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EFFECT OF TEMPERATURE ON DEVELOPMENT, DRY-MATTER PRODUCTION, DRY-MATTER DISTRIBUTION AND QUALITY OF FORAGE MAIZE (*ZEA MAYS* L.). AN ANALYSIS

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INTRODUCTION

In maize, temperature strongly influences growth, morphology, development, production, quality and the time necessary to reach maturity. The following discussion will be limited to temperature conditions that are not injurious to the plant.

Germination processes (both imbibition and elongation) are strongly temperature dependent (BLACKLOW, 1972a, 1972b; GRZESIAK et al., 1981). The maximum rates of shoot and radicle elongation are achieved at approximately 30 °C, but elongation ceases at temperatures below 9 °C and above 40 °C. Soil temperature during the first month after sowing is the most relevant growth-limiting climatic factor in many maize-growing areas. Soil temperature during germination may also affect the rate of development at later stages of growth (COLIGADO and BROWN, 1975a).

After emergence, higher soil and air temperatures accelerate leaf appearance (see, among others: GROBBELAAR, 1963; BROUWER et al., 1973; GMELIG MEYLING, 1973; TOLLENAAR et al., 1979), but also advance tassel initiation (COLIGADO and BROWN, 1975a, 1975b; BREUER et al., 1976). This effect of temperature on the duration of the pre-tassel initiation period is independent of photoperiod (BREUER et al., 1976). At temperatures between 25–30 °C the shortest pre-tassel initiation period is achieved (COLIGADO and BROWN, 1975b); the fastest rate of leaf appearance occurs at a temperature of 31–32 °C (TOLLENAAR et al., 1979). Although they curtail the pre-tassel initiation period, higher temperatures lead to an increase in final number of leaves of about 2 leaves per plant per 10 °C increase in temperature (TOLLENAAR et al., 1979; TOLLENAAR and HUNTER, 1981), independent of photoperiod. This increase in leaf number can only be induced during a short period prior to tassel initiation (TOLLENAAR and HUNTER, 1981).

Little is known about specific reactions to temperature during the period from tassel initiation to silking. STRUIK (1982a) found that plant height, stem thickness, leaf area, number of tillers, date of anthesis and silking, synchronization of anthesis and silking, and tassel and ear size may all be influenced by temperature during this period.

After grain set, the rate of kernel growth is stimulated, but the duration of leaf area and of grain filling is shortened at higher temperatures, and therefore the optimum temperature for grain yield is low. This is true for maize, other cereals and pulses (SOFIELD et al., 1974; HUNTER et al., 1977; SPIERTZ, 1977; CHOWDHURY and WARDLAW, 1978; JONES et al., 1981; VOS, 1981; WIEGAND and

CUELLAR, 1981; TJ. WIJNGAARDEN, 1982, personal communication).

Photosynthesis, respiration, transpiration, transport and cell growth are also promoted by higher temperature. Net photosynthesis, however, is stimulated less than development, although both achieve their maximum rates at about 30–33 °C (DUNCAN and HESKETH, 1968; DUNCAN, 1975). Maximum whole-plant yields are therefore obtained when the temperatures during late vegetative and reproductive development are rather low. Moreover, development, respiration, transport and cell growth are stimulated by a higher mean 24-hours temperature, whereas transpiration and photosynthesis are promoted by the temperatures prevailing during the light phase (DUNCAN, 1975). High night temperatures are therefore particularly deleterious (GRZESIAK et al., 1981).

Crop quality as ruminant feed

Digestibility is one of the primary factors in the conversion of forage to animal product. Other factors, not discussed in this paper, are intake and feed efficiency.

A plant is composed of cellular contents and cell walls. The cellular contents are almost completely digestible by ruminants (VAN SOEST, 1965, 1967; DEINUM, 1974; HACKER and MINSON, 1981), but digestibility of cell walls is much lower and it varies. Cell walls are composed of pectin, hemicellulose, cellulose, lignin, glycoprotein and silica. The proportion of these compounds may vary. The quality of hemicellulose, cellulose and lignin is also variable.

Temperate grasses are generally more digestible for ruminants than tropical grasses. In addition to specific and genotypic differences and differences in crop structure, climatic conditions seem to be responsible for this general rule. It is commonly assumed that temperature is the major determinant for the digestibility of Gramineae (MINSON and MCLEOD, 1970; DEINUM and DIRVEN, 1975; WILSON et al., 1976; DIRVEN and DEINUM, 1977); light intensity is of minor importance (DEINUM and DIRVEN, 1976; DEINUM, 1979; WILSON, 1982), whereas atmospheric humidity and fertilization show small or inconsistent effects (MINSON, 1973; WILSON et al., 1976; DEINUM, 1979; WILSON, 1982). WILSON and NG (1975) reported that there is no consistent effect of soil-moisture level, although PITMAN et al. (1981) found that prolonged severe moisture stress produced large negative effects. Unpublished data on maize, collected by the present author, indicated that cell-wall digestibility increased slightly as a result of moisture stress during stem growth; the cell-wall content depended on the severity of the stress (the lowest cell-wall content occurred at mild stress) and the physiological stage at which the stress was applied.

Photoperiod may affect crop quality by its effects on morphogenesis (DEINUM, 1981; WILSON, 1982).

High temperature causes a decrease in herbage digestibility by its effects on morphological development, physiological age, cell-wall content and cell-wall digestibility. The latter is reduced by lignin (e.g. DEINUM, 1974; MINSON, 1976), the production of which is relatively boosted at higher temperatures (DEINUM and DIRVEN, 1976). Lignin is a polymeric compound of phenylpropanoid units and forms complexes with other cell-wall components, thus protecting them

from microbial degradation in the fore-stomachs of polygastric animals (see, e.g.: MINSON, 1976; AKIN and BURDICK, 1981, HARTLEY, 1981). In some forage species, plant silica may play the same role as lignin in the microbial degradation of cell walls (VAN SOEST and JONES, 1968; HARTLEY, 1981).

There is, however, another temperature effect on cell-wall digestibility independent of lignin content (DIRVEN and DEINUM, 1977; DEINUM, 1979). This effect is probably connected with the organization characteristics of the cell walls, such as the manner in which hemicellulose is associated with polyphenol esters (CHESSON, 1982), the crystallinity of hemicellulose and cellulose (BAILEY et al., 1976; DEINUM, 1979), the interactions between hemicellulose and cellulose (BAILEY et al., 1976), the occurrence of O-acetyl groups (BAILEY et al., 1976), whether bacteria are physically impeded from adhering (cf. RICHARDS, 1976) or the available surface of the cell walls and their fragility (SMITH et al., 1971).

These two effects of temperature on cell-wall digestibility may be distinguished by estimating the potential cell-wall digestibility and the rate of cell-wall digestion. Lignin and silica affect the potential extent of cell-wall digestibility, but lignin content, the ratio of lignin to cellulose or of lignin to acid-detergent fibre do not correlate with the rate at which potentially digestible cell walls can be digested (SMITH et al., 1971; SMITH et al., 1972; WALDO et al., 1972; MERTENS, 1977). The rate of disappearance of digestible fibre is related to the morphological and physical nature of the cell walls (MERTENS, 1977; GOODRICH and MEISKE, 1979), although SMITH et al. (1971) have stated that the content of cell solubles (or 100 – cell-wall content!) may also be relevant for cell-wall digestion kinetics during in vitro fermentation. Other factors limiting rates of degradation, such as the pH in the rumen, are not relevant in the in vitro technique.

Literature about the effects of temperature on maize digestibility is scarce. DEINUM (1976) found that higher temperatures caused a slight increase in cell-wall content, but a strong decline in the cell-wall digestibility of leaf blades, leaf sheaths and stems. Data on the effects of temperature on whole-plant digestibility of forage maize have previously been based on comparisons made under uncontrolled conditions (e.g. CUMMINGS and DOBSON, 1973; ANDRIEU, 1976). This paper deals with the effects of temperature during certain stages of growth, partly in combination with low light intensity, on the development, production and quality of forage maize under controlled conditions.

MATERIALS AND METHODS

Three experiments were carried out in greenhouses in 1979, 1980 and 1981. To obtain high and relatively constant light intensities for all treatments during periods in which the area of green leaf was large, experiments were started in March or April. Four seeds were sown per plastic pot containing 10 l of a mixture of equal volumes of sandy soil and peat. After emergence, the seedlings were reduced to 2 per pot. Nutrient solution, adjusted to soil type, and water were

provided adequately. Weeds were removed by hand or controlled by applying a low dose of atrazin. Plants (including their root systems) were kept as healthy as possible and were finally arranged in a density of 10 m^{-2} with a row distance of 75 cm, a plant arrangement similar to cultural practice in The Netherlands. Thus it was possible to place 8 rows of 26 pots (i.e. 416 plants including the border rows) in each greenhouse.

In early stages of growth, supplemental light was provided with 0.8 Philips HPLR 400 W mercury lamps per m^2 for 14 (1979 and 1980) or 16 (1981) hours per day. During vegetative development, the photoperiod was extended to 16 h by means of 12 incandescent bulbs (100 W) per 40 m^2, except for hybrid Dara in the 1979 trial. Relative humidity was kept at 75%.

Pollination in greenhouses may be suboptimal because air currents are locally strong and always flow in the same direction. Therefore, pollen was collected and sprinkled over the silks by hand daily. The date on which silk extrusion was first visible was noted for each plant in all experiments. In the 1981 experiment the dates of the first visible extrusion of anthers were noted as well. Plants were checked twice daily every day.

Prior to treatment, plants were rearranged to cancel out any differences that might have arisen in different greenhouses during pre-treatment growth.

In 1979, the hybrid Dara was sown one week earlier than Ula. In combination with different photoperiods, this ensured a better synchronized silking for the early and late genotypes.

Treatments

Maize development can be divided into four physiologically distinct periods:

1. from sowing until the double-ridge stage of the shoot apex (approx. 6.5-leaf stage)
2. from double-ridge stage until 50% ♂ flowering
3. from 50% ♂ flowering until onset of linear dry-matter accumulation in kernels
4. grain-filling period.

These phases differ greatly in duration.

