

MEDEDELINGEN LANDBOUWHOGESCHOOL  
WAGENINGEN • NEDERLAND • 81-5 (1981)

# THE INFLUENCE OF PHYSICAL FACTORS ON THE NUTRIENT CONTENT OF FORAGES

B. DEINUM

*Department of Field Crops and Grassland Science,  
Agricultural University, Wageningen, The Netherlands*

(Received 9-XII-1980)

H. VEENMAN & ZONEN B.V.-WAGENINGEN - 1981

BIBLIOTHEEK  
PER  
LANDBOUWHOGESCHOOL  
WAGENINGEN

AN 123724-02

# THE INFLUENCE OF PHYSICAL FACTORS ON THE NUTRIENT CONTENT OF FORAGES

## INTRODUCTION

### *What are nutrients*

All plants have in common that their cells are surrounded by walls. This cell wall mainly constitutes from cellulose, hemicellulose, lignin and sometimes silica, whereas the cellular contents mainly consists of protein, minerals, soluble carbohydrate, starch, and organic acids.

Herbivorous animals are able to digest the cellular contents of plants almost completely, but digestion of cell walls varies greatly with animal species. Therefore it is very useful to know the proportions of cellular contents and cell-wall constituents in different fodders. In monogastrics like rat and man, which have a small digestion system, digestion of plant cell walls is minute. Horse and deer do better because of a fair microbial digestion in caecum and colon, but ruminants do best because the cell walls are thoroughly degraded in the rumen. Table 1 demonstrates the ability of different animals to digest the cellulose and hemicellulose of a legume and a grass, and reveals that grass cell walls are especially poorly digested by monogastrics. Cell-wall digestion would have been greater in these monogastrics if the retention time in the digestive tract had been longer (VAN SOEST, personal communication, 1975). In ruminants in which retention time is extended to about two days, the digestibility of plant cell walls mainly depends on whether the cells are from non-lignified, highly digestible tissues (such as parenchyma) or from lignified tissues (such as xylem, sclerenchyma and cuticle). In the latter tissues the lignin content greatly determines digestibility (MINSON, 1976).

A century ago the undigested cell wall fractions were considered to be retained in the crude-fibre determination, but subsequent research has disclosed that about 70–95% of the cellulose, 5–50% of the lignin and about 20% of the hemicellulose is retained in this determination, of which cellulose and hemicellulose can be very digestible (VAN SOEST, 1976). Figure 1 shows the average composition of Dutch herbage estimated by the old proximate analysis and by the new techniques of VAN SOEST using detergents.

TABLE 1. Digestibility (%) of cellulose and hemicellulose from lucerne (*Medicago sativa*) and brome grass (*Bromus enermis*) in various species (VAN SOEST and MC QUEEN, 1973).

Species	Lucerne		Brome grass	
	Cellulose	Hemicellulose	Cellulose	Hemicellulose
Sheep	50	47	67	71
Pig	40	43	39	47
Vole	33	39	18	24
Rat	21	47	1	11

cellular contents (44%)					cell-wall constituents (56%)		
crude protein	ash	total	sol carbo-hydrates	org acids	hemicellulose	lignin	cellulose
15	8	2	10	9	26	5	25
15	8	2	nitrogen-free extract			crude fibre	
crude protein	ash	total					

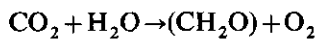
Figure 1. Average chemical composition of Dutch herbage according to the old proximate analysis (bottom) and with the procedures of Van Soest using detergents (top) (DEINUM, 1974).

Amino-acid compositions of protein is a criterion for nutrient content of plants for monogastrics, but not so much in ruminants, as these animals do not absorb the plants protein but the protein from the rumen microflora. As the amino-acid composition of plant protein is determined genetically rather than environmentally no attention will be paid to it in this paper.

#### *Plant production*

Three processes are involved in the production of dry matter in plants grown for animal fodder with regard to their quality. These three processes are clearly described by BROUWER (1962, 1962a) and they help explain the effects of the environmental factors described below. The kinetics of each of these three processes affects the chemical composition of the plant. Therefore it is clear that these processes form the basis of the effects of environmental factors on nutrient content of plants.

Photo-autotrophic plants produce their dry matter by the process of photosynthesis, which is briefly and very simply described in the following way:



This process is stimulated by higher light intensity and higher concentration of carbon dioxide in the air if the supply of minerals and of water for transpiration is adequate, whereas it is also controlled by temperature. The initial product of this reaction is phosphoglycerate in plants from temperate regions which show the Calvin metabolism for photosynthesis (called C<sub>3</sub> plants after the 3 C-atoms in phosphoglycerate). In many tropical plants oxaloacetate is also a first product (C<sub>4</sub> plants) which coincides with their high photosynthesis at high temperature. The excess of both initial products may be stored in the cellular contents as water-soluble carbohydrate or starch.

A second process in the plant is the uptake of nitrogen as nitrate or ammonia from the soil and its incorporation into protein. This reaction proceeds at the expense of the reserve carbohydrate produced by photosynthesis. Therefore, as the protein content increases with higher nitrogen uptake, the amount of reserve

carbohydrate decreases. If the nitrogen is taken up as nitrate and not used to form protein, the excess accumulates in the plant and becomes toxic if it is reduced to nitrite in the digestive tract of the animal that eats the plant.

The products of photosynthesis are not only used for protein formation and carbohydrate accumulation but also for building new tissues and organs. This development and morphogenesis is greatly influenced by temperature and sometimes by day length.

In this paper, the examples of plant nutrient content are mainly derived from trials on forages for ruminants. However, as all plants species are subject to similar processes of nutrient production, some examples from seeds and vegetables are included for comparison.

