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Effects of temperature during different stages of development on growth and digestibility of forage maize (*Zea mays* L.)

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Summary

Growth and digestibility of a forage-maize crop were studied when it was exposed to low (18 °C day/12 °C night) or high (30 °C/24 °C) temperatures during the following three periods of development: from sowing until the 8-leaf stage; from the 8-leaf stage until grain set; during grain filling.

High temperatures increased the rate of production and the rate of development. Temperature also affected leaf number, leaf area, plant height, stem diameter and ear characteristics. Therefore the proportions and amounts of several plant fractions were influenced. High temperature before tassel initiation increased dry-matter production, mainly because of its effect on leaf area. After the 8-leaf stage a rise in temperature increased rate of development more than rate of production, thus reducing final dry-matter yield.

Differences in digestibility were caused by differences in cell-wall content and in cell-wall digestibility. Differences were greatest around anthesis but declined considerably thereafter. High temperatures during the period from the 8-leaf stage until grain set were most effective in reducing the digestibility.

The final amounts of indigestible cell wall were surprisingly similar for all treatments. The amount of cellular contents varied only slightly. The amount of truly digestible cell wall, however, was greatly reduced by high temperatures during vegetative growth.

Differences in the proportion or in the digestibility of the plant fractions resulted only in small differences in whole-plant digestibility. Temperature affected digestibility much less than it affected yield. In addition, high temperatures were needed for a prolonged period to obtain a noticeable reduction of digestibility. A large reduction in digestibility is only possible if the amount of indigestible cell wall can be increased by a concomitant decline in cell-wall digestibility and an increase in cell-wall content. This could not be realized by one simple temperature treatment. In

this respect forage maize is different from most other forage grasses. The reasons for this are discussed.

Introduction

Temperature affects growth, development, morphology, production, quality and time necessary to reach maturity of maize. Most physiological processes in the maize plant show their fastest rate at temperatures around or above 30 °C (Struik, 1983a). Below this optimum, an increase in rate of these processes caused by a rise in temperature depends on other growing conditions (e.g. light intensity) and is not the same for all processes. For example, net photosynthesis is stimulated less by a rise in temperature than plant development. Growing conditions vary over time and some plant processes (e.g. leaf initiation) mainly occur during certain stages of development; thus maturation, final yield and quality are not merely a result of cumulative temperature or accumulated heat units but also depend on temperature during limited time spans (Struik, 1983a). This is especially true for digestibility.

Digestibility is a major factor in the conversion of forage to animal product. The digestibility of the organic matter (D_{om}) of a plant is determined by its cell-wall content (cwc%) and cell-wall digestibility (D_{cwc}). Both cwc% and D_{cwc} are influenced by temperature (Dirven & Deinum, 1977). Poorly digestible cell-wall components, very digestible cell-wall components and wholly digestible cell contents are produced in different – though partly overlapping – stages of maize development (cf. Deinum & Dirven, 1971) and their relative amounts are also affected by the morphogenetic effects of growing conditions.

Thus both the quality and the amount of these components can be affected by temperatures during different stages. This impact of a rise in temperature during a certain period depends on the temperature prevailing during earlier and later stages of growth. This means that differences in digestibility can only be explained by a comprehensive description of production rates, development and chemical composition of the plant. Struik (1983b) analysed how these parameters were affected by temperature rises during different periods in the case of forage maize by discussing data from several experiments and from the literature. This study indicated that temperature influences the digestibility of forage maize by affecting:

- rate of production and utilization of photosynthates after tassel initiation
- rate of development during different stages of growth (e.g. characterized by silking date or rate of grain fill)
- morphogenesis (e.g. number of leaves, leaf area, number of kernels, midrib:mesophyll ratio) and histology (e.g. parenchyma:sclerenchyma ratio)
- cell-wall content, cell-wall composition and cell-wall structure.

The temperature effects depended on timing and duration of the rise in temperature.

In this paper we describe research in which an attempt was made to integrate all relevant temperature treatments in one comprehensive greenhouse experiment.

Materials and methods

The greenhouse experiment was carried out in 1983. Four seeds of the hybrid LG 11 were sown per plastic pot containing 10 litres of a mixture of equal volumes of sandy soil and peat. 250 pots were sown on 2 May (i.e. day 122) and placed in a greenhouse set at a day (12 h)/night (12 h) temperature of 18/12 °C (code 'L'). Another 250 pots were sown on day 141 and placed in a greenhouse set at a day (12 h) temperature of 30 °C and a night (12 h) temperature of 24 °C (code 'H'). These sowing dates were chosen so that the 8-leaf stage for both temperature treatments would be reached on the same day.

After emergence the seedlings were thinned to 2 per pot. Nutrient solution (adjusted to soil type) and water were provided adequately. Relative humidity was kept at approximately 75 %. Photoperiod was limited to 14 h until day 157. Thereafter photoperiod was kept at 16 h. Outdoor light intensity was reduced by about 20-25 % by the hammered glass and greenhouse framework. Pests were controlled with nicotine. Weeds were controlled by a low dose of atrazin and by hand.

The temperature switches at day 194 and day 196 could only be made by moving the plants to an extra greenhouse with similar conditions, set at 18 °C day/12 °C night. After several weeks these plants could be moved to the original low-temperature greenhouse.