In this paper, experiments are described in which temperature was varied in period 2 or 4. Data from the literature or unpublished results on the influence of temperature during periods 1 and 3 will be mentioned. Comparisons will be made with maize grown in the field under different conditions. In addition to temperature, light intensity was also varied during period 4 in the 1979 and 1980 experiments. Each greenhouse was divided into two compartments, separated by shading nets. The outer glass of low-light compartments was sprayed with temperzon (Hermadix). Care was taken to ensure, that the light was reduced by the same amount in all temperature treatments. The hybrids were chosen according to the aims of the experiments. Only LG 11 is in current use in The Netherlands. Ula, LG 11 and Nicco have been described in earlier reports (STRUIK, 1982b; STRUIK and DEINUM, 1982). Dara is a late, dent hybrid registrated in France.

In Table 1, climatic conditions are presented for each of the three experiments

and for normal Dutch conditions. The data of normal conditions are based on average climatic data and on average rate of crop development. The treatments have been coded according to the day/night temperature during the period in which the temperature was varied and with the relative amount of light or according to whether they were shaded or unshaded. Treatment 18/12 represents average temperature conditions in The Netherlands during periods 2, 3 and 4. Treatment 24/18 represents an extremely warm year, while treatment 30/24 reflects American and tropical or subtropical conditions. Average light intensity during period 4 was calculated as follows:

$$\frac{\text{cumulative outdoor irradiance in period 4 (J . cm}^{-2})}{\text{duration of period 4 (days)}} \times 0.75 \times a$$

in which 0.75 accounts for the light reduction, caused by the greenhouse itself
a accounts for the light reduction obtained by shading.
$a = 1.00$ for unshaded treatments and $a = 0.40$ (1979) or 0.33 (1980) for shaded treatments.

For Experiment 1 the same procedure was followed for period (3 + 4).

Light intensity was relatively low for treatment 18/12 in 1981 and treatment 24/18 in 1980 and was relatively high for treatment 30/24 in 1979. In all years the radiation received by unshaded treatments exceeded or was similar to the amounts of radiation maize crops would normally receive under field conditions in The Netherlands during grain filling.

Data on crop development

The number of visible leaves per plant and the plant height were estimated twice weekly to record and monitor rates of development in different greenhouses. The surface area of fully expanded leaves was calculated from the equation length × maximum width × 0.75 (MONTGOMERY, 1911). The maximum diameter of the middle of the second above-ground stem internode was measured with a marking gauge, to provide an estimate of stem thickness. Leaf angles were estimated with a clinometer (WHIGHAM and WOOLLEY, 1974). At each sampling date after female flowering, the ear length, number of unshrivelled kernels and total number of visible kernels or florets per ear were estimated for all ears arising from leaf axils. Plant height and flowering date were also noted.

Light extinction was measured using a 97.5 cm long light meter containing silicon cells and calibrated against a solarimeter.

Yield estimates

Plants were cut off at soil level, separated into stover (i.e. tassel + stem + leaves + leaf sheaths), husk + shank, top ear and lower ears and cut into pieces by hand. After recording their fresh weight, fractions were dried for each plant separately and without subsampling at 70 °C in forced ventilation ovens. After reaching constant weight, they were re-weighed. For the uppermost ears, shelling percentage (dry grain weight divided by whole-ear weight) was estimated in 1979

and 1980. In 1980, the root systems of six plants per treatment and per sampling date were also analysed.

In Experiment 1, 40 plants were harvested at the 6.5-leaf stage. For each temperature treatment, 40 plants were harvested 4 times during period 2, at 50% ♂ flowering and 4 weeks after 50% ♂ flowering. The final sample was taken 8 weeks after 50% ♂ flowering and comprised 30 plants.

In Experiment 2, 32 plants of each hybrid were harvested prior to climate differentiation. 20 plants from each treatment were sampled some time thereafter and 20 plants were harvested at the first visible black-layer formation in normal kernels for Ula and the next day for Dara.

In Experiment 3, 36 plants were harvested at initiation of treatment: 6 harvests

TABLE 1. Climatic conditions in Experiments 1, 2 and 3 and estimated normal conditions in The Netherlands.*

Experiment and hybrid	Day/night temperatures (°C)				Shading treatment during period 4	Estimated mean light intensity ($J.cm^{-2}.day^{-1}$) during periods 3+4 or 4
	period 1	period 2	period 3	period 4		
Experiment 1 (1981) LG 11 (FAO 260)	18/12	18/12 24/18 30/24	18/12	18/12	unshaded	1031 1090 1086
Experiment 2 (1979) Ula (FAO 190)	20/15	20/15	20/15	18/12	unshaded shaded	1206 482
				24/18	unshaded shaded	1197 479
				30/24	unshaded shaded	1305 522
Dara (FAO 320)	20/15	20/15	20/15	18/12	unshaded shaded	1202 481
				24/18	unshaded shaded	1178 471
				30/24	unshaded shaded	1300 520
Experiment 3 (1980) Nicco (FAO 300)	20/15	20/15	20/15	18/12	unshaded shaded	1107 365
				24/18	unshaded shaded	1031 340
				30/24	unshaded shaded	1080 356

Normal conditions	period 1	period 2	period 3	period 4
Mean light intensity ($J.cm^{-2}.day^{-1}$)	1650	1650	1350	1000
Mean air temperature (°C)	11.8	16.0	17.3	14.3

* Calculations of normal conditions are based on climatic data (source: KNMI, The Bilt) and on the average rate of development of a standard crop.

of 20 plants from each treatment were taken after climate differentiation and the final harvest was at the end of the grain-filling period. The samples from one intermediate harvest of treatment 30/24 were lost, because of a malfunction of the oven.

Experiments 2 and 3 differed in frequency of sampling, hybrid choice (and thus crop structure and crop reaction), and light reduction for shaded crops.

Chemical analyses

Samples were bulked per fraction and per treatment at each sampling, ground with hammer mills and subsampled. Subsamples were analysed for true digestibility in vitro of organic matter, using the method described by VAN SOEST et al. (1966). These values were standardized and converted to apparent digestibility by means of a series of standard samples of fresh maize, ensiled maize and parts of the maize plant with known apparent in vivo digestibility (sheep).

All the digestibilities of organic matter presented in this paper are standardized values, unless otherwise stated.

Digestibility of the whole plant was calculated from digestibilities of the fractions and their proportions of organic matter. According to JOANNING et al. (1981) it is permissable to calculate the in vivo digestibility of a feed from the in vivo digestibility of its components at feeding levels below 1.5–2 times maintenance. The calculations done by van DONSELAAR and STEG (1980) agree with this. Therefore I assumed that such calculations are permissable for the in vitro technique too.

Organic cell-wall content in dry matter (neutral-detergent fibre) after removal of the starch was estimated according to VAN SOEST's (1977) method. In vitro cell-wall digestibility (D_{cwc}) was calculated from true digestibility (D_{true}), cell-wall content (cwc%) and ash content (ash%), using the formula:

$$D_{cwc} = 100 - \frac{(100\text{-}D_{true}) \times (100\text{-ash}\%)}{cwc\%}.$$

Acid-detergent fibre, cellulose, lignin and insoluble ash were estimated according to the methods described by GOERING and VAN SOEST (1970). Hemicellulose was calculated as the difference between neutral-detergent fibre and acid-detergent fibre. Rates of cell-wall digestion were estimated as described by SMITH et al. (1971) and GOODRICH and MEISKE (1979), assuming that the maximum extent of digestion was reached at a retention time of 96 h. For ear samples this assumption was certainly true, as was evident from the calculations of maximum extent of digestion done according to the method described by MERTENS and VAN SOEST (1972). For some stover samples, indigestibility was probably slightly overestimated. The potential extents of cell-wall digestibility after 96 h of incubation in a certain amount of rumen liquor are thus not strictly comparable with potential digestibilities after several weeks of incubation in mixed rumen microorganisms (see, e.g. PRINS et al., 1981), or with potential digestibility after long-term incubation with refreshed inoculum (e.g. WILKINS, 1969). Water-soluble carbohydrates were colorimetrically determined with an automatic ana-

lysing device using ferricyanide. To ascertain the total non-structural carbohydrates the same procedure was followed after hydrolizing the starch with amyloglucosidase.

N, P and Ca were determined after the dry material had been digested in a solution of salicylic and sulphuric acid with hydrogen peroxide. N and P were measured colorimetrically; Ca was measured by flame-emission spectrometry. Crude-protein content was calculated as N content times 6.25.

Results and discussion

Period 1. Some unpublished data

In this stage of growth, the growing point of the maize plant is still below the soil surface. Thus temperatures in the upper soil layer influence the processes in the shoot apex. Soil temperatures may increase by several degrees centigrade under field conditions if a plastic mulch is applied. This technique has already been practised by French growers for some years. Much of the resulting increase in yield, however, consists of structural material, as is illustrated in Table 2. This increase in cell-wall yield may result because more plant cells are produced, especially in the vegetative parts of the plant. The effect on digestibility of a small rise in temperature during early growth is therefore variable.

In the trials done by Deinum and Struik, the plastic cover caused the temperature in the upper soil layer during period 1 to rise by about 2 °C. Therefore there were only slight differences in the number of leaves (and thus the number of stem internodes) between mulched and unmulched treatments. If temperature rises more than this during early stages of growth, the increase in cell-wall yield will be much greater, because of an increase in number of stem internodes and thus an increase in duration of the period of cell-wall formation. In that case, whole-plant digestibility may even decline, especially if cell-wall digestibility is low.

Table 2. Dry-matter yield, cell-wall yield (cwc yield), cell-wall content (cwc%), apparent digestibility (D_{om}) and cell-wall digestibility (D_{cwc}) of hybrid LG 11 with and without plastic mulch. (Field conditions; Deinum and Struik, 1977; unpublished data).

Location and sowing date	Wageningen 28 April		Swifterbant 17 May	
	control	mulched	control	mulched
whole-crop yield ($Mg.ha^{-1}$)	15.86	18.37	13.56	16.40
ear yield ($Mg.ha^{-1}$)	7.19	8.95	5.51	7.13
cwc yield ($Mg.ha^{-1}$)	7.28	8.22	6.56	8.06
D_{om} (%)	73.5	74.1	72.0	70.8
cwc% (%)	45.9	44.8	48.4	49.2
D_{cwc} (%)	65.4	65.7	64.1	62.0

Period 2. Experiment 1.