### *Nomenclature*

Various abbreviations, not found in the IUPAC-IUB combined commission bulletins, are used in the tables of this paper.

dm = dry mass, cp = crude protein (% organic nitrogen  $\times$  6.25), ash = the amount of minerals retained after ashing at 550°C, wsc = water-soluble carbohydrate, tnc = total non-structural carbohydrate (wsc + starch, measured as  $(C_6H_{12}O_6)_n$ ), cwc = cell-wall constituents, cf = crude fibre, cell. = cellulose, hemic. = hemicellulose, l. = lignin,  $D_{om}$  = *in-vivo* apparent digestibility of organic matter, ( $D_{vitro}$  = *in vitro* true digestibility of organic matter with rumen micro flora ( $D_{vitro} \approx D_{om} + 13$ )),  $D_{cwc}$  = *in vitro* digestibility of cell-wall constituents, calculated from  $D_{vitro}$ , cwc and ash.

The reserve carbohydrate is water-soluble carbohydrate in temperate grasses and total non-structural carbohydrate in all other plants, as the temperate grasses contain hardly any starch in their vegetative parts. No attention is paid to the mineral composition of the plants or to anti-quality components such as alkaloids, steroids and glycosides. Information on these items has recently been summarized by BUTLER and BAILEY (1973).

Nutrient content is generally expressed in percentages. As all percentages together make 100%, this implies that a rise of the content of one or more constituents must cause a drop in content of others. Consequently the explanation is sometimes rather complex.

## THE INFLUENCE OF VARIOUS ENVIRONMENTAL FACTORS

The various factors to be studied are usually highly correlated in nature. So a high light intensity usually coincides with a high temperature, a high barometric pressure and a low relative humidity. Similarly, water shortage often prevails in bright and hot conditions. This implies that the true effects of these factors can only be measured properly if each of them is varied independently from the others. So light intensity can be varied by using screens and lamps in the greenhouse and in the field. Temperature and humidity can be varied in temperature- and humidity-controlled greenhouses, but it is very difficult to

manipulate barometric pressure. Water supply can be manipulated by irrigation and drainage.

#### Light intensity

Light intensity is expressed in  $\text{Wm}^{-2}$  (in controlled environment) or in  $\text{J cm}^{-2} \text{ day}^{-1}$  (in controlled environment and in nature) either in the visible range (400–700 nm) or total (400–10000 nm). Table 2 shows the effects of light intensity in a field trial revealing that at higher light intensity the content in the dry matter of nitrate, crude protein and ash decreased, whereas the reserve carbohydrate content increased, just the opposite of the effect of nitrogen fertilization. The quantity and composition of the cell walls were hardly affected; neither was digestibility. This can be explained by the rule that given the same limited amount of nitrogen, the higher light intensity causes more photosynthesis and dry matter production, thus diluting the available nitrogen over a greater amount of dry mass. Moreover the increases photosynthesis causes a greater accumulation of reserve carbohydrate. So a high light intensity can cause nitrogen shortage.

This marked effect of light intensity on the content of water-soluble carbohydrate is common in grasses such as *Lolium perenne*, *L. multiflorum* and a few other temperature grasses that can accumulate fair amounts of soluble carbohydrate. As the lower content of protein and ash at higher light intensity was counterbalanced well by the higher content of water-soluble carbohydrate in this experiment, the percentage of cellular contents and of cell-wall constituents was not affected much by light intensity. However in many former experiments with *L. perenne* the positive effect of light intensity on % water-soluble carbohydrate overcompensated the negative effect on protein and ash content so much that % crude fibre decreased appreciably with higher light intensity, especially in case of low nitrogen fertilization (DEINUM, 1966).

In most grasses the effect of light intensity on carbohydrate content is less, for example in the tropical species *Setaria sphacelata* (Table 3), whereas the effect on % protein is about the same. A great effect was found on % nitrate and ash, possibly because of the abundant mineral application. Filling of the plant cells declined in this trial with higher light intensity, because of the decline in nitrate

TABLE 2. The effect of light intensity on chemical composition of a sward of *Lolium perenne* in a vegetative stage (in % of dry matter) (after DEINUM et al, 1968).

Light intensity $\text{J.cm}^{-2}.\text{day}^{-1}$	$\text{NO}_3\text{-N}$	cp	ash	wsc	cwc	l.	cell.	hemic.	cf	$D_{om}$
527	0.09	24.3	9.7	9.5	46.1	2.07	22.6	21.5	23.0	86.5
1758	0.05	21.1	8.5	15.7	45.0	1.54	22.3	21.2	20.8	85.6

Growth conditions: growth period April 13 – May 10, 1967, average max. and min. temperature: 13.7 and 2.7°C resp. Fertilization: 100 kg N/ha as  $\text{NH}_4\text{NO}_3$ . The high light intensity is above average for this period. The low light intensity was established by shading with cheesecloth and yielded an intensity normal for October in the Netherlands.

TABLE 3. The effect of light intensity on yield and chemical composition of *Setaria sphacelata* (Schum) Stapf & Hubbard in a reproductive stage (in % of dry mass).

Light intensity J.cm <sup>-2</sup> .day <sup>-1</sup>	g dm		% dm		tiller number	NO <sub>3</sub> -N	cp	ash	tnc	cwc	cf	D <sub>nitro</sub>	D <sub>cwc</sub>
	g dm	% dm	% leaf blade	% dm									
758	26.2	12.0	61.2	38	0.87	23.8	12.0	6.5	47.3	27.2	72.4	48.7	
1515	83.4	15.2	47.2	87	0.21	20.3	6.2	7.3	59.9	31.5	81.5	71.0	
3022	105.9	16.5	49.5	132	0.10	19.4	5.8	8.1	61.3	30.5	84.9	76.9	

Growth conditions: small swards grown in sand in 5-litre plastic pots. Fertilizer application abundant. Greenhouse temperature 25–20°C, day and night resp.; High light intensity from HPL-R 400 W mercury lamps added to daylight. Day length: natural, about 16 hrs; growth period: May 10 – June 17, 1975.

TABLE 4. The effect of light intensity on chemical composition of leaf blade and stem of *Setaria sphacelata* (SCHUM) STAPF & HUBBARD (in % of dry mass).