Until the 8-leaf stage, pots were arranged in a square to minimize the number of guard pots. After this stage, pots were arranged in east-west rows in the north-south oriented greenhouse. Simulating field conditions, the distance between rows was 75 cm resulting in a density of 11 plants/m^2. Plants designated for sampling were surrounded by guard rows or guard ends of a row. To simulate the crop situation even more precisely, light penetration from the glazed side walls was reduced by spraying the outer glass with temperzon (Hermadix) up to a height of 1.80 m above soil level. Care was taken to ensure that the light was reduced by the same amount in both greenhouses and in all parts of each greenhouse.

Maize development can be divided into four main, physiologically distinct, periods:
(1) from sowing until the double-ridge stage of the shoot apex (tassel initiation)
(2) from double-ridge stage until 50 % ♂ flowering
(3) from 50 % ♂ flowering until onset of linear dry-matter accumulation in kernels (grain set)
(4) period of grain filling.
These periods differ greatly in duration.

In this experiment, temperature was varied during period 1, period 2 + 3 and period 4 resulting in 8 different treatments. To prevent a switch in temperature from resulting in serious desynchronization of silking and pollen shed (Struik, 1982a, 1983b) period 1 was extended to the 8-leaf stage; during the transition from period 2 to period 3 the temperature could not be switched, because of lack of space.

The time table of the eight treatments is presented under 'Results and discussion' (Fig. 1). Treatments have been coded by the sequence of the temperature codes for the three periods during which the temperature was varied (e.g. LHL indicates the

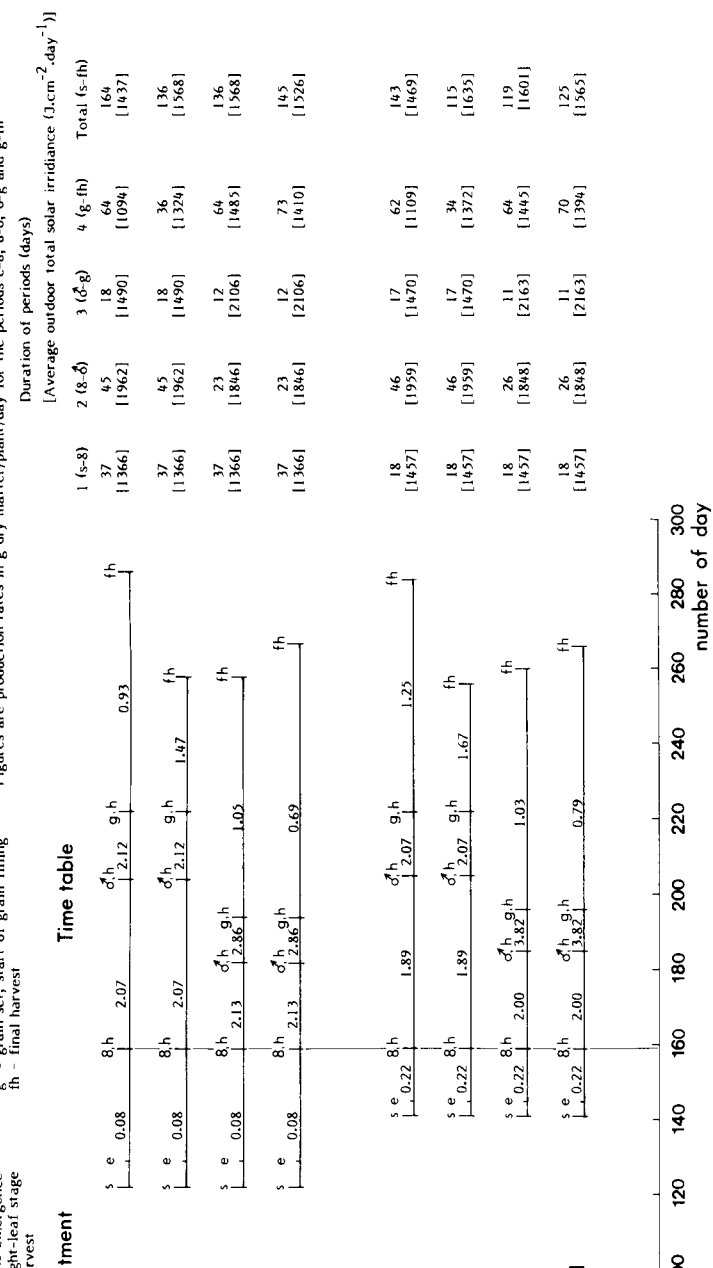


Fig. 1. Time table, and some experimental data on eight temperature treatments.

treatment with 18/12 °C during period 1, 30/24 °C during period 2 + 3 and 18/12 °C during period 4). ♂ and ♀ flowering dates were recorded for each plant. Harvests took place at the end of each of the four periods (Fig. 1). 28 plants (second, third and fourth harvests) or as many as possible (first harvest) were cut off at soil level. Morphological data, such as number of leaves, leaf area, plant height, stem diameter and number of kernels, were measured from each plant harvested. Leaf area was measured with an area meter. Stem diameter was measured with a marking gauge. If possible, plants were separated into the following fractions: tassel, green leaf laminae, dead leaf laminae, leaf sheaths, stem, kernels top ear, cob top ear, husks + shank top ear and complete lower ears. Per plant these fractions were weighed and dried at 70 °C in forced ventilated ovens until they reached constant weight. After determining the dry weight, samples were bulked per fraction and per treatment, ground in hammer mills with 1 mm sieves and subsampled. Subsamples were analysed for cwc%, D_{om} and D_{cwc} according to methods described by Struik (1983b).