Development

In Experiment 1, the effects of temperature on leaf number were deliberately avoided. The rate of development increased dramatically when temperature rose (Table 3); yet final differences in vegetative development were small. Plant height showed a maximum in the 24/18 treatment, but was not affected much (cf. BLONDON and GALLAIS, 1976). Stem thickness decreased markedly with a rise in temperature. Thus stem volume declined if temperature rose. The cumulative area of all leaves was somewhat greater in the 24/18 treatment than in the other treatments. Leaves just below and above the top ear were smaller in treatment 30/24 than in the other two treatments but the uppermost leaves were larger when temperatures were higher (Fig. 1). This pattern is similar to the one described by ALLISON and DAYNARD (1979), although the differences found in Experiment 1 were smaller, possibly because the temperature differentiation occurred at a later stage. Although leaf areas only showed minor differences between treatments, the maximum length and maximum width of the leaves differed greatly between temperature treatments. At lower temperatures, leaves were shorter and wider. This difference in shape may alter the ratio of rib to mesophyll and therefore may affect digestibility (DEINUM, 1976).

Reproductive development was greatly accelerated at higher temperatures but anthesis was hastened more than silking. In treatment 30/24 this resulted in a very long anthesis-to-silking interval, combined with a delayed ear development (cf. dry-matter content of top ear at final sampling) and in the severely limited development of second ears. The dominance of the terminal inflorescence is more marked at higher temperatures (BLONDON and GALLAIS, 1976) and inhibition of reproductive axillary buds may be greater if climatic conditions are altered in the very early stages of their development (STRUIK, 1982a). In addition, a high plant density may be unfavourable for a good synchronization (BUREN et al., 1974; EDMEADES and DAYNARD, 1979), thus emphasizing the effects of other adverse factors.

Dry-matter production

At first, the rate of dry-matter production increased with temperatures, but dry-matter production was stimulated less than development. Maximum dry-matter production rates were found during tassel emergence and were similar for all treatments (Fig. 2a).

Total dry-matter at 50% anthesis correlated negatively with temperature (Fig. 2b). Climatic conditions during period 2 affected production rates after anthesis: the decline in rate of dry-matter production was more rapid if temperatures during period 2 were higher, resulting in great differences between final whole-plant yields (cf. NELSON and TREHARNE, 1973). As a result of the above-mentioned effects of temperature on reproductive development, ear yields for treatments 18/12 and 24/18 were the same, but the ear yield of treatment 30/24 was only half as much.

TABLE 3. Effect of temperature treatment during the period from 6.5-leaf stage to 50% ♂ flowering on vegetative and reproductive development.

	Day/night temperatures during period 2 (°C)		
	18/12	24/18	30/24
Vegetative development			
rate of leaf appearance (leaves.day^{-1})	0.25	0.36	0.50
final number of leaves per plant*	14.85	14.80	14.80
final height of plant (cm)†	291	300	284
stem diameter (cm)§	2.48	2.23	1.97
cumulative leaf area (dm^2/pl)§	50.9	52.6	49.2
Reproductive development			
date of 50% anthesis (days after emergence)	73	57	50
portion of silking plants at 50% anthesis (%)	81	50	15
date of 50% silking (days after emergence)	72	57	63
number of kernels (top ear)†	413	481	452
length of top ear (cm)†	15.1	18.5	17.3
length of the second ear (cm)†	7.9	4.7	2.3
dry-matter content top ear at final sampling (%)	47.8	46.0	33.6

* average of 80 plants † average of 70 plants § average of 20 plants

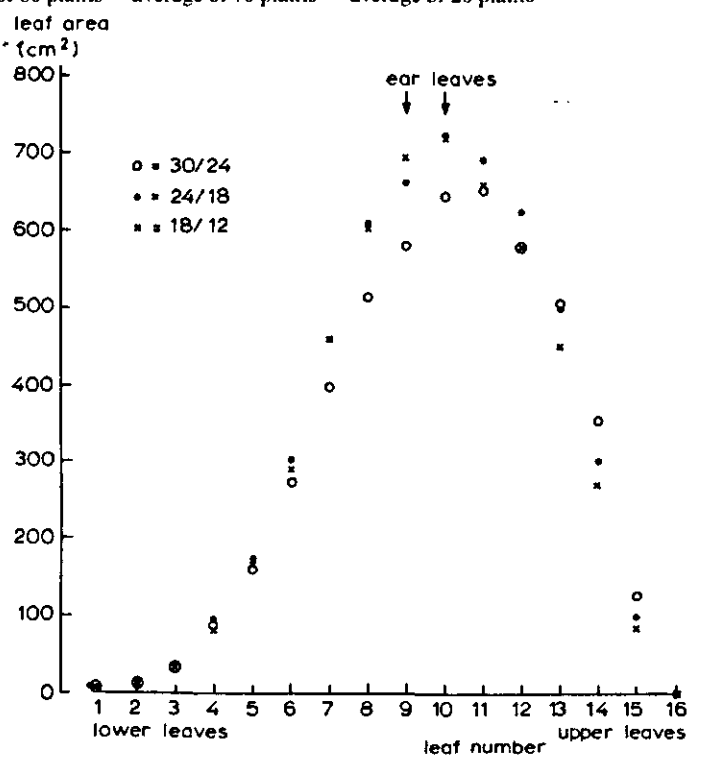

FIG. 1. Mean surface area of leaf laminae of plants grown at three different temperatures during period 2. Each point represents the mean of 20 leaves.

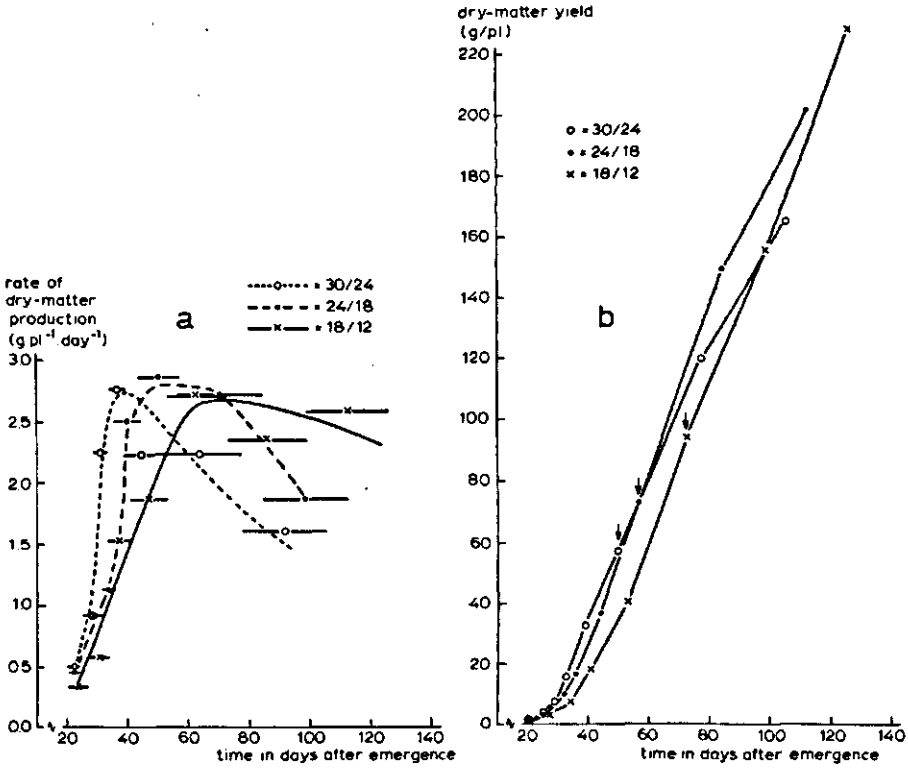

FIG. 2. Rate of dry-matter production (a) and dry-matter yield (b) in Experiment 1. Horizontal lines indicate the duration of the period, for which the production rate has been calculated. Arrows indicate 50% anthesis.

The course of quality up to anthesis

During period 2, maize generally shows a decline in the in vitro digestibility of the organic matter (D_{om}), because of an increase in cell-wall content and a decrease in the cell-wall digestibility (STRUIK, 1982b). In the present experiment, the increase in cell-wall content and the decrease in cell-wall digestibility were both stimulated by a rise in temperature, as occurs in other Gramineae (Table 4). This resulted in a marked temperature effect on D_{om} at 50% anthesis, as is shown in Fig. 3.

Temperature had a much greater effect on cell-wall digestibility than on cell-wall content, especially if ear shoots, including husks and shanks, are excluded (Table 4). The chemical composition of stover-cell walls was not greatly affected by temperature, although there were small temperature-induced effects on lignification and on silica content (insoluble ash). Yet, the cell-wall digestibility differed greatly, especially between treatments 30/24 and 24/18. Unidentified physical/chemical factors must have been responsible for most of the observed effects on digestibility. Incidentally, it is mainly these factors that prevent in vitro data being accurately extrapolated to in vivo parameters.

TABLE 4. Some quality parameters (all expressed as % of organic matter or cell walls) of the whole crop and of the stover in Experiment 1 at 50% anthesis.

		Day/night temperatures during period 2 (°C)		
		18/12	24/18	30/24
whole crop				
D_{om}		68.7	66.7	60.9
cwc%		59.5	61.3	62.9
D_{cwc}		68.2	66.1	58.7
stover				
D_{om}		67.2	65.4	60.3
cwc%		62.1	63.4	63.6
cell-wall composition:				
	hemicellulose	39.4	38.9	38.3
	cellulose	52.7	51.5	51.7
	lignin	7.7	8.7	8.7
	insoluble ash	0.2	0.9	1.3
D_{cwc}		67.4	65.4	58.4

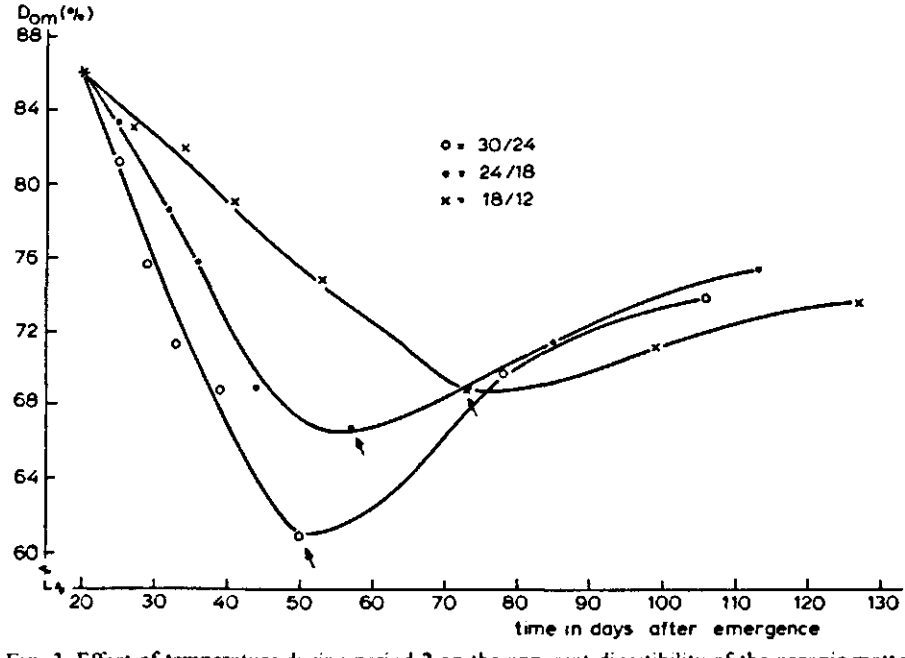

FIG. 3. Effect of temperature during period 2 on the apparent digestibility of the organic matter (D_{om}). Arrows indicate 50% ♀ flowering.