Light intensity J.cm <sup>-2</sup> .day <sup>-1</sup>	Tissue	NO <sub>3</sub> -N		cp	ash	tnc	cwc	cf	D <sub>nitro</sub>	D <sub>cwc</sub>
		NO <sub>3</sub> -N	cp							
758	leaf blade	0.49	29.7	11.4	5.0	45.2	23.1	81.9	64.5	
1515	leaf blade	0.07	27.1	5.9	6.3	54.6	25.4	84.6	73.5	
3022	leaf blade	0.03	22.1	5.5	7.0	56.8	26.1	88.2	78.7	
758	leaf sheath + stem	1.47	14.6	13.0	8.8	58.8	33.7	(57.0)	(36.4)	
1515	leaf sheath + stem	0.33	14.2	6.5	8.1	59.9	37.0	78.7	66.8	
3022	leaf sheath + stem	0.16	16.8	6.1	9.1	65.8	34.8	82.7	75.3	

Growth conditions as in Table 3.

(–3.4%), crude protein (–4.4%) and ash (–6.2%) and the small rise of total non-structural carbohydrate (+1.6%), so the % cell-wall constituents and % crude fibre had to rise. Digestibility of organic matter increased with light intensity in this trial, as did digestibility of cell-wall constituents.

New tiller growth and stem development had been stimulated by higher light intensity (see tiller number and % leaf), so Table 3 reveals a mixture of direct and indirect effects of light intensity on plant production and chemical composition. Therefore, Table 4 shows the effect of light intensity on leaf blade and leaf sheath + stem separately. Leaf sheaths + stems were much lower in % protein and digestibility than leaves, much richer in nitrate and cell-wall constituents, and a little higher in total non-structural carbohydrate.

Stems were even less nutritious than leaf sheath, not only in this trial but also in all other examples yet to be mentioned in this paper.

What has been mentioned for the effect of light intensity of the whole crop in general, holds also for the effect on leaf blade and leaf sheath + stem separately. In leaves light intensity had about the same qualitative effect as in the vegetative

TABLE 5. The effect of light intensity on yield of dry mass and chemical composition of *Medicago sativa* L (in % of dry mass)

Light intensity J.cm <sup>-2</sup> .day <sup>-1</sup>	g dm	% dm	% leaf blade	tiller number	NO <sub>3</sub> -N	cp	ash	tnc	cwc	cf	D <sub>vitro</sub>	D <sub>cwc</sub>
758	33.4	17.4	44.9	56	0.88	24.2	12.7	6.1	36.3	29.2	81.8	56.2
1515	101.5	22.6	39.8	54	0.14	20.6	8.2	9.0	43.3	32.9	77.6	52.5
3022	102.3	29.3	36.7	56	0.06	16.3	6.5	12.0	46.4	34.2	76.7	53.0

Growth conditions: as in Table 3. Nitrogen uptake occurred from fertilizer nitrogen and not via *Rhizobium* in this trial.

grass of *Lolium perenne* from Table 2.

In stems, increased light intensity reduced the percentage of nitrate and ash, but it had hardly any effect on the content of crude protein and total non-structural carbohydrate, presumably because of the adequate supply of nitrate in all treatments. Yet the content of cell-wall constituents increased with higher light intensity. Digestibility of organic matter and of cell-wall constituents increased considerably as the light intensity increased like in the other grasses grown in this trial. The reasons for this increase are not yet clear.

Tables 5 and 6 show the effect of light intensity on the legume lucerne (*Medicago sativa*) grown in the same trial as the *Setaria* (Tables 3 and 4). The effects of light intensity in this forage legume were of the same direction as in *Lolium* and *Setaria*: nitrate, protein and ash content decreased with higher light intensity in

TABLE 6. Effect of light on chemical composition of leaf blade and stem of *Medicago sativa* L (in % of dry matter).

Light intensity J.cm <sup>-2</sup> .day <sup>-1</sup>	Tissue	NO <sub>3</sub> -N	cp	ash	tnc	cwc	cf	D <sub>vitro</sub>	D <sub>cwc</sub>
758	leaf blade	0.98	35.1	16.4	7.2	12.1	11.8	95.4	69.6
1515	leaf blade	0.11	31.6	12.3	8.5	15.2	11.8	94.5	68.3
3022	leaf blade	0.05	26.3	9.8	17.6	16.3	11.9	95.4	74.5
758	petiole + stem	0.80	15.3	9.6	5.3	56.0	43.3	71.4	53.8
1515	petiole + stem	0.16	13.3	5.4	9.4	61.9	46.8	67.3	50.0
3022	petiole + stem	0.07	10.5	4.5	8.7	63.8	47.2	66.9	50.5

Growth conditions: as in Table 5.

leaf and stem and in the whole crop, whereas content of total non-structural carbohydrate increased. The latter increase was greater than in *Setaria* but smaller than in *Lolium*. Again there was some increase in percentage of cell-wall constituents and crude fibre with higher light intensity, whereas digestibility of organic matter decreased somewhat. It is not yet clear at this moment why digestibility of the grasses increased with higher light intensity and why digestibility of lucerne decreased.

There appears some additional information from Tables 5 and 6. The average content and digestibility of cell-wall constituents is lower in *Medicago* than in *Setaria*, but the greater share of cellular contents cannot compensate for the lower digestibility of cell-wall constituents. So digestibility of organic matter was less in *Medicago* than in *Setaria*, at least at normal light intensities.

Especially leaf blades of *Medicago* were low in cell walls, which in turn were low in hemicellulose ( $\approx$  cwc-cf). Stems were also low in hemicellulose compared to grass. Summation of percentages of nitrate, protein, ash, total non-structural carbohydrate and cell-wall constituents reveals a discrepancy of about 30% in the leaves and about 10% in stems. This gap can almost certainly be filled by the organic acids formed in the protein formation from nitrate and by the fats normally extracted with ether. These tables also suggest that lucerne may be a good food for monogastrics because of their high percentage of cellular contents.