Standard statistical tests are not valid because of the lack of real replication of temperature treatments.

Results and discussion

Characterization of treatments, rate of development and rate of production

Fig. 1 shows the timetable of the experiment, data on the duration of the four periods, the rates of production, and the average outdoor light intensity.

A high temperature boosted the rate of germination and early growth to such an extent that the 8-leaf stage was reached on the same date for both temperature treatments during period 1, even though there was a difference in sowing date of 19 days. Period 2 was 20-22 days shorter if temperatures were high during this period regardless of what the temperatures had been during period 1. The absolute value of the duration of period 2 was also independent of the temperature of period 1. This is striking, because the temperature before the 8-leaf stage did affect the number of leaves per plant (see below). The same was observed for period 3: only the temperature during the period itself affected the duration of period 3. For period 4, however, this was only true for the low temperature: the duration of period 4 was 62-64 days, irrespective of the temperature regimes during earlier development. When temperature was high during period 4, the duration of this period strongly depended on the temperature during period 2 + 3: a *high* temperature during these periods *prolonged* the longevity of the leaf apparatus at a high temperature during period 4. Therefore LHH had a *longer* growing season than LLH, and HHH had a *longer* growing season than HLH. The durations of period 4 of the treatments LHH and HHH were the longest of all treatments! This result was influenced by the definition of period 4: the final harvest was carried out when only a few green leaves were still present. The general trend, however, was that plants with large numbers of kernels and high rates of grain filling (LLH and HLH; see below) showed the fastest rate of senescence. Only in these cases was the sink:source ratio unbalanced (cf. Wilson & Allison, 1978).

Because rates of development differed, the average outdoor light intensity during each period varied between treatments. Differences in light intensity were fairly insignificant during periods 1 and 2 but were large for periods 3 and 4. Thus light intensity should be taken into account when discussing the results. The average outdoor radiation over the entire growing period was closely negatively correlated with the duration of the period from sowing until final harvest. This is in agreement with the natural situation in areas at a high latitude.

The rates of dry-matter production were maximum during period 3 for all treatments, even when light intensity during period 3 was low. In some cases, production rates were well above normal rates in field trials. The effects of temperature treatments on rate of production during a certain period were large and depended not only on the temperature during that period but also on the temperature during earlier periods. This is illustrated in Table 1, in which treatments are compared with the control LLL. High temperatures boosted the production rate during period 1 and during the period immediately following a switch from low to high temperatures. During period 4, positive after-effects of earlier high temperatures were observed in HLL, HHL and LHL. High temperatures reduced the rate of production during periods 2 and 4 if the temperature during the preceding period had also been high. High temperatures during period 1 appeared to reduce the rate of production during period 3 if the temperature during the latter period was low. Other effects during period 3 were closely related to radiation. All treatments showed a higher overall rate of production than LLL, except for LHL and LHH. Periods 2 and 3 in the latter treatments had the shortest relative durations.

The total amounts of dry matter produced during a certain period were usually lower when temperature during that period had been high. Thus a rise in temperature had a greater effect on rate of development than on rate of production; this pattern is also found in other crops (e.g. van Dobben, 1962; Spiertz, 1977). The obvious exception occurred during period 1 (Table 1). The positive effects observed

Table 1. Effects of temperature treatments on the rate of dry-matter production and on the amount of dry matter produced during four different periods of development (treatment LLL is benchmark).

Code	High temperature during period	Relative rate of production					Relative amount of dry matter produced				
	period	1	2	3	4	total	1	2	3	4	total
HLL	1	+	−	−	+	+	+	−	−	+	+
HHL	1, 2, 3	+	−	(+)	(+)	+	+	−	(+)	(+)	−
HHH	1, 2, 3, 4	+	−	(+)	−	+	+	−	(+)	−	−
HLH	1, 4	+	−	−	(+)	(+)	+	−	−	−	−
LHL	2, 3		+	(+)	(+)	−		−	−	(+)	−
LHH	2, 3, 4		+	(+)	−	−		−	−	−	−
LLH	4				+	+				−	−

+, higher value than LLL.
−, lower value than LLL.
(+), higher value than LLL, but difference greatly exaggerated by high outdoor radiation.

during period 3 were mainly the result of the higher radiation. The only positive after-effects of a temporary rise in temperature on amount of dry matter produced during a certain period were, as mentioned above, observed for period 4 in HLL, HHL and LHL; these after-effects were mainly caused by differences in radiation, except in the case of HLL, where the after-effect was particularly large (approx. 18 g/plant).

Over the entire growing season only HLL yielded more than LLL.