Changes in quality after anthesis

In Experiment 1, the course of digestibility after anthesis was affected by:

1. amount of cell wall, cell-wall content and cell-wall digestibility at anthesis (mentioned above)
2. amount of cell wall produced after anthesis
3. digestibility of cell walls produced after anthesis
4. amount of cell solubles produced after anthesis and the extent of decrease in cell-wall content after anthesis.

In Fig. 4 the courses of cell-wall yields are presented. During period 2, 50–57% of the final total amount of cell walls was produced in all treatments. Temperature during period 2 not only determined the cell-wall yield before anthesis but also the plant's capacity for subsequent cell-wall production, since the success of ear development determines how much structural material may be produced in ear shoots. Poor ear development, however, stimulated the progress of cell-wall formation in stems to some extent; this was also found by DEINUM and KNOPPERS (1979).

Thus successful ear development promotes termination of cell-wall production in vegetative parts but initiates cell-wall production in ear shoots: i.e. it

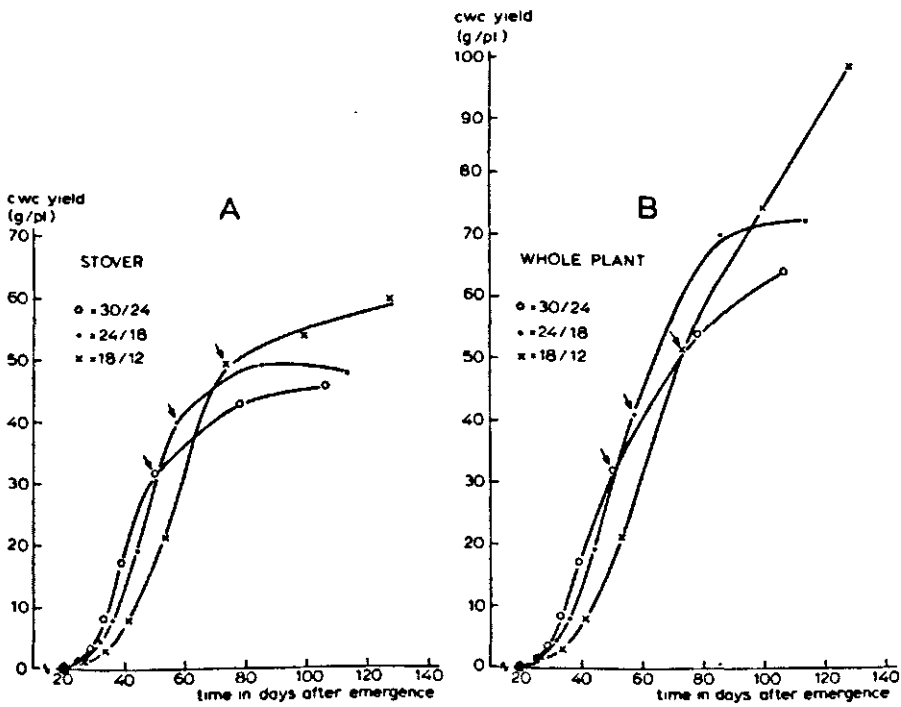

FIG. 4. Development over time of cell-wall yields in the stover (A) and in the whole plant (B) in Experiment 1. Arrows indicate 50% anthesis.

TABLE 5. Quality parameters at final sampling and their changes during the post-anthesis period in Experiment 1 (all expressed as % of organic matter or as % of cell walls).

	Day/night temperatures during period 2 (°C)		
	18/12	24/18	30/24
whole crop			
D_{om}	73.5	75.3	73.8
cwc%	45.5	37.9	41.1
D_{cwc}	67.7	65.4	64.9
(Δ cwc yield/Δ om yield) × 100	36.1	25.3	30.7
(Δ (cwc yield × D_{cwc})/Δ cwc yield) × 100	66.4	64.5	70.9
Δ cwc %	-14.1	-23.4	-21.7
stover			
D_{om}	65.6	64.4	66.8
cwc%	55.0	53.2	49.3
cell-wall composition:			
hemicellulose	41.0	33.5	35.8
cellulose	48.6	52.8	51.7
lignin	9.1	11.9	10.3
insoluble ash	1.3	1.8	2.2
D_{cwc}	60.5	57.2	58.0
(Δ cwc yield/ Δ om yield) × 100	28.8	28.7	32.4
(Δ (cwc yield × D_{cwc})/Δ cwc yield) × 100	27.6	13.4	57.1
Δ cwc %	-5.5	-8.4	-10.6

affects the proportion of photosynthates produced after anthesis invested in cell walls in two ways (Table 5). The final cell-wall yields of the stover in treatments 24/18 and 30/24 were similar, but the cell-wall yield of treatment 18/12 was much higher. Cell-wall formation in the ears was also most extensive in treatment 18/12. Finally, cell-wall content in the whole crop was highest in treatment 18/12 and lowest in treatment 24/18. Cell-wall content in stover was lowest in treatment 30/24, as storage of non-structural carbohydrates in the stem was more pronounced because of the absence of a strong ear sink.

The cell walls produced before anthesis became diluted with cell walls produced after anthesis. Since the temperature after anthesis was the same for all treatments, differences in cell-wall digestibility decreased even though the histology of the new cell walls was different. As shown in Fig. 5, however, cell-wall digestibility at final sampling differed much less than the dilution of old cell walls with new ones was anticipated to cause.

The D_{cwc} of newly synthesized cell-wall constituents cannot be calculated directly, since the D_{cwc} of cell walls already present may decrease during the new production. The combined effect of cell-wall maturation and cell-wall accretion can be estimated by dividing the increase in yield of digestible cell walls by the increase in total cell-wall yield (Table 5). The D_{cwc} of cell-wall constituents produced after anthesis appeared to be affected by temperatures during period 2,

but not in the same direction as the digestibility of cell walls produced before anthesis. Cell walls present in husks, shanks and ears were almost completely formed during periods 3 and 4, i.e. after the three temperature treatments were reduced to one. The digestibility of cell walls present in husks and shanks was not affected by the temperature treatments. The D_{cwc} of upper ears increased as temperatures rose during period 2. During periods 3 + 4 the stover D_{cwc} did not decline in treatment 30/24, but fell markedly in treatments 24/18 and 18/12 (Fig. 5). On the basis of the whole crop, the most digestible cell-wall constituents produced after anthesis were those from treatment 30/24. Differences in the D_{cwc} of the whole crop therefore faded in the post-anthesis period.

The digestibility of stover-cell walls appeared to be strongly correlated with plant height (Fig. 6). The regression coefficient decreased slightly with increasing temperatures. However, the greatest deviations from the joint regression line were found at 50% anthesis, when mean plant height only ranged between 266 and 277 cm, but the digestibility of stover-cell walls ranged from 58.4% to 67.4%.

This relation is meaningful: it indicates that the decline in stover D_{cwc} is connected with stem elongation and that this decline stops when stem extension has ceased (Fig. 6). The more rapid decline of the D_{cwc} with increasing plant height at higher temperatures is caused by the effect of temperature on digestibility irrespective of morphological stage.

For leaves, stems and ears longitudinal growth exceeded growth in width and thickness at higher temperatures. FRIEND and POMEROY (1970) found for wheat that leaf length was stimulated by increasing temperatures over a wide range and that length increase was mainly due to an increase in cell length. The number of cells along the lamina could even decline with increasing leaf length. Extrapolating these findings for wheat leaves to all plant parts in the present maize trial, we might surmise, that at higher temperatures the stem, leaves and cobs had fewer cells along their longitudinal (and perhaps also along the lateral and radial) axes, and that these were longer, narrower and thinner. This would mean that the cell-wall content could be higher at higher temperatures since the ratio of surface area to volume increases when longitudinal growth dominates. This agrees with the data given in Table 4, but differences are very small, especially when the expected lower mass fraction of water-soluble carbohydrates is taken into account. This means that the cell walls must be thinner at higher temperatures. The possibilities for the formation of secondary walls are greater at lower temperatures since total area of cell walls is larger (because stem volume is larger and there are more cells). Thickening was also more pronounced at lower temperatures. Surface availability for microbial attack therefore declined when temperatures were lower during period 2.

The Q_{10} for lignin synthesis is higher than the Q_{10} for the synthesis of other cell-wall components. The lignin content is therefore higher at higher temperatures but the time lag between accretion of cellulose and hemicellulose and encrustation of lignin will also be smaller. A better synchronized lignin encrustation will give more opportunity for the formation of linkages and will therefore change the nature of the hemicellulose/cellulose fraction of the cell wall, especially when surface area of the primary cell wall is large. This structural effect will influence both potential digestibility and rate of cell-wall digestion and will be consistent throughout the growing season.

In an extra in vitro run, an attempt was made to gain more insight into these (partly hypothetical) influences of temperature by estimating potential digestibility of cell walls and the rate of digestion of potentially digestible cell walls.