A final information from Tables 3 and 5 is that the dry-matter content of the forages is stimulated by higher light intensity. Thus a drier product is harvested in these conditions.

The same effects of light intensity are present in vegetables. Thus in spinach, a high light intensity stimulates dry matter production and reduces nitrate content (Table 7). At low nitrogen fertilization the content of crude protein was also reduced, as expected. However at the high nitrogen treatments the crude protein content (which is free of nitrate-N) increased in conditions of high light intensity. This seems strange but it becomes explainable if one realizes that a high light intensity not only stimulates carbon dioxide reduction (photosynthesis) but also nitrate reduction and consequently stimulates protein formation. Similar stimu-

TABLE 7. Effect of light intensity and nitrogen nutrition on yield and chemical composition of spinach leaves (after CANTLIFFE, 1972).

Light intensity	g dm/pot		% NO <sub>3</sub> -N		% cp	
	high	low	high	low	high	low
Nitrogen mg/kg soil						
0	0.22	0.22	0.09	0.14	16.8	19.9
100	1.27	0.57	0.35	1.09	22.6	20.3
200	1.25	0.42	0.72	1.61	23.5	18.3

Growth conditions; soil Honeyone. Temperature 18–13°C day and night resp. Age: 68 days. Light intensity low:  $\approx$  32 W.m<sup>-2</sup>; high:  $\approx$  96 W.m<sup>-2</sup> (400–700 nm) Day length: 14 hrs. Cultivar: Winter Bloomsdale.



lations have been reported on *Lolium perenne* (DEINUM, 1971) and *L. multiflorum* (DARWINKEL, 1975). This increase in protein content can only occur if the nitrogen supply is abundant and if nitrate reduction is stimulated more than carbon dioxide reduction by high light intensity. Thus CANTLIFFE (1972) found this did not occur in table beets.

Similar processes prevail in nutrient production in seeds (which generally constitute a fair part of the diet of domestic animals). Seedfilling occurs after flowering when the plant has usually finished vegetative growth. It occurs by translocation of protein and soluble carbohydrate from the vegetative parts.

Crops such as wheat normally exhaust the nitrogen from the soil before flowering and therefore protein accumulation in the seed occurs completely from redistribution of protein from the straw. However, with abundant supply of nitrogen, uptake may proceed longer.

Leaf photosynthesis continues for some time after flowering, so carbohydrate accumulation in the seed may proceed both from actual photosynthesis and from reserves stored earlier in the straw. It will be clear that the kinetics of both protein and carbohydrate translocation determine the content of protein and carbohydrate in the grain. Thus it has been established that during grainfilling the protein content declines gradually from a high level to a minimum, with a small increase in the final phase of ripening.

From the processes mentioned above it may be inferred that a higher light intensity will stimulate photosynthesis and consequently translocation of carbohydrate to the grain. The grain yield will be greater and the starch content higher (Table 8). As about the same amount of nitrogen is translocated to the seed, it is diluted over the greater amount of dry matter, so the protein content drops with higher light intensity. The water-soluble carbohydrate content of the wheat grains in Spiertz's trial was still rather high at the final sampling and not much affected by light intensity.

Table 8. Effect of light intensity on yield and chemical composition of grain in wheat at the final harvest (after SPIERTZ, 1977).

	Light intensity during grain filling ( $\text{W}\cdot\text{m}^{-2}$ )		
	33	62	98
Grain-filling period (days)	41	41	41
mg dm/ear	1103	1526	1783
mg N/ear	39.7	41.8	42.8
% protein ( $\text{N} \times 5.7$ )	20.5	15.6	13.7
% wsc	15.0	17.9	17.1
% starch ( $\text{C}_6\text{H}_{10}\text{O}_5$ ) <sub>n</sub>	50.5	51.8	54.2

Growth conditions: phytotron, temperature 20°C, photoperiod 16 hrs, light intensity (400–700 nm) from Philips fluorescent tubes TL-33 + incandescent bulbs. Plants in sandy soil in 5-litre plastic pots, adequately supplied with minerals and water. Cultivar: Orca. Plants were grown in a glasshouse from planting to flowering at 15°C and 80% of natural daylight (April-June 1971).

Thus it may be concluded that with a sufficient supply of nitrogen a higher light intensity stimulates crop production and causes plants with a lower content of nitrate, crude protein and ash, and a higher content of non-structural carbohydrate, whereas the effects on content and digestibility of cell-wall constituents are variable. However with a limited supply of nitrogen the effect of light intensity on content of crude protein and total non-structural carbohydrate can be very great. This suggests that in conditions of high light intensity, a high nitrogen supply is needed to prevent shortage of protein in the food, whereas in low light intensity a lower nitrogen fertilization is required to prevent nitrate toxicity and lack of digestible carbohydrate.

### Temperature

Table 9 describes the effect of temperature on reproductive *Lolium multiflorum*. In this grass stem development was greatly influenced by temperature, which had a marked effect on chemical composition via morphological development. At the temperature closest to the optimum, 25–20°C for this grass, yield of dry mass was highest and contents of protein and ash were lowest. The per-

TABLE 9. Effect of temperature on yield of dry matter and chemical composition (in % of dry mass) of the temperate grass species *Lolium multiflorum* Lam.

Temperature	g dm	% dm	% leaf blade	tiller number	NO <sub>3</sub> -N	cp	ash	wsc	cwc	cf	D <sub>Nitro</sub>	D <sub>cwc</sub>
15–10°C	45.7	14.2	58.6	112	0.73	24.5	9.9	14.6	35.2	18.4	94.6	86.2
25–20°C	65.0	15.5	40.7	225	0.68	20.7	9.1	9.5	46.5	25.9	84.7	69.9
35–30°C	13.9	23.3	36.2	121	1.86	22.0	14.8	8.6	44.4	21.8	67.6	37.8

Growth conditions: average light intensity: 1515 J.cm<sup>-2</sup>.day<sup>-1</sup>  
other conditions: as in Table 3.