Development

Table 2 lists the effects of the various treatments on some characteristics of the full-grown plants. As expected, the final number of leaves was mainly affected by the temperature during period 1. Data also suggest frequent abortion of the youngest leaf in early stages of its development after a sudden temperature increase. This agrees with other unpublished data of ours. The increase of 0.18 leaf per °C rise in temperature is within normal ranges. Final harvest took place when most leaves were no longer green. Only treatment LLL was harvested somewhat earlier in the development. In all treatments plant height was great and was mainly affected by temperature during period 1 (thus by number of internodes). However, plant height in treatment HLH was aberrantly low, for reasons that were not clear. The maximum leaf area, which was reached around anthesis, was increased by a higher temperature during period 1, but was somewhat reduced by higher temperatures during period 2 + 3. These two effects were cumulative. The former (positive) effect was caused by the increase in leaf number; the latter (negative) effect was caused by an increase in leaf length associated with a decline in leaf width. This second effect also resulted in a larger midrib:mesophyll ratio. In all cases the maximum LAI exceeded 4, sufficient to intercept at least 95 % of the radiation. The diameter of the stem base was greater when temperatures were low during stem formation (i.e. period 2 + 3).

Table 2. Some characteristics of maize plants grown at high or low temperatures during different stages of development.

Treatment →	LLL	LLH	LHL	LHH	HLL	HLH	HHL	HHH
Total number of leaves per plant[a]	14.0	14.0	13.5	13.5	15.9	15.9	15.9	15.9
Number of green leaves at final harvest/plant[b]	4.0	0.8	1.2	1.4	2.5	0.5	0.7	1.8
Plant height (cm)[b]	267	267	263	266	288	268	291	291
Green leaf area (dm^2/plant)[c]	42.3	42.3	39.2	39.2	48.4	48.4	45.6	45.6
Stem diameter (cm)[b]	2.1	2.2	1.9	1.8	2.3	2.3	1.9	1.9
Desynchronization (days)[d]	−1	−1	+4	+4	0	0	+1	+1
Number of filled kernels per top ear[b]	311	279	141	128	302	263	177	141
Dry-matter content top ear (cob + kernels; %)[b]	54.5	59.6	56.9	65.2	57.8	57.3	55.0	59.7

a, average of 26-28 plants, determined at 3rd harvest.
b, (weighed) average of 26-28 plants, determined at 4th harvest.
c, average of 27-30 plants, determined at 2nd harvest.
d, silking date minus anthesis date based on all plants from which data were recorded.

High temperatures during period 2 + 3 caused an increase in desynchronization especially when the temperatures during period 1 had been low. The delay of the transition from period 1 to period 2 did not completely prevent the desynchronizing effect of a temperature switch. However, desynchronization was not large enough to hamper effective pollination. Yet there was a significant linear correlation between desynchronization (days) and number of filled kernels in the top ear ($r = -0.854$; $b = -33.5$; $P < 0.01$) despite correct hand pollination, possibly because of interactions between plant organs which are not fully understood. Conditions during periods 2 and 3 were very important for the final number of kernels. However, the negative effect of high temperature during period 4 on kernel number was also consistent. There was no clear trend in dry-matter content (dm%) of the top ear. The date of the final harvest was not based on the maturity of the ear but on leaf senescence. These two did not correlate.

Plant development may influence digestibility by affecting the morphological composition, because plant parts vary greatly in digestibility. Table 3 shows the proportions of 8 fractions at final harvest as affected by the 8 temperature treatments. Only three fractions showed large differences in their proportion: stem, kernels and lower ears. The proportion of stem correlated closely with the number of kernels ($r = -0.933$; $P < 0.01$) and with the proportion of kernels ($r = -0.935$; $P < 0.01$): the more dry matter had to be invested in grain filling the greater the need for dry matter to be translocated from the stem to the kernels. The stem proportion, however, was also considerably stimulated by high temperatures during period 1. This is in accordance with the plant height differences, shown in Table 2. The proportion of kernels correlated with the number of kernels ($r = 0.907$; $P < 0.01$) and with desynchronization ($r = -0.734$; $P < 0.05$). Development of lower ears was most successful if the temperature was low throughout the growing period. High temperature during every period hampered the development of the lower ears. This negative effect was more pronounced the earlier the high temperature treatment was applied. Later periods of high temperature were less effective in inhibit-

Table 3. Dry-matter proportion (%) of eight morphological fractions at final harvest as affected by the different temperature treatments.

Fraction Treatment →	LLL	LLH	LHL	LHH	HLL	HLH	HHL	HHH
Tassel	1.2	1.4	1.6	1.6	1.0	1.1	1.1	1.2
Stem	18.4	22.8	32.6	40.2	22.9	29.3	35.2	41.7
Leaf laminae	10.8	10.9	12.9	13.9	10.7	12.4	12.0	13.6
Leaf sheaths	5.6	5.7	5.8	6.4	5.7	6.4	5.8	6.7
Top ear husks + shank	8.1	8.2	7.1	7.7	7.9	8.5	6.8	6.6
Top ear kernels	35.1	34.2	26.6	18.3	36.9	30.0	29.4	19.8
Top ear cob	7.4	7.9	5.4	5.9	8.3	8.6	7.2	7.4
Lower ears	13.4	8.9	8.0	6.1	6.5	3.7	2.6	3.0
Total	100.0	100.0	100.0	100.1	99.9	100.0	100.0	100.0
100 = . . . g dry matter/plant	192.9	186.5	152.9	136.0	202.6	182.0	163.6	152.5

ing the lower ears if such periods had been preceded by other periods of high temperature. These temperature effects on the development of lower ears are caused by an increase in the apical dominance of the tassel or of the top ear at high temperatures. This increased dominance was also shown by the abortion of the youngest leaf and the desynchronization (Table 2). A more marked dominance of the tassel at higher temperatures has also been reported by Blondon & Gallais (1976).