Husk + shank samples were not investigated, since temperature during period 2

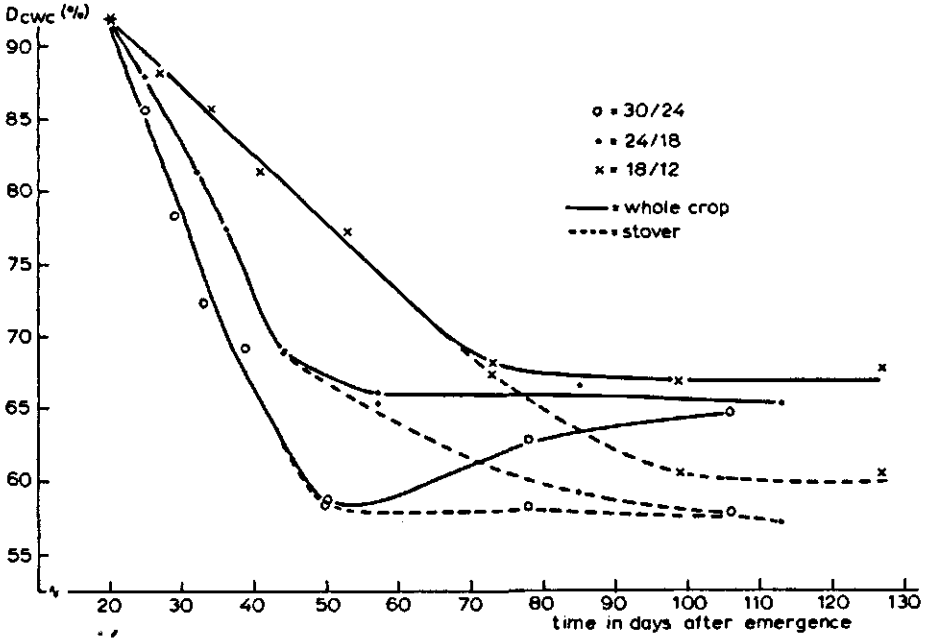

FIG. 5. Effect of temperature during period 2 on cell-wall digestibility (D_{cwc}) of the whole plant and of the stover.

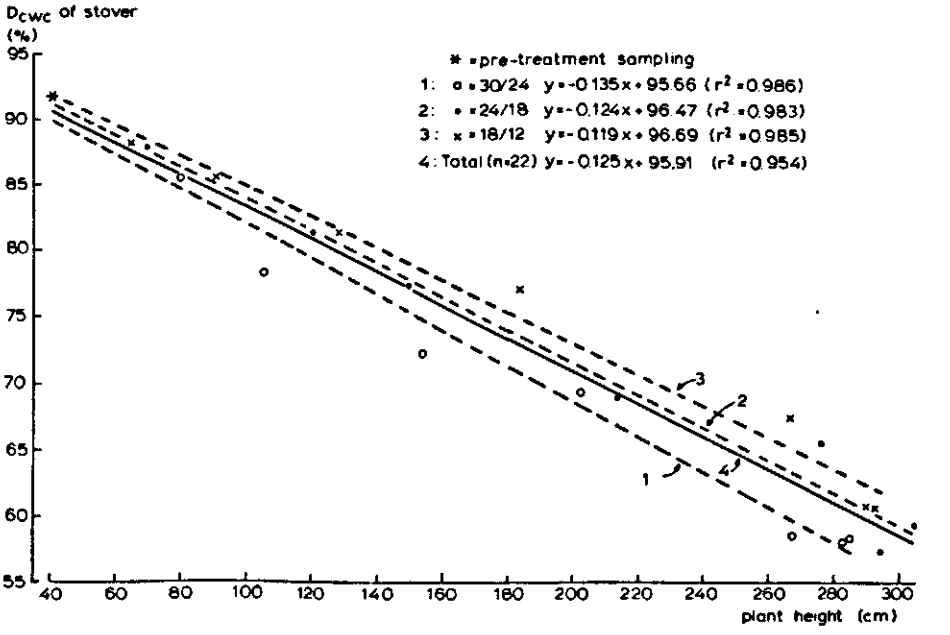

FIG. 6. Relation between plant height and cell-wall digestibility of the stover in Experiment 1.

did not affect their D_{cwc}. The data from ear samples will not be presented: their cell-wall digestion showed a considerable time lag, but was very rapid after 6 hours of incubation, so that accurate estimation of digestion rate was impossible. Stover samples taken about 2 weeks after temperature differentiation, at 50% ♂ flowering and 4 and 8 weeks after anthesis were analysed and gave workable results. Fig. 7 illustrates the method with stover samplings at 50% ♂ flowering and gives the relation between rate of cell-wall digestion and sampling date.

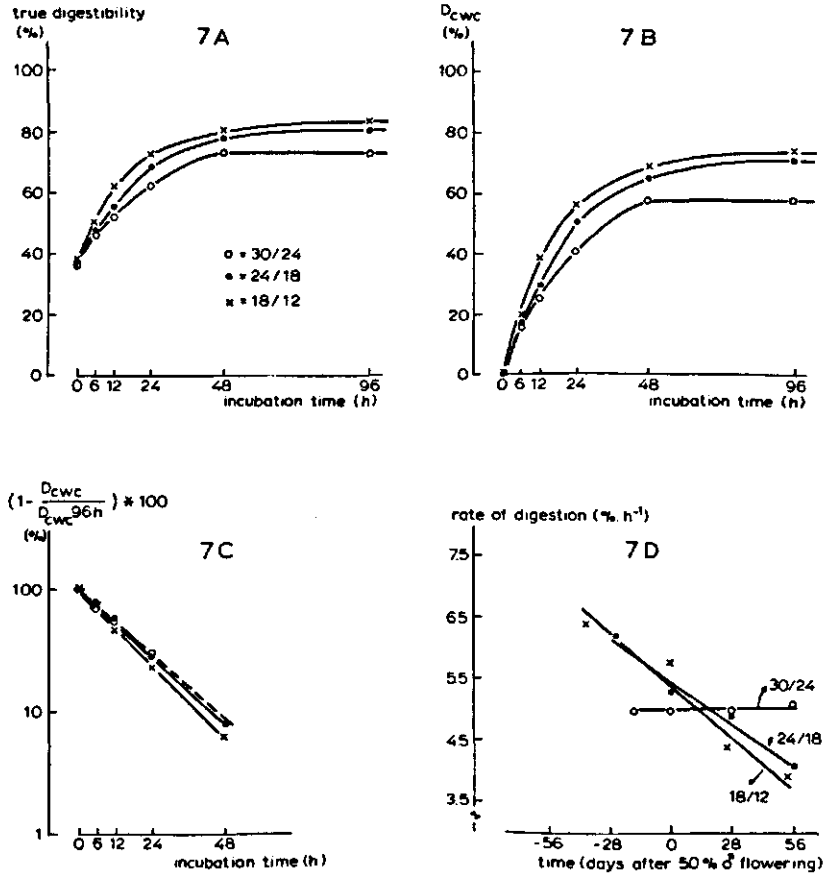

FIG. 7. Illustration of method for estimating digestion rate of potentially digestible cell walls.
7A. True digestibility in relation to incubation time; residues contain indigestible cell walls and potentially digestible cell walls that have not yet been digested.
7B. Digestibility of cell walls as a function of incubation time; D_{cwc} at 96 h is assumed to equal potential D_{cwc}. $1 - \frac{D_{cwc} \text{ at time t}}{D_{cwc} \text{ at 96 h}}$ indicates the fraction of the cell walls that have not been digested at time t, although they are digestible within 96 h of incubation.
7C. Semilog plot of fraction of potentially digestible cell walls that remained undigested versus incubation time; the regression coefficient is an estimator of the rate of digestion of potentially digestible cell walls.
7D. Rates of cell-wall digestion plotted against sampling date (cf. Table 6).

Table 6 shows the potential digestibilities of cell walls, the semilog regression equations and the correlation coefficients (all significant at $P < 0.01$; $n = 5$).

Potential digestibility depended on content of lignin and silica but even more on the structural organization of the cell-wall components. Differences in potential digestibility of cell walls achieved their maximum at 50% ♂ flowering and decreased during the first weeks of the post-anthesis period. Although for final samplings only slight differences were recorded after 48 h of incubation (Table 5), the potential digestibility of cell walls still differed considerably between temperature regimes. On the other hand, stover samples from early sampling dates showed smaller differences in D_{cwc} (96 h) than in D_{cwc} (48 h). This discrepancy is caused by differences in rate of cell-wall digestion (Table 6).

These digestion rates have been plotted against sampling date in Fig. 7D. The effect of temperature on lignification and structural organization apparently accelerated the maturity of the cell walls before flowering, which agrees with the above-described hypothesis. After anthesis, the content of cell solubles (i.e. 100 – cwc%) increased considerably in treatment 30/24, because ear development was inhibited. These increasing contents of cell solubles could have compensated for the normal decline in the rate of cell-wall digestion. SMITH et al. (1971, 1972) reported very significant positive correlations between the rate of cell-wall digestion and content of cell solubles.

TABLE 6. Potential cell-wall digestibilities (D_{cwc} after 96 h of incubation), and the regression equations and correlation coefficients (r) of the relation between $(1 - \frac{D_{cwc,\,t_i}}{D_{cwc,\,96\,h}}) \times 100\%$ and time of incubation, for stover samples taken on four sampling dates.

Temperature regime during period 2 (°C)	D_{cwc} after 96 h of incubation (%)	Regression equation	r
2 weeks after temperature differentiation			
30/24	76.1	$y = -0.050\,x + 4.544$	–0.99
24/18	81.7	$y = -0.062\,x + 4.489$	–0.98
18/12	84.5	$y = -0.064\,x + 4.431$	–0.96
at 50% ♂ flowering			
30/24	57.3	$y = -0.050\,x + 4.604$	–1.00[1])
24/18	70.0	$y = -0.053\,x + 4.643$	–1.00
18/12	72.6	$y = -0.058\,x + 4.583$	–1.00
4 weeks after 50% ♂ flowering			
30/24	63.7	$y = -0.050\,x + 4.580$	–1.00
24/18	65.3	$y = -0.049\,x + 4.569$	–1.00
18/12	69.6	$y = -0.044\,x + 4.502$	–0.99
8 weeks after 50% ♂ flowering			
30/24	63.2	$y = -0.051\,x + 4.591$	–0.99
24/18	64.7	$y = -0.041\,x + 4.520$	–0.98
18/12	70.0	$y = -0.039\,x + 4.495$	–0.99

[1]) $n = 4$, since the potential D_{cwc} had already been reached after 48 h of incubation.

Rates of digestion decreased for both other temperature treatments because of changes in the chemical composition of the cell walls after anthesis (cf. Tables 4 and 5) and because of a reduction of the surface availability. These effects reduced the rate of cell-wall digestion to such an extent that they overcompensated the still existing differences in physical structure.

The method illustrated in Fig. 7 clearly reveals the effect of temperature on digestibility as caused by its effect on the organization of the cell-wall components.