TABLE 10. Effect of temperature on chemical composition of leaf blade and stem of *Lolium multiflorum* Lam (in % of dry mass).

Temperature	Tissue	NO <sub>3</sub> -N	cp	ash	wsc	cwc	cf	D <sub>Nitro</sub>	D <sub>cwc</sub>
15–10°C	leaf blade	0.70	30.2	10.8	12.2	29.7	15.9	96.2	88.6
25–20°C	leaf blade	0.81	30.7	12.4	9.2	32.1	17.9	95.1	86.6
35–30°C	leaf blade	1.79	26.1	16.7	11.2	31.6	15.9	80.9	49.7
15–10°C	leaf sheath + stem	0.78	16.5	8.6	18.0	43.0	21.9	92.4	83.9
25–20°C	leaf sheath + stem	0.59	13.9	6.8	9.7	56.4	31.4	77.9	63.5
35–30°C	leaf sheath + stem	1.91	19.6	13.8	7.1	51.6	25.2	60.4	33.8

Growth conditions: as in Table 9.

centage of water-soluble carbohydrate decreased as temperature increased especially in the range below the optimum temperature, certainly because of the enhanced metabolism and respiration at higher temperature. Nitrate content increased with higher temperature. The proportions of cell-wall constituents and crude fibre were greatest at the optimum temperature, but digestibility of organic matter and of cell-wall constituents decreased considerably as temperature increased, also above the optimum.

Table 10 describes the influence on leaf blade and leaf sheath + stem of *L. multiflorum* separately. As expected, leaf sheath + stems were much poorer in nutrient quality than leaves. The Table shows that with adequate supply of nitrogen, the percentage of  $\text{NO}_3\text{-N}$  and crude protein of the leaf blade hardly changed with rising temperature below the optimum, whereas the percentage of ash increased somewhat and percentage of water-soluble carbohydrate decreased. The percentage of cell-wall constituents and crude fibre were enhanced a little with higher temperature, but digestibility declined. However at 35–30°C, far above the optimum, nitrate and ash content were very high compared to 25–20°C; the percentage of crude protein was somewhat lower and that of water-soluble carbohydrate a little higher, which seems exceptional. The percentages of cell-wall constituents and crude fibre were somewhat lower, but a great reduction was found in digestibility of organic matter and of cell-wall constituents.

In this trial, the leaf sheaths + stems had a poorer quality, with a lower crude protein content and digestibility than the leaves, whereas the effect of temperature on the chemical composition was much greater than in leaves. This was certainly caused by the great effect of temperature on stem development (the samples of leaf sheath and stems at the 35–30°C treatment had to be combined because of shortage of material). If nitrogen supply had been restricted in this experiment, then the temperature effect on crude protein content would have been much greater because the limited amount of nitrogen would have been diluted over the great amount of dry matter at 25–20°C.

Table 10 shows that the content of cell-walls and crude fibre of leaves increased from 15–10°C to 25–20°C, whereas cell-wall digestibility decreased somewhat. This is partially the result of a direct effect, but also the result of an indirect effect via the morphological development. Rate of leaf appearance was greater at 25–20°C than at 15–10°C, so stems bore more leaves at 25–20°C

TABLE 11. Chemical composition of different leaves along the stem of *Panicum maximum* in a young adult stage (leaves numbered from bottom to top) (after WILSON, 1976).

Leaf number	leaf length	% cp	% cwc	% $D_{\text{vitro}}$
3	15.6	29.4	36.5	90.3
7	42.8	23.1	51.5	86.0
10	52.8	20.0	59.2	80.8
13	48.9	15.6	62.5	82.5
16 (flag)	14.4	20.6	63.8	78.0

Table 12. Effect of temperature on yield and chemical composition (in % of dry mass) of the tropical grass species *Setaria sphacelata* in a reproductive stage.

Temperature	g dm	% dm	% leaf blade	tiller number	NO <sub>3</sub> -N	cp	ash	tnc	cwc	cf	D <sub>nitro</sub>	D <sub>cwc</sub>
25–20°C	83.4	15.2	47.2	87	0.21	20.3	6.2	7.3	59.9	31.5	81.5	71.0
35–30°C	90.5	16.4	44.0	163	0.20	17.6	6.3	5.4	61.5	33.0	75.6	62.9

Growth conditions: as in Table 9

Table 13. Effect of temperature on chemical composition of leaf blade and stem of the tropical grass species *Setaria sphacelata* in a reproductive stage (in % of dry matter)

Temperature	Tissue	NO <sub>3</sub> -N	cp	ash	tnc	cwc	cf	D <sub>nitro</sub>	D <sub>cwc</sub>
25–20°C	leaf blade	0.07	27.1	5.9	6.3	54.6	25.4	84.6	73.5
35–30°C	leaf blade	0.08	25.3	6.2	5.5	53.6	26.6	83.1	70.4
25–20°C	leaf sheath + stem	0.33	14.2	6.5	8.1	59.9	37.0	78.7	66.8
35–30°C	leaf sheath + stem	0.30	11.6	6.4	5.4	67.7	38.1	69.8	58.2

Growth conditions: as in Table 9

than at 15–10°C, whereas these extra leaves are higher in cell walls and less digestible (Table 11).

Table 12 and 13 illustrate the effect of temperature on the tropical grass *Setaria sphacelata* grown in the same trial as *L. multiflorum* (Tables 9 and 10). The data show that the effect of temperature in this tropical grass and in *L. multiflorum* are similar, taking into account the different optimum temperature (22°C for *L. multiflorum* and 29°C for *S. sphacelata*). However the one exception was that in the content of the total non-structural carbohydrate which did not decrease so much with temperature as in *L. multiflorum*. This is presumably because in tropical grasses photosynthesis and formation of new tissues are affected to the same degree by temperature, whereas in the temperate species tissue formation is stimulated more by higher temperature than photosynthesis. This results in a great accumulation of reserve carbohydrate at low temperature in the temperate grasses, and hardly any accumulation in the tropical species (WILSON, 1975).