Quality of plant fractions at final harvest

Plant parts differed greatly in digestibility both between fractions and between temperature treatments (Table 4). These differences were due to differences in cell-wall amount, translocation and accumulation of cell contents, and cell-wall digestibility.

The most digestible part of the forage-maize plant is the kernel. Kernel digestibility was not affected by temperature. In general, the tassel showed the poorest digestibility, because it senesced long before the other plant parts. Tassel digestibility was mainly affected by temperatures during periods 1 and 4. High temperature during period 1 had a positive effect on digestibility of the tassel, whereas high temperature during period 4 had a negative effect. Considerable differences between treatments were also found for the fractions husks + shank, cob and lower ears. These differences were caused by a variety of temperature effects on development, redistribution, senescence and cell-wall digestibility, which are difficult to unravel.

The digestibility of the leaf laminae was reduced by high temperature during any period of development. The effect, however, was largest during period 2 + 3, when temperature also had an effect on the morphology of the larger leaves. The digestibility of the leaf sheaths was strongly reduced by high temperatures after period 1.

The digestibility of the stem was fairly independent of temperature during periods 1 and 4 if the temperature during period 2 + 3 was high. Stem digestibility was improved by high temperatures during periods 1 and (especially) 4 when temperature during period 2 + 3 was low. The cell-wall digestibility of the stem was mainly determined by the temperature during period 2 + 3. However, when temperature during period 2 + 3 was low, high temperature during period 1 had a small *positive*

Table 4. Digestibility (% of organic matter) of plant fractions at final harvest as affected by the different temperature treatments.

Fraction Treatment →	LLL	LLH	LHL	LHH	HLL	HLH	HHL	HHH
Tassel	56.7	54.7	58.0	50.7	65.0	56.5	62.0	50.8
Stem	64.0	71.1	68.7	68.4	67.4	73.7	68.3	70.8
Leaf laminae	72.3	70.7	70.0	66.5	70.7	69.9	65.3	65.8
Leaf sheaths	63.3	58.4	61.1	58.5	64.4	59.0	59.1	58.0
Top ear husks + shank	68.2	67.1	70.0	61.3	71.7	67.7	69.8	68.3
Top ear kernels	84.7	84.4	84.6	84.7	84.9	83.9	85.3	84.0
Top ear cob	63.6	60.3	70.6	58.5	65.3	65.5	68.0	61.9
Lower ears	74.1	75.0	76.6	72.0	79.5	75.0	74.9	77.0
Total	73.9	74.0	73.5	69.5	75.1	74.1	72.8	71.2

effect on cell-wall digestibility of the stem. Cell-wall content of the stem was low for all .H. treatments (37.9-44.6 %), associated with their poor grain set, and was lower for HHH than for LHL, LHH and HHL. Cell-wall content of the stem was high for all .L. treatments (48.5-70.2 %) but was then boosted by *low* temperatures during period 4.

Although the treatments had a great impact both on the proportion of dry matter and the quality of the fractions, the final digestibility of the whole plant only ranged between 69.5 % (LHH)-75.1 % (HLL).

Development over time of the quality of the whole plant

Although final differences in whole-plant digestibility were smaller than expected, large differences between treatments were found earlier in the growing season. Fig. 2 illustrates the development over time of the whole-plant digestibility.

Digestibility started highest for L.. and gradually declined for treatment LLL. This decline was faster before silking than after silking. The digestibility of HHH was always lower than that of LLL. The difference was greatest at anthesis. After anthesis the difference was considerably reduced because of the formation of the ear, whose digestibility was fairly independent of temperature (Table 4), and the slow-down of vegetative growth. In fact, the digestibility in treatment HHH increased rapidly during period 3.

The temperature during period 1 quickly lost its impact on digestibility during later stages of growth. This is clearly illustrated by the atypical pattern shown by HLL: the initial low digestibility was maintained with scarcely any change throughout the entire growing period, ultimately resulting in the highest value of all treat-

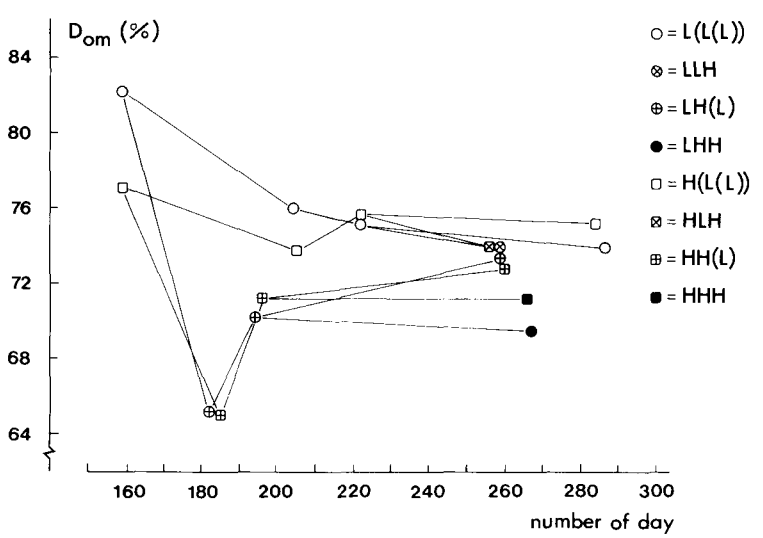


Fig. 2. Development over time of the whole-plant digestibility of the organic matter (D_{om}) for all temperature treatments.