The dilution of cell walls with completely digestible organic matter was most efficient in treatment 24/18 and 30/24 (Table 5: $\triangle$ cwc%). The rate of the dilution process was determined by the cell-wall content present at anthesis, the cell-wall production after anthesis and the production rate of cell contents.

Résumé: *During period 2, the main processes that were dependent on temperature were leaf appearance, stem growth and reproductive development. High temperatures during period 2 led to lower amounts of dry matter at 50% ♂ flowering and a lower productivity thereafter. Temperature affected final digestibility by its effects on cell-wall content, cell-wall digestibility and amounts of cell wall. Its effects, however, were limited, since cell-wall production* after *anthesis was reduced by higher temperatures* before *anthesis and since most of the difference in cell-wall digestibility present at anthesis subsequently disappeared. Considerable differences in potential digestibility of cell walls remained at final samplings, but the rate of digestion of stover-cell walls was ultimately greater for the crop that received higher temperatures during period 2. This effect was probably partly caused by the high content of cell solubles in the stover that resulted from poor ear development.*

Period 3. Data and inferences from literature and unpublished research

The period from anthesis to grain set is a very critical period in the development of the maize crop. Stresses such as drought, low light intensity and heat produce very detrimental effects on ear development during this period. Although in Western Europe high temperatures are generally accompanied by high light intensity and high evaporation, in this discussion only temperature will be considered. High temperatures during pollination result in poor grain set because anther emergence is curtailed and pollen viability reduced (HERRERO and JOHNSON, 1980). According to these authors pollen viability remains almost unaffected up to 32 °C. JOVANOVIĆ and JOVANOVIĆ (1963) found that the success of pollination strongly depended on time of day associated with the concomitant temperature and the concomitant atmospheric humidity. Poorest grain set was obtained by pollination at 1 p.m. when the temperature was 26.4 °C and air humidity was 37%. Extremely high temperatures during silking are rare in The Netherlands. However, it is known that both pollen shed and silk extrusion may be inhibited by a succession of cool days (F. DE WOLFF, 1982; personal communication). Tolerance of cool weather during flowering shows great genotypic variability.

The effects of successful pollination on dry-matter production and D_{om} are illustrated in Fig. 8. In this example both yield and quality are greatly reduced by partial sterility of the ear. Smaller effects of sterility, however, have also been reported (e.g. BUNTING, 1975; DEINUM and KNOPPERS, 1979).

Fig. 4 illustrates that at least 43% of the cell-wall yield was attained after 50% anthesis. Much of this increase in cell-wall yield will occur during period 3. Thus during this stage too, an increase in temperature will reduce D_{om} by increasing the cell-wall content and reducing the cell-wall digestibility. The quantity of cell-wall constituents produced during period 4 will be little affected by the temperatures prevailing in period 3, unless adverse temperature reduces fertilization. In that case, cell-wall production during period 4 will be promoted (see above).

Period 4. Experiments 2 and 3

Developmental stage at climatic shift and climatic conditions

In Fig. 9 the physiological stages at which climatic differentiations took place are illustrated for all three hybrids in Experiments 2 and 3. Ula was treated at a later stage of kernel development than Nicco and Dara.

Rapid dry-matter accumulation in the kernels normally starts 12 to 18 days after silk emergence (JOHNSON and TANNER, 1972; DAYNARD and KANNENBERG, 1976; TOLLENAAR and DAYNARD, 1978), although cell division of the endosperm is not completed until 28 days after pollination (INGLE et al., 1965). Tip kernels

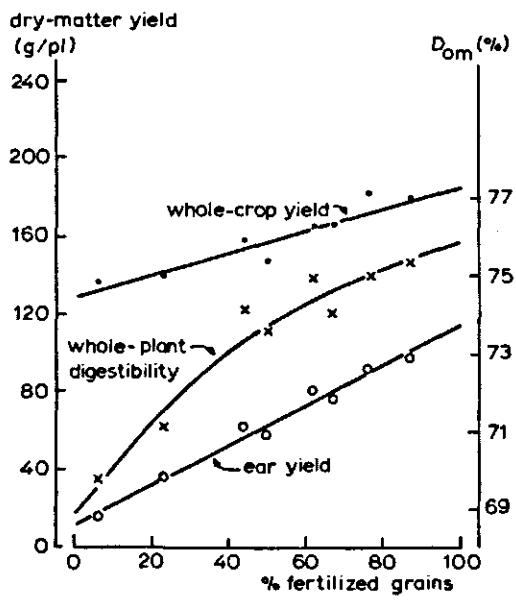

FIG. 8. Ear yield, whole-crop yield and whole-plant digestibility as affected by artificially prevented pollination. Plant density: 8.9 m^{-2}. (STRUIK, 1980; unpublished data).

start their linear phase of dry-matter accumulation about 4–5 days later than basal kernels (TOLLENAAR and DAYNARD, 1978). Hence, climate differentiation occurred almost at the start of rapid dry-matter accumulation of Nicco and Dara and a few days thereafter for Ula.

Light extinction depends on crop structure. The leaf angles were distinctly larger in Ula than in the other two hybrids. The tassels of Ula were relatively long compared to those of the other two hybrids but there were few branches. The leaves of Dara and Nicco were wider and shorter than those of Ula, thus enabling better light penetration in the crop.

Light extinction in the crop for shaded und unshaded treatments is illustrated in Fig. 10A for Ula and in Fig. 10B for Dara. The linear regression coefficient in the equation:

light intensity at leaf number n for shaded crop $= b \times$ light intensity at leaf number n for unshaded crop + constant

was 0.40 for Ula ($r = 0.992$; $n = 21$) and 0.41 for Dara ($r = 0.947$; $n = 22$). In both cases the constant only slightly exceeded zero. In 1980, light reduction caused by shading was greater ($b = 0.33$).

Shading affected the temperatures of plant tissues too (cf. STRUIK and DEINUM, 1982). Ear temperatures (recorded hourly with a data logger in 1979) appeared to be higher than air temperature for almost the entire day: they showed a minor lag phase compared with air temperature and were higher for unshaded plants than for shaded plants during the entire temperature cycle. Other climatic factors such as atmospheric humidity and water availability were hardly affected by shading in these controlled environments.

Crop development

As expected, final plant heights were not affected by treatments during period 4 and were 290 cm, 247 cm and 276 cm for Ula, Dara and Nicco, respectively. The number of leaves (Ula: 13.4; Dara: 15.5; Nicco: 14.4), total area of all leaves produced (Ula: 41.2 $dm^2.pl.^{-1}$; Dara: 51.0 $dm^2.pl.^{-1}$; Nicco: 50.5 $dm^2.pl.^{-1}$) and number of kernels in the top ear (Ula: 489; Dara: 602; Nicco: 427) were also unaffected.

Table 7 shows that ear size decreased with increasing temperatures and decreasing light intensity. This reduction of ear elongation at equal kernel numbers affected ear quality (see below).

Since rate of grain filling and availability of assimilates are both influenced by temperature and irradiance, the climatic shift will alter the activity of the kernels or the number of kernels that accumulate dry matter (henceforth called 'active kernels') (cf. STRUIK and DEINUM, 1982). The latter phenomenon is illustrated for Nicco in Fig. 11: the higher the temperature, the more rapid the decline in number of visibly active kernels. Finally, the plants at the lowest temperatures retained the greatest number of active kernels. As a rule, differences between

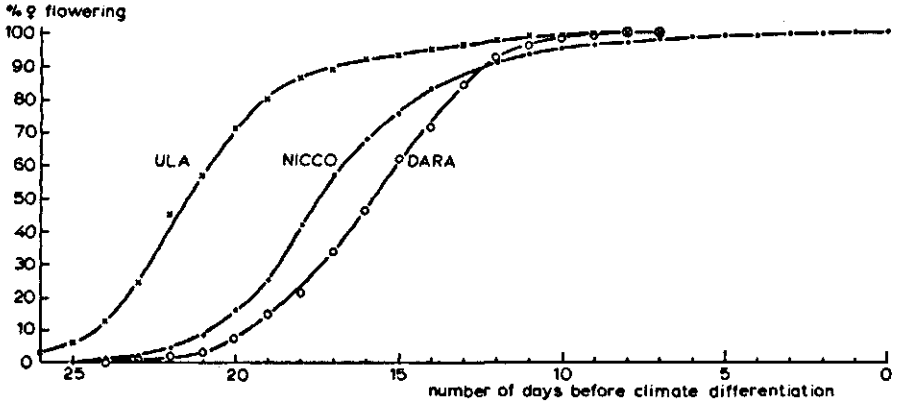

FIG. 9. Portion of silking plants as a function of time before climate differentiation.

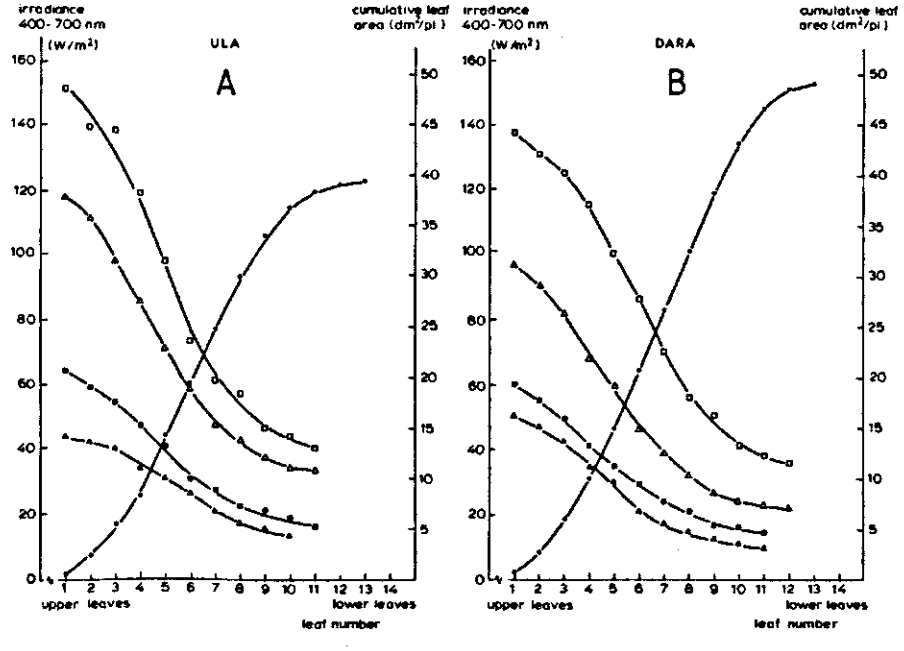

FIG. 10. Light extinction for shaded (■, ▲) and unshaded (□, △) crops in 1979 on a clear day (□, ■) and an overcast day (△, ▲) in relation to cumulative leaf area (•). Each point represents the mean of 15 (irradiance) or 20 (leaf area) values. Note that the x axis is not the same as in Fig. 1.