The temperature effect on lucerne (*Medicago sativa*) is presented in Table 14 and 15. The results show that at the temperature closest to the optimum in this experiment (25–20°C) yield of dry matter was highest causing the lowest content of ash, nitrate and crude protein. Stems were also best developed causing the highest content of cell-wall constituents of the complete crop as well. In leaves the effect of temperature was minute, except on the reserve carbohydrate; but

Table 14. Effect of temperature on yield and chemical composition (in % of dry mass) of the legume *Medicago sativa* in a reproductive stage

Temperature	g dm	% dm	% leaf blade	tiller number	NO <sub>3</sub> -N	cp	ash	tnc	cwc	cf	D <sub>nitro</sub>	D <sub>cwc</sub>
15-10°C	44.5	17.1	46.9	66	0.25	26.1	9.3	11.7	29.0	21.5	88.3	63.4
25-20°C	101.5	22.6	39.8	54	0.14	20.6	8.2	9.0	43.3	32.9	77.6	52.5
35-30°C	60.4	25.8	47.3	53	0.29	22.4	9.5	6.3	39.0	28.7	77.5	47.5

Growth conditions: as in Table 9. Nitrogen uptake occurred from fertilizer nitrogen and not via *Rhizobium* in this trial.

Table 15. Effect of temperature on chemical composition of leaf blade and stem of *Medicago sativa* in a reproductive stage (in % of dry mass)

Temperature	Tissue	NO <sub>3</sub> -N	cp	ash	tnc	cwc	cf	D <sub>nitro</sub>	D <sub>cwc</sub>
15-10°C	leaf blade	0.15	36.9	10.4	12.4	13.2	10.0	95.9	72.2
25-20°C	leaf blade	0.11	31.6	12.3	8.5	15.2	11.8	94.9	70.6
35-30°C	leaf blade	0.27	33.1	12.6	7.5	14.4	11.5	94.8	68.4
15-10°C	petiole + stem	0.34	16.6	8.3	11.2	43.0	31.6	81.8	61.2
25-20°C	petiole + stem	0.16	13.3	5.4	9.4	61.9	46.8	67.3	50.0
35-30°C	petiole + stem	0.30	13.0	6.8	5.2	61.0	44.4	63.1	43.6

Growth conditions: as in Table 14

stems deteriorated substantially with higher temperature: crude protein and total non-structural carbohydrate content decreased, whereas the content of cell-wall constituents increased and their digestibility decreased. Many more results could be shown on the effect of temperature on forage quality, all revealing its dramatic deleterious effect on cell-wall digestibility.

There are only a few examples available in literature on the effect of temperature on vegetables but they are confined to nitrate accumulation (Table 16) which, together with keepability in fresh condition seems to be a more important criterion than nutrient content. This table shows that spinach has a very wide optimum temperature range for growth, but a much narrower range for nitrate uptake from the soil, resulting in a large nitrate accumulation and high protein content at intermediate temperatures. Of course, there was an interaction of temperature with nitrogen nutrition, revealing that with low nitrogen, accumulation of nitrate only occurred above 20°C, at intermediate nitrogen nutrition it occurred above 10°C and at high nitrogen nutrition it occurred at all temperatures. So here again the kinetics of the three basic processes mentioned in the second paragraph determine into which direction the nutrient composition will proceed.

Table 16. The effect of temperature on average yield, nitrate and crude protein content of spinach (after CANTLIFFE, 1972a).

Temperature °C	yield g dm/pot	% NO <sub>3</sub> -N	% crude protein
5	1.024	0.06	18.5
10	1.063	0.10	19.4
15	1.031	0.34	25.0
20	1.011	0.42	25.1
25	0.966	0.85	23.3
30	0.810	0.55	20.9

Growth conditions: cultivars Northland and Virginia Savoy

Soil medium: Ontario fine sandy loam

Nitrogen nutrition: 0,50 and 200 mg N/kg soil

Seedling growth: 28 days at 20°C, followed by 28 days at the mentioned temperature

Day length: 12 hrs. Light intensity  $\approx 51 \text{ W.m}^{-2}$  (400–700 nm).

Temperature also significantly affects the nutrient content of seeds. SPIERTZ (1977) has shown in wheat that a higher temperature accelerates both the translocation of protein and of soluble carbohydrate to the grain, thus increasing grain-filling rate. As ripening occurs even faster than grain filling at high temperature, seed yield decreases significantly with higher temperature (Table 17). The amount of nitrogen recovered in the seed was not affected in this experiment, so the protein content was increased considerably by higher temperature. Starch content decreased with temperature in this trial as expected, but the effect on percentage of water-soluble carbohydrate was irregular for unknown reasons. Nitrogen translocation was not affected in this trial, but after the hot and bright summer of 1976 he found extremely high seed yield and protein content, indicating that a high temperature can favour protein translocation so much, that it extracts almost all the protein from the straw.

Table 17. Influence of temperature on yield and chemical composition of grain in wheat at the final harvest.

	Temperature during grain-filling (°C)			
	10	15	20	25
Grain-filling period (days)	80	62	41	41
mg dm/ear	2570	2146	1783	1466
mg N/ear	42.4	38.2	42.8	39.3
% protein (N $\times$ 5.7)	9.4	10.1	13.7	15.3
% wsc	22.0	25.1	17.1	26.6
% starch (C <sub>6</sub> H <sub>10</sub> H <sub>5</sub> ) <sub>n</sub>	57.7	54.7	54.2	51.6

Growth conditions: phytotron, light intensity  $97 \text{ W.m}^{-2}$  (400–700 nm)

Other conditions as in Table 8

From these results it may be concluded that yield of vegetative plant parts is highest at the optimum temperature for growth, but that the nutrient content is best at low temperature which gets worse with rising temperature. This poor quality of forage grown in the warm regions of the world is the major reason for the low animal production in these areas, even when sufficient forage is available for *ad libitum* consumption. In seeds protein content seems to be highest at high temperature, whereas the carbohydrate content is highest at low temperature.