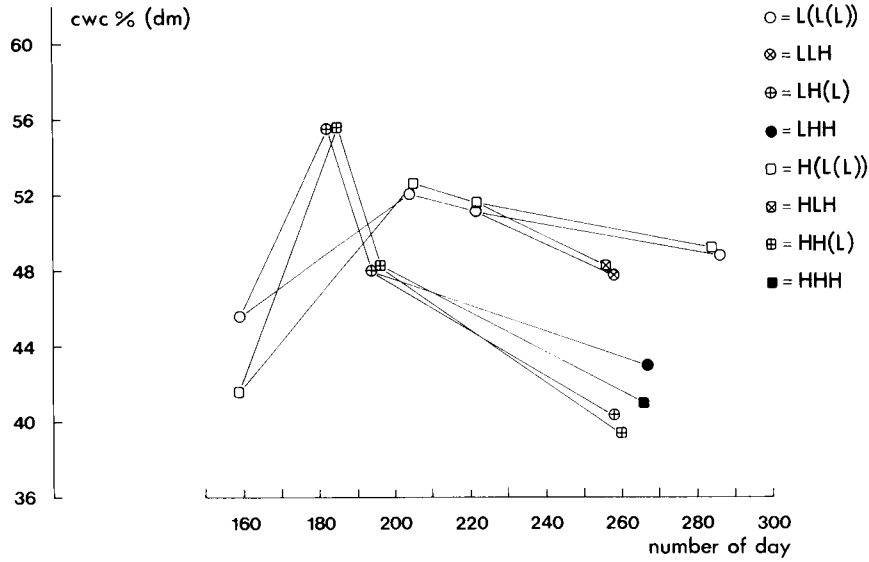


Fig. 3. Development over time of the cell-wall content (cwc%) in the dry matter of the whole plant for eight temperature treatments.

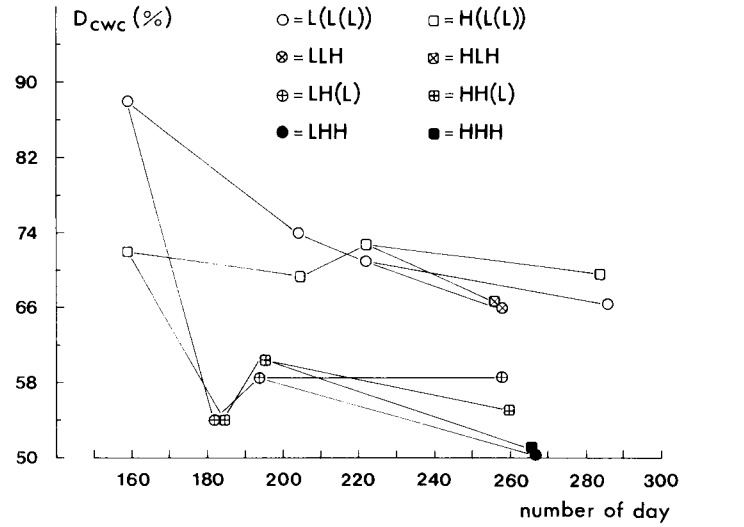
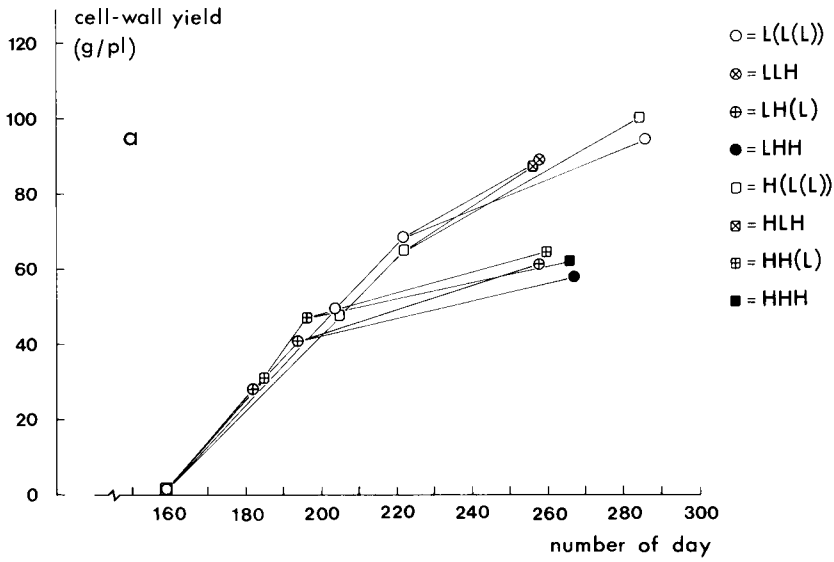


Fig. 4. Development over time of the cell-wall digestibility (D_{cwc}) of the whole plant for different temperature treatments.

ments. Up to the beginning of period 4 it was the temperature during period 2 + 3 that was the most decisive. Temperature during period 4 had no effect on digestibility if temperatures during period 2 + 3 had been low. If temperatures during period 2 + 3 had been high, however, significant variation in digestibility arose during period 4: low temperatures during period 4 caused a rise of 1.5-3.2 units. Ultimately, LLH, HLH, LHL and HHL all reached about the same value. High temperatures are needed during periods 2 + 3 and 4 to obtain a large reduction of digestibility.