TABLE 7. Length of the top ear (in cm) ± standard error of the mean, as affected by light intensity and temperature during period 4 (hybrid Nicco, 1980; means of 80 plants).

Day/night temperatures (°C)	Length of top ear at 100% rel. light intensity	Length of top ear at 33% rel. light intensity	Mean length of top ear
30/24	14.9 ± 0.31	13.9 ± 0.29	14.4
24/18	15.3 ± 0.28	13.8 ± 0.34	14.6
18/12	16.1 ± 0.23	15.2 ± 0.28	15.7
Mean length of top ear	15.4	14.3	

treatments 18/12 and 24/18 were greater than differences between treatments 24/18 and 30/24. The shading treatment showed a prompt and strong effect on the number of active kernels at all temperatures; the final differences between shaded and unshaded treatments were temperature-independent for Ula and Nicco, but not for Dara, where the shading effect was more pronounced at higher temperatures.

Leaf-area duration after grain set was temperature-dependent and was also affected by light intensity. An example of the leaf-senescence pattern is presented in Fig. 12. The pattern, however, varied between genotypes. The differences between light treatments in the number of green leaves per plant increased as temperatures fell. This was true for all genotypes, but the degree of the difference between the number of green leaves at final sampling for the shaded crop and the number of green leaves at final sampling for the unshaded crop depended on genotype. The difference was always large and positive for Ula. The differences were smaller, but still positive or zero for Nicco (Fig. 12). For Dara the difference declined from + 3.6 leaves at 18/12 to – 2.8 leaves at 30/24.

These differences in type of reaction may be connected with the physiological stage at which shading was applied (Fig. 9), or with genotypic background.

Dry-matter production

Ear. The final ear yields of unshaded crops were always highest in treatment 18/12, slightly lower in treatment 24/18 and much lower in treatment 30/24. For Ula and Dara this was also true for shaded crops; for hybrid Nicco a very low ear yield was found for the shaded crop in treatment 24/18. The duration of grain filling increased as temperature fell; grain-filling rate increased as temperatures rose, but not enough to compensate fully for the decrease in duration of filling. The growth rates of ears in Nicco are presented in Table 8. Ear growth can also be derived from Fig. 13. The penultimate harvest of the shaded crop in treatment 24/18 gave an atypical high ear yield, that arose because the average number of aborted kernels was low in that sample (see also Fig. 11). At a relative light intensity of 100%, rate of ear growth was higher in treatment 30/24 than in treatments 24/18 and 18/12. For shaded crops, however, the growth rate was

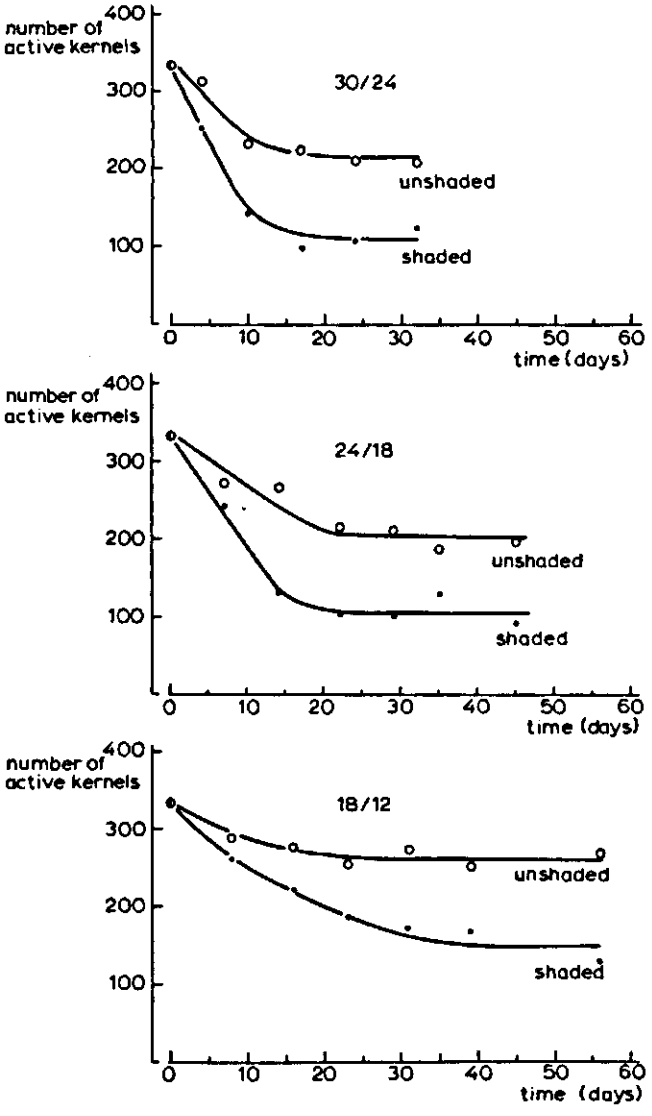

FIG. 11. Decline in the number of active kernels at three temperatures and two light treatments during period 4 (hybrid Nicco, 1980; means of 20 plants). Day 0 = date of initiation of treatment.

highest in treatment 18/12. The higher the temperature, the greater the negative effect of shading on the growth rate of ears was (cf. the lower the temperature the greater the positive effect of shading on leaf-area duration; see above). The effects of shading on duration of ear filling were inconsistent in these trials.

The final shelling percentages of the top ear were negatively affected by temperature but unaffected by light intensity in Ula and Dara; in Nicco no significant or consistent differences were found.

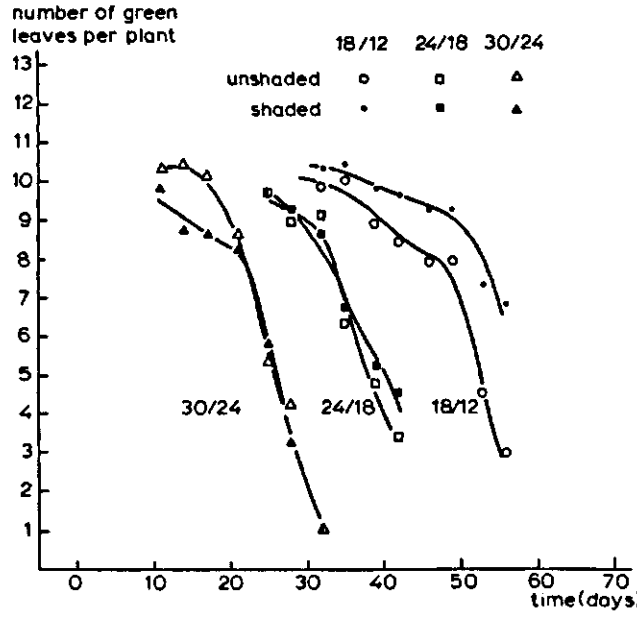

FIG. 12. Leaf senescence at three temperatures and two light intensities during period 4. Hybrid Nicco. Day 0 = date of initiation of treatment.

In all hybrids, ear yields were closely related to leaf-area duration during period 4 if data from the two light treatments were pooled separately.

Stover and husk + shank. A large portion of the dry matter present in the ears is produced after flowering. This portion may be 100% in regions with abundant irradiance and conditions that favour a long duration of leaf area (ALLISON

TABLE 8. Correlation coefficients (r) and regression coefficients (b) of the linear relation between ear yield and time for Nicco, grown under three temperature regimes and two light intensities during period 4.

Day/night temperatures (°C)	Relative light intensity (%)	n	r	90% interval of confidence of b (g.day^{-1})
30/24	100	5	0.99**	2.30 ± 0.42
	33	6[1])	0.99**	1.06 ± 0.13
24/18	100	6	0.99**	1.91 ± 0.34
	33	6	0.92**	0.85 ± 0.38
18/12	100	6	0.99**	1.82 ± 0.29
	33	6	0.99**	1.16 ± 0.17

[1]) This treatment did not reach a constant level of ear yield.
** = significant at $P < 0.01$.

and WATSON, 1966). In many other regions a significant reduction in weight of stem, leaves, husks and shanks has been recorded (DAYNARD et al., 1969; GENTER et al., 1970; DEINUM and DIRVEN, 1971; ADELANA and MILBOURN, 1972; BUNTING, 1976; AERTS et al., 1978; PHIPPS and WELLER, 1979; DEINUM and KNOPPERS, 1979; LUCAS, 1981; STRUIK, 1982b). This reduction is caused by redistribution of soluble carbohydrates, minerals and nitrogenous compounds (HAY et al., 1953; HANWAY, 1963; DAYNARD et al., 1969; GENTER et al., 1970; BEAUCHAMP et al., 1976; BELOW et al., 1981; STRUIK, 1982b). The intensity of redistribution depends on the difference between the rate of ear growth and that of crop growth. Since high temperature stimulates kernel growth more than crop growth, redistribution will be more intensive at higher temperatures, providing the light intensity is the same. In addition, low light intensity will dramatically increase the necessity for redistribution, unless complete ear abortion occurs.

Table 9 shows the final increases in dry matter, non-structural carbohydrate ($C_6H_{12}O_6$) and protein (N × 6.25) in non-ear parts at the 6 combinations of temperature and light intensity in Experiments 2 and 3. The rates of decline in component yield differed even more than final absolute values. Kernel abortion, induced by high temperatures or low light intensity, slowed down the redistribution of nitrogenous compounds (Table 9) and also of phosphorus (data not presented). Although the accumulation of N and P in the above-ground parts of the plant was reduced by shading (data not presented), the need for these minerals in the ear was reduced even more. If climatic conditions enable the plant to continue its ear growth successfully, N and P depletion in the stover occurs. This depletion may accelerate the senescence of the leaves under normal conditions.

The Ca content was also estimated. Ca plays a role in cell-wall formation and neutralization of organic acids. It tends to accumulate in the leaves (PAIN, 1978) where the light-dependent and organic-acid producing nitrate reduction

TABLE 9. Constituent yield in non-ear parts at final sampling minus constituent yield in non-ear parts at the climatic shift in g per plant for six climatic regimes during period 4 (means of three hybrids).