#### Water supply

Many parts of the world suffer from water shortage during the growing season. This shortage retards the rate of crop production. As the nitrogen supply is generally also limited, all available nitrogen is absorbed by the plants. Consequently the same amount of nitrogen is distributed over the smaller yield, causing a higher nitrate and protein content and a lower soluble carbohydrate content (Table 18). However, with an adequate supply of nitrogen it appears from the results in Table 19 that nitrogen uptake by the *L. perenne* was limited more by water shortage than dry mass production, causing lower crude protein content and higher water-soluble carbohydrate content. The results shown in Tables 18 and 19 suggest that water shortage has a negative effect on the crude fibre content, but it is not yet certain whether this has consequences for digestibility.

Table 18. The effect of water supply on production and chemical composition of herbage from *Lolium perenne* with limited nitrogen supply (DEINUM, 1966).

Treatment	g dm/pot	% dm	% NO <sub>3</sub> -N	% cp	% ash	% wsc	% cf
adequate moisture	11.5	17.8	0.02	17.1	7.7	18.6	23.4
limited moisture	7.1	25.4	0.21	23.7	8.9	16.1	20.4

Growth conditions: vegetative grass in sandy soil in 5-litre plastic pot  
 Light intensity: 1070 J.cm<sup>-2</sup>.day<sup>-1</sup> (400–10000 nm); temperature: 20–14°C day and night;  
 Nitrogen 450 mg/pot; Age: 28 days.

Table 19. The effect of water supply on production and chemical composition of herbage from *Lolium perenne* with an adequate nitrogen supply (DEINUM, 1966).

Treatment	g dm/pot	% dm	% NO <sub>3</sub> -N	% cp	% ash	% wsc	% cf
adequate moisture	10.5	16.2	0.90	29.0	11.2	5.7	23.0
limited moisture	4.9	26.9	0.72	24.5	9.9	15.1	21.6

Growth conditions: vegetative grass in sandy soil in 5-litre plastic pot  
 Light intensity: about 350 J.cm<sup>-2</sup>.day<sup>-1</sup> (400–10000 nm); temperature: 15–9°C day and night;  
 Age: 28 days; Nitrogen: adequate moisture: 670 mg/pot; limited moisture: 450 mg/pot.

### *Relative humidity*

Low humidity causes greater transpiration which in turn may lead to a better development of the vascular bundles (SINNOTT, 1960). This might cause a higher percentage of cell-wall constituents in the plant. However detailed research has shown only small and inconsistent effects on percentage cell-wall constituents and on digestibility of dry matter (WILSON et al, 1976, DEINUM, unpublished data, 1971).

As low humidity stimulates evapotranspiration it may happen that with a limited supply of water for plant growth this water is consumed faster. Thus plants suffer sooner from water shortage and reduce growth sooner, with higher protein content and less reserve carbohydrate, as described in the former paragraph.

### *Day length*

Day length itself has only minor effects on the nutrient content of plants. However in nature, a longer day is concomitant with a greater amount of solar radiation and often a higher temperature, the effects of which are described in previous paragraphs. Day length can also control morphogenesis in plants. So a longer day may prevent, inhibit, stimulate or force stem formation and flowering, depending on the plant species. If a longer or shorter day has caused stem formation, a more fibrous crop is produced with a lower nutritive value, like may be inferred from Tables 4, 6, 10, 13 and 15.

### *Barometric pressure, altitude and topography*

From the available information on plant physiology it is clear that these three factors are only of minor importance with regard to plant production and nutrient content. Moreover their possible effects are greatly overshadowed by the effects of light intensity, temperature and water supply, which factors have changed concomitantly.

The variation in barometric pressure is very small compared to the mean value, so its effect cannot be very great. Furthermore, atmospheric high pressure conditions are generally associated with bright, sunny weather, whereas low pressure systems usually mean cloudy weather and hence low solar radiation. Thus the effect of light intensity and water supply will greatly overshadow any possible effect of barometric pressure.

To the best of my knowledge altitude has not shown to have any direct importance on the nutrient content of plants, but it will have some indirect influence on quality via the effect of light intensity, temperature and rainfall. At higher altitudes, light intensity is higher and temperature and barometric pressure are lower. Therefore it may be expected that if the same plant species and variety grows at low and high altitudes, the high altitude plants will be higher in reserve carbohydrate and digestibility and lower in cell-wall constituents. In  $C_3$ -plants the percentage of total non-structural carbohydrate will be higher because of the higher solar radiation and lower temperature, in  $C_4$ -plants this will be true possibly only because of the higher solar radiation. In both groups digestibility will be higher because of the lower temperature (CUMMINGS and DOBSON, 1973).



Crude protein content depends on the optimum temperature for growth of the species. If the high-altitude temperature is closest to the optimum then production rate is highest and the generally limited amount of nitrogen is diluted over the greater yield, so the percentage of crude protein is lowest. If plants of the same species are grown at low and high altitudes respectively, and if the temperature at both heights is the same, then the reduced barometric pressure at high altitude will stimulate transpiration and initiate water stress sooner. However, the temperature drop of about 7°C per 1000 m rise in altitude compensates this effect of barometric pressure on transpiration (GALE, 1972, 1973).

Sunfacing slopes receive more solar radiation and are warmer than the opposite slopes. Evaporation and transpiration are consequently higher and water shortage may occur sooner. Air temperature and especially soil temperature will be much higher on the sunfacing slope than on the opposite one. This is beneficial at higher latitudes for subtropical plants like maize but it can be detrimental at lower latitudes for cool temperature plants like *Poa pratensis* (BENNETT et al, 1972). Soil temperature may rise so much on warm, bright days that the plant roots are almost killed. From this it may be inferred that if temperature on the sunfacing slope is closer to the optimum for that crop, crop production will be greater and content of reserve carbohydrate lower than on the opposite slope. In addition, crude protein content and cell-wall digestibility will generally be lower. If the sunfacing slope is too hot for the plant, a poor, low quality crop may be expected.