The results indicated in Fig. 2 are a reflection of the results presented in Figs. 3 and 4. The cell-wall content (cwc%) started at a lower value when temperature up to the 8-leaf stage was high. Cwc% increased until anthesis. This increase was faster when the temperature during period 2 was high, and in that case the maximum reached was also higher. Cwc% at anthesis and at grain set were independent of temperatures during period 1. The decline in cwc% during period 3 was very rapid when temperatures during period 3 were high, because of the high light intensity and the poor grain set. The same was true for period 4. This will be discussed later in this paper. Ultimate cwc% was mainly determined by temperature during period 2 + 3.

Cell-wall digestibility (D_{cwc}) declined continuously for LLL (Fig. 4). This decline did not occur in HLL, as high temperature during period 1 caused a low D_{cwc} at the 8-leaf stage. During period 2 a rise in temperature caused a faster decline of the D_{cwc}. If temperature during this period was high, the impact of the high temperature during period 1 was nullified. D_{cwc} increased during period 3 even though the temperature was high as well. Only the D_{cwc} of LL declined during this period! During period 4, D_{cwc} remained constant (LHL) or declined. This decline was faster if temperature was higher.



Production of cell wall

Fig. 5 shows the development over time of the cell-wall production of the whole plant. High temperatures had only a minor effect on rate of production of total cell wall during the period of exposure to warmth. However, high temperatures during period 2 + 3 had clear repercussions on the duration of cell-wall production. When temperatures during period 4 were high but those of the preceding period had been

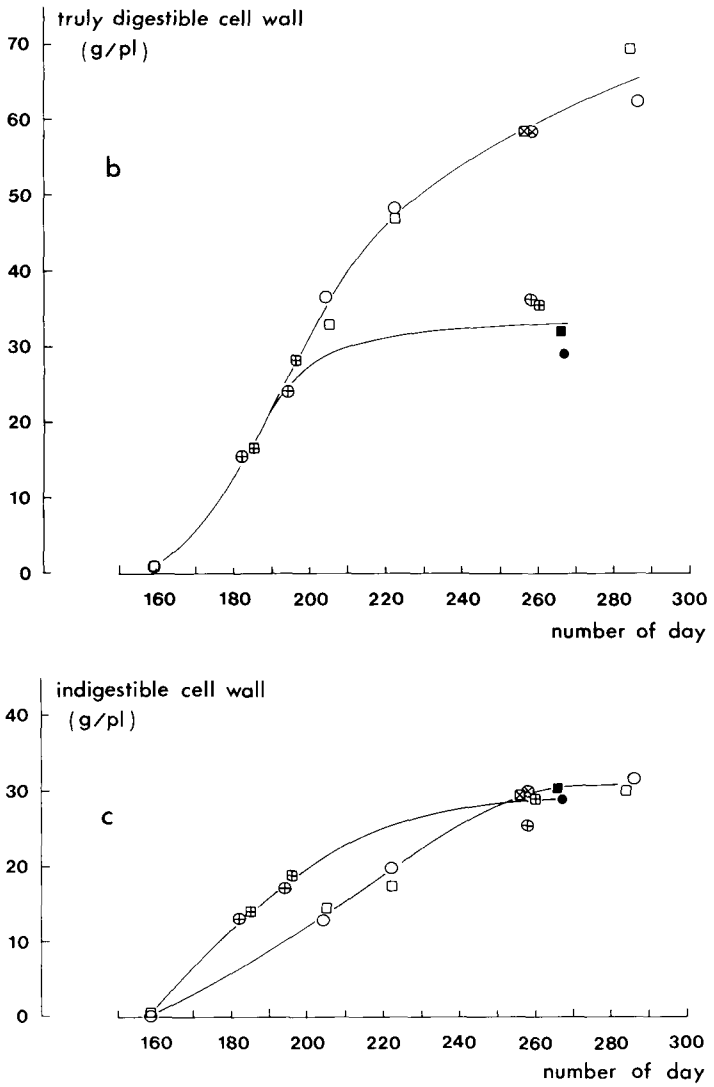


Fig. 5. Development over time of the whole-plant production of cell wall (a), truly digestible cell wall (b) and indigestible cell wall (c), as affected by temperature during different stages of growth. Samples were fermented by rumen microflora for 48 h. Note the differences in scale along the y-axis.

low, the period of cell-wall formation was somewhat shortened. Although high temperatures during period 1 increased the number of internodes and the final plant height, they did not stimulate cell-wall production. The trends observed for HLL and LLL are atypical. Usually, cell-wall formation stops some time after grain set (Struik, 1982b, 1983c). In this greenhouse experiment, cell-wall formation continued until final harvest. The same phenomenon was also found by Struik (1983b) in a greenhouse experiment with different temperatures during period 2: it resulted from a strong and prolonged formation of cell wall in the ear fractions. The trends observed for LHL, LHH, HHL and HHH, however, made the normal rapid decline of the cwc% possible. During period 4 hardly any photosynthates were used in the production of cell wall in these 4 treatments.