Temperature regime (°C)		30/24	24/18	18/12	*Mean*
dry matter	unshaded	− 7.1	− 4.9	+ 3.0	*− 3.0*
	shaded	−22.1	−20.4	−14.1	*−18.8*
	Mean	*−14.6*	*−12.7*	*− 5.6*	
non-structural carbohydrates	unshaded	− 5.6	− 1.3	+ 0.7	*− 2.1*
	shaded	−11.4	− 9.9	− 6.4	*− 9.2*
	Mean	*− 8.5*	*− 5.6*	*− 2.8*	
protein	unshaded	− 3.8	− 4.5	− 5.0	*− 4.5*
	shaded	− 3.6	− 3.5	− 3.8	*− 3.6*
	Mean	*− 3.7*	*− 4.0*	*− 4.4*	

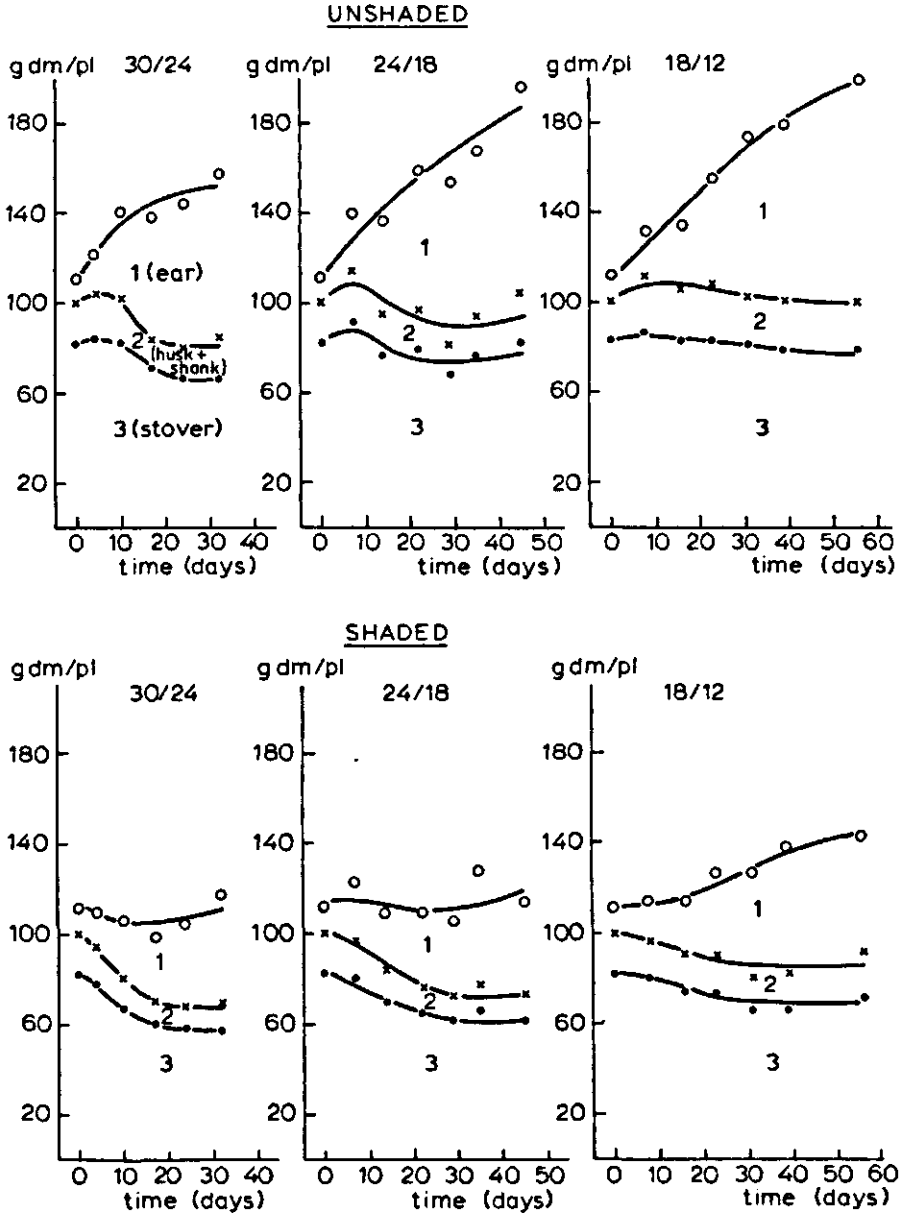

FIG. 13. Dry-matter production and distribution for all treatments in Experiment 3. Day 0 = date of initiation of treatment.

occurs. The accumulation of Ca in the above-ground parts of the plant was reduced by shading during period 4, but the amounts of Ca in ears were very low and it was not remobilized in the plant. Ca does not play a role in the redistribution pattern.

Kernel abortion also decreases the amount of carbohydrates that has to be translocated from the vegetative parts to the ears. The redistribution of carbohydrates, however, was still intensive. Much of the fraction that was not identified as ash, cell wall, non-structural carbohydrate or crude protein also left the vegetative parts if redistribution of other compounds was intensive.

Whole plant. As an example, Fig. 13 illustrates the dry-matter production and distribution of Nicco. Although fewer sampling dates were available for Ula and Dara, the general pattern was essentially similar. Since some data were deviant because there were few plants in the samples, curves were drawn using the cell-wall yield as a standardizing criterion. Final yields increased with falling temperature and increasing light intensity. Initially, the production rates of all hybrids in the unshaded treatments tended to increase with rising temperatures. If shaded, however, crop-production rate was highest in treatment 18/12.

Low light intensity resulted in a strong reaction during the first part of the grain filling, but dry-matter production rate was higher in the later part associated with a decrease in rate of redistribution. This is especially evident in treatment 18/12 (Fig. 13) but was also clear in Ula and Dara in treatments 24/18 and 30/24. This phenomenon of habituation to a growth-limiting climatic factor during a rather fixed, unplastic stage of the crop is conspicuous. The phenomenon might be explained by the hypothesis presented by STRUIK and DEINUM (1982), who stated that shading promptly curtailed root activity. Reduced root activity might have induced the observed kernel abortion. If abortion occurs early in the grain-filling period, a new balance might be obtained, since partial sterility favours translocation of sugars to the roots. When this new balance is achieved, the plants may function better than expected on the basis of their previous performance. Data from the root samples of Experiment 3 tended to support this hypothesis, but the difficulties of separating roots from root medium affected the reliability of the data. The linear correlation coefficient between non-structural carbohydrate content in the roots and number of active kernels, however, was highly significant ($P < 0.01$; $n = 35$).

Quality of the organic matter

Fig. 14 illustrates the trend in D_{om} of the most relevant plant parts in each treatment in Experiment 3. The development of the proportion of the most digestible part (i.e. the ear fraction) is also given.

Ear digestibility increased slightly during early stages of grain filling but subsequently remained constant. The same pattern was found in Experiment 2. This agrees with results obtained by PERRY and COMPTON (1977) and AERTS et al. (1978). Temperature did not influence ear digestibility. Continuous shading also barely affected ear digestibility, since shelling percentage and thus cell-wall con-

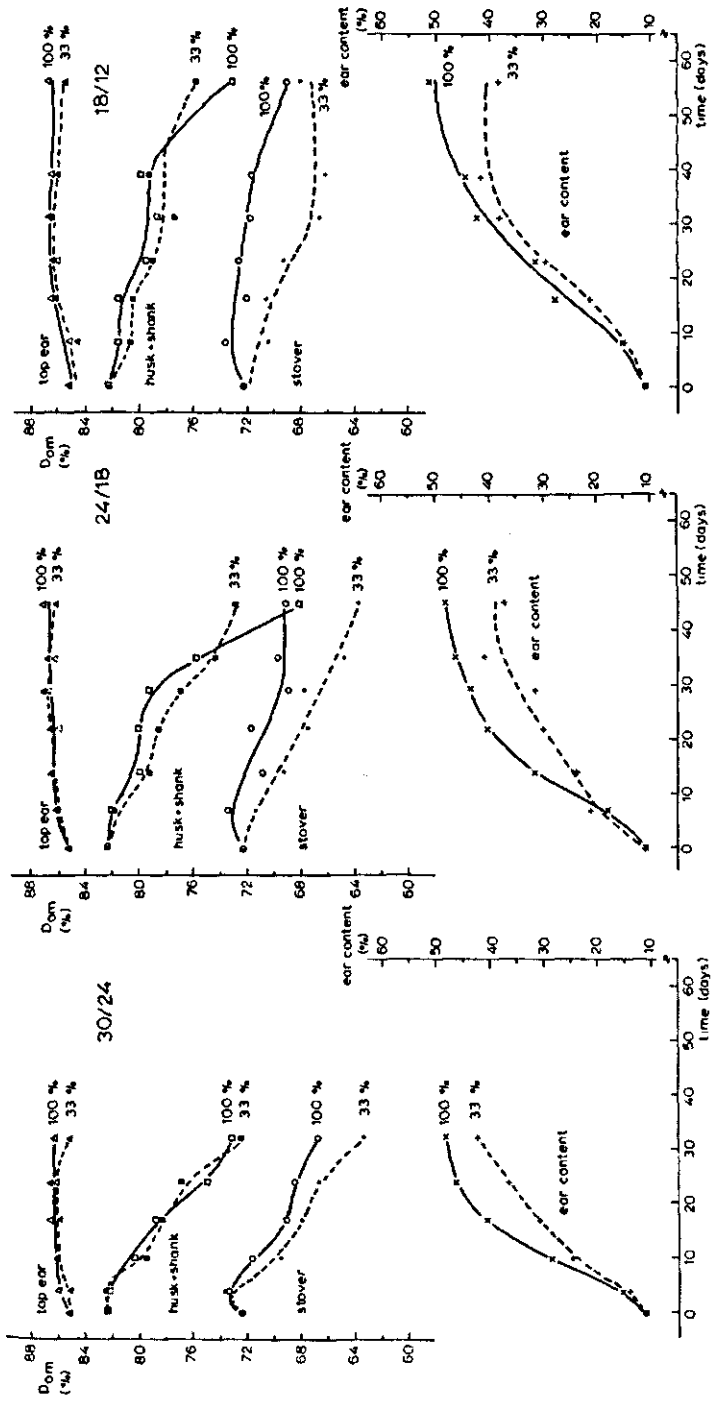

FIG. 14. Development of ear content and digestibility of the main plant parts over time after grain set for two light intensities at 30/24, 24/18 and 18/12 °C. Day 0 = date of initiation of treatment.