#### *Wind velocity*

Windbreaks improve the microclimate of the protected area by retarding wind velocity and transpiration. Thus water stress is delayed and production can proceed longer. Consequently yield can be greater in the protected area, causing a lower protein content and a higher non-structural carbohydrate content in case of limited supply of nitrogen. An additional effect of windbreaks is that average temperature in the protected area is higher, which may stimulate plant development and consequently the percentage of cell-wall constituents, whereas cell-wall digestibility and content of reserve carbohydrate may become lower.

### CONCLUSION

From the information presented it may be concluded that light intensity and temperature are the major physical factors that affect nutrient content of forages and other plants. A high light intensity promotes a high crop yield with a low protein content and a high content of non-structural carbohydrate, whereas nitrate toxicity may occur at low light intensity. Both situations can be balanced by adapted fertilization of nitrogen. Light intensity has not much effect on forage digestibility for ruminants.

Plant production is best at the optimum temperature for growth, but protein content and soluble carbohydrate are low. These concentrations are better at low

temperature whereas digestibility is also better. Consequently animal performance is better on fodder grown below the optimum temperature, provided sufficient material is available for optimum consumption.

## REFERENCES

- BENNETT, O. L., E. L. MATHIAS and P. J. HENDERLONG: 1972. Effects of north- and south-facing slopes on yield of Kentucky bluegrass (*Poa pratensis* L.) with variable rate and time of nitrogen application. *Agron. J.*, **64**: 630–685.
- BROUWER, R.: 1962. Distribution of dry matter in the plant. *Neth. J. agric. Sci.*, **10**: 361–376.
- BROUWER, R.: 1962a. Nutritive influences on the distribution of dry matter in the plant. *Neth. J. agric. Sci.*, **10**: 399–408.
- BUTLER, G. W. and R. W. BAILEY, (Eds): 1973. *Chemistry and Biochemistry of Herbage*. Academic Press London and New York, 3 Vols.
- CANTLIFFE, D. J.: 1972. Nitrate accumulation in table beets and spinach as affected by nitrogen, phosphorus and potassium nutrition and light intensity. *Agron. J.*, **65**: 563–565.
- CANTLIFFE, D. J.: 1972a. Nitrate accumulation in spinach grown at different temperatures. *J. amer. Soc. hort. Sci.*, **97**: 674–676.
- CUMMINGS, D. G. and J. W. DOBSON jr.: 1973. Corn for silage as influenced by hybrid maturity, row spacing, plant population and climate. *Agron. J.*, **65**: 240–243.
- DARWINKEL, A.: 1975. Aspects of assimilation and accumulation of nitrate in some cultivated plants. *Agric. Res. Reports*, Wageningen, nr. 843, 64 pp.
- DEINUM, B.: 1966. Climate, nitrogen and grass. Research into the influence of light intensity, temperature, water supply and nitrogen on the production and chemical composition of herbage. *Meded. Landbouwhogeschool*, 66–11, 91 pp.
- DEINUM, B.: 1971. Climate, nitrogen and grass. 3. Some effects of light intensity on nitrogen metabolism. *Neth. J. agric. Sci.*, **19**: 184–188.
- DEINUM, B.: 1974. Structural inhibitors of quality in forages. *Växtodling*, **28**: 42–51.
- DEINUM, B., A. J. H. van Es and P. J. van SOEST: 1968. Climate, nitrogen and grass. 2. The influence of light intensity, temperature and nitrogen on *in vivo* digestibility of grass and the prediction of these effects from some chemical procedures. *Neth. J. agric. Sci.*, **16**: 217–233.
- GALE, J.: 1972. Availability of carbon dioxide for photosynthesis at high altitudes: theoretical considerations. *Ecology*, **53**: 494–497.
- GALE, J.: 1973. Experimental evidence for the effect of barometric pressure on photosynthesis and transpiration. In: *Plant response to climate factors*. Proc. Uppsala symposium, Unesco, Paris, France, 289–294.
- MINSON, D. J.: 1976. Relationship between digestibility and composition of feed. In: *Carbohydrate Research in Plants and Animals*. Misc. Papers Agric. Univ. Wageningen, **12**: 101–104.
- SINNOTT, E. W.: 1960. *Plant morphogenesis*. McGraw Hill Co, New York, 308–373.
- SOEST, P. J. van and R. E. McQUEEN: 1973. The chemistry and estimation of fibre. *Proc. Nutr. Soc.*, **32**: 123–130.
- SOEST, P. J. van: 1976. The estimation of digestibility from chemical composition. In: *Carbohydrate Research in Plants and Animals*. Misc. Papers Agric. Univ., Wageningen, **12**: 137–145.
- SPIERTZ, J. H. J.: 1977. The influence of temperature and light intensity on grain yield in relation to the carbohydrate and nitrogen economy of the wheat plant. *Neth. J. agric. Sci.*, **25**: 182–197.
- WILSON, J. R.: 1975. Influence of temperature and nitrogen on growth, photosynthesis and accumulation of non-structural carbohydrate in a tropical grass, *Panicum maximum* var *trichoglume*. *Neth. J. agric. Sci.*, **23**: 48–61.
- WILSON, J. R.: 1976. Variation of leaf characteristics with level of insertion of a grass tiller. I. Development rate, chemical composition and dry-matter digestibility. *Aust. J. agric. Res.*, **27**: 343–354.
- WILSON, J. R., A. O. TAYLOR and G. R. DOLLY: 1976. Temperature and atmospheric humidity effects on cell-wall and dry-matter digestibility of some tropical and temperate grasses. *New Z. J. agric. Res.*, **19**: 41–46.