The trends observed for total cell wall are even more pronounced for truly digestible cell wall: differences between treatments appeared after 50 days and were wholly attributable to variation in duration of formation of truly digestible cell wall. Again, the temperature during period 2 + 3 was found to have the greatest effect, whereas temperature during period 4 had a minor effect if temperature during period 2 + 3 had been low.

The trends observed for indigestible cell wall, however, were completely different. The higher the temperature before grain set, the faster the rate of formation of indigestible cell wall but the shorter the duration of this formation. This resulted in a more or less constant final amount of indigestible cell wall. The results of the analyses for lignin content not mentioned in this paper suggest that these observations can be attributed to lignin formation and encrustation being more synchronized with the formation of cellulose and hemicellulose at high temperatures during period 2 + 3 (cf. Struik, 1983b) thus causing a higher rate of production and a larger amount of indigestible cell wall in the vegetative parts. Yet, final amounts of indigestible cell wall were the same because

- the additional cell wall formed in the ear fractions from treatments with low temperatures during period 2 + 3 was also partly indigestible
- the cell-wall digestibility of the stem in treatment LLL continued to decline up to final harvest.

Table 5 summarizes the main results described in this paper. High final dry-matter yield depended mainly on high temperatures during period 1. This positive effect resulted from the large increase in leaf area caused by high temperatures during period 1. High temperatures during periods 2, 3 and 4 reduced the final yield, because they accelerated development more than they increased rate of production.

Dry matter consists of cell contents + ash and cell wall. By means of in vitro digestion the cell wall can be fractionated into truly digestible cell wall and indigestible cell wall. Differences in dry-matter yield could only partly be attributed to differences in yields of cell contents and were mainly caused by differences in the yield of truly digestible cell wall: in contrast, the yield of indigestible cell wall proved to be surprisingly constant.

The most important yield factor, however, is the yield of digestible organic matter. Since differences in digestibility at the same stage of maturity were relatively

Table 5. Yields of different quality fractions (in g/plant) for the different temperature treatments.

Treatment	Dry matter	Cell contents + ash	Cell wall	Truly digestible cell wall	Indigestible cell wall	Apparently digestible organic matter
LLL	192.9	99	94	63	32	137
LLH	186.5	98	89	59	30	132
LHL	152.9	91	62	36	26	107
LHH	136.0	78	58	29	29	88
HLL	202.6	103	100	70	30	146
HLH	182.0	94	88	59	29	129
HHL	163.6	99	64	35	29	113
HHH	152.5	90	63	32	31	106
Normal value*	150	80	70	45	25	105

* Values for field conditions in the Netherlands, based on Struik (1983a).

small after grain set, temperature affected this trait in the same way as it affected dry-matter yield. Short-term differences in temperature have only a minor effect on whole-plant digestibility (see also Struik, 1983b). Their effects on yield and maturation are much more important. This is true for a wide range of temperatures. It is probably also true for other climatic factors such as light intensity and water availability (cf. Struik, 1983a, b, c).

This study also underlines the importance of high temperatures during seedling growth. Even when temperatures are not marginal, considerable increases in yield can be obtained by a rise in temperature.

Dry-matter yield, yield of apparently digestible organic matter, and yield of indigestible cell wall for the control (LLL) were about 30 % higher than normal values for a good field crop. The individual differences were 34 % for cell-wall yield and 40 % for truly digestible cell wall, but only 24 % for cell contents + ash.

Implications

The reaction of forage maize to temperature is unlike the reaction of most other forage grasses.

- Modern maize hybrids do not tiller. That means that the production of cell wall is determinate. It also means that the duration of photosynthesis is limited.
- Maize stems contain very digestible pith tissue, which can be used as an alternative storage organ for non-structural carbohydrates. If much carbohydrate is available it can be stored in a completely digestible form instead of being used for the production of (partly indigestible) new tissue.
- Maize plants produce ear shoots in which the products of photosynthesis can be stored as starch. These shoots start their development at the end of the vegetative growth and change the physiology of the plant completely.

These characteristics of forage maize ensure:

– that there is a limited amount of indigestible cell wall. If a rise in temperature causes a reduction in cell-wall digestibility it simultaneously causes a reduction of cell-wall amount and halts the decline in cell-wall digestibility earlier;
– 'dilution' of the indigestible cell wall with digestible cell wall or digestible cell contents. If crop growth after grain set is fast and prolonged, more photosynthates can be invested in the production of cell wall, both digestible and indigestible (LLL). However, if there is a balance between rate of crop growth and grain-filling rate, all newly produced photosynthates will be translocated to the kernels. This situation is very desirable for the digestibility, the rate of production and for the longevity of the plant.

The results also imply that high quality forage can be produced in hot regions. The digestibility in treatment HHH was still 71 %. If digestibility is found to be poor, hybrid choice and cultivation techniques should be reconsidered.

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