Mean P1–P5	Mean P3–P5
Clarine N1	L	51·05	41·42	70·91	63·41	52·03	55·76	62·12
	H			69·24	71·75	74·33		68·44
Clarine N2	L	61·12	44·52	95·11	102·39	76·72	75·97	91·41
	H			103·14	117·74	77·85		99·58
Barcel N1	L	66·47	42·00	69·39	54·12	51·17	56·63	58·23
	H			71·09	71·78	56·02		66·30
Barcel N2	L	87·05	51·35	105·24	99·53	69·79	82·59	91·52
	H			100·86	112·64	69·08		94·19
s.e.		7·376	4·303	6·386	6·381	3·048		
Probability attributable to each treatment								
Nitrogen		0·0001	0·0020	0·0005	0·0002	0·0004		
Variety		0·0001	0·0130	0·4300	0·1500	0·0040		
Nitrogen/variety		0·0210	0·0320	0·4700	0·8800	0·1600		
LAI				0·7100	0·0070	0·0110		
LAI/nitrogen				0·7100	0·7900	0·0100		
LAI/variety				0·3900	0·4900	0·0700		

L denotes swards maintained at low LAI and H at high LAI.
N2, N1 denote low and high N application rates.

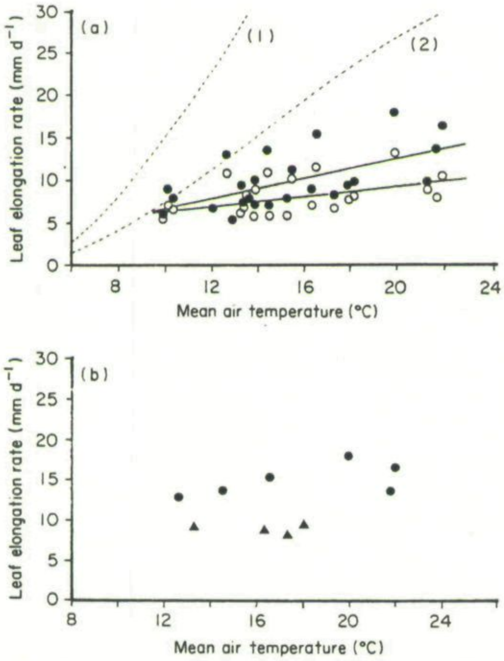

Figure 3. (a) Relationships between LER and air temperature during the different periods for high (●) and low (○) N. Dotted lines represent the relationships for undisturbed swards in spring (1) and in summer (2) according to Gastal *et al.* (1992). (b) Comparison of LER for summer 1987 (●) and summer 1988 (▲) at high N.

nutrition *per se* on the elementary processes of cell division and cell elongation which drive the leaf elongation rate.

Herbage growth

Herbage growth may be considered as the product of growth per tiller and tiller density. LER is the major component of the growth per tiller. Therefore, for analysing the effect of N and of interactions with variety or LAI on herbage growth, it is necessary to examine these effects on each of these components. The average effects of N, genotype and LAI are summarized in Table 9. High N application increased herbage growth by 39% as a consequence of the 13% increase in growth rate per tiller (Table 6) and the 21% increase in tiller density (Table 3). The effect of N on LER remained limited to 23%, as explained in the preceding section, and was partly counterbalanced by a reduction in specific leaf weight. Therefore the importance of LER as a component of the response of herbage growth to N appeared to be less in continuously grazed than in infrequently defoliated swards and was partly offset by the effect of N on tiller density. The analysis of the effect of genotype shows a total compensation between growth per tiller and tiller density. Thus, despite the great morphological differences between the two genotypes, the homeostatic response of the swards results in a similar herbage growth and similar response to N. This homeostasis can also be observed by analysing the response of swards to level of LAI, an increase of 19% in growth rate per tiller being partly compensated by a decrease of 8% in tiller density. This phenomenon was described by Bircham (1981) on perennial ryegrass dominated swards.

In order to analyse the potential for herbage production of continuously grazed swards of tall fescue over the different seasons we expressed the herbage growth in relation to the quantity of intercepted photosynthetically active radiation (PAR). The intercepted PAR was estimated by the means of the light interception model described by Lemaire (1985) and by Gastal and Lemaire (1988) for tall fescue, following the approach of Monteith (1977). By this model we obtained an estimation of the energy conversion in herbage dry matter: 2·1–2·4 g MJ^{-1} in spring 1988 (P3) and 1·3–1·5 g MJ^{-1} in summer and autumn 1988 (P4 and P5). These values are similar to those obtained in an adjacent site and during the same year on an infrequently defoliated sward of tall fescue (cv. Clarine) and reported by Belanger *et al.* (1992): 1·9–2·2 g MJ^{-1} in spring and 1·6 g MJ^{-1} in summer.

Conclusions

In the absence of strong interactions between N fertilizer and the other two factors, LAI and genotype, it may be possible to extrapolate these results to a wide range of sward conditions. The initial hypothesis suggested that the continual

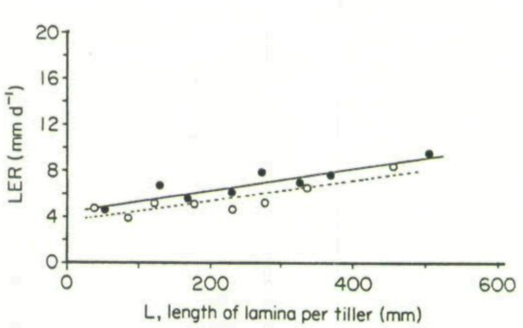

Figure 4. Relationship between LER and the total length of green lamina (L) for grazed tillers (○) or protected tillers (●).

Table 9. Effect of N fertilizer, genotype and LAI on herbage growth and its components

	LER	Growth rate per tiller	Tiller density	Herbage growth
N2/N1	1·23	1·13	1·21	1·39
Clarine/Barcel	0·99	1·15	0·81	0·96
	(1·03)†	(1·20)	(0·80)	(1·00)
H/L	1·19	1·19	0·92	1·08

† Excluding period P1.

removal of the additional leaf tissue production due to N fertilizer application by a corresponding increase in stocking density, adjusted to maintain a constant given sward LAI, should limit the sward response to N fertilizer application. This hypothesis was based on the predominance of the leaf area expansion as the chief mechanism contributing to the response of an infrequently defoliated sward to variation in N nutrition level. The results obtained during this experiment showed that in continuously grazed swards, as well as responses in LER, the promotion of tillering rate provides an alternative additional pathway for N response. The absence of any difference in herbage growth between the two morphologically contrasting genotypes was due to counterbalanced homeostatic mechanisms whereby differences in growth rate per tiller were offset by differences in tiller density. The detailed mechanisms involved in the herbage growth dynamics under different grazing managements remain relatively unknown and will require further study in the future.

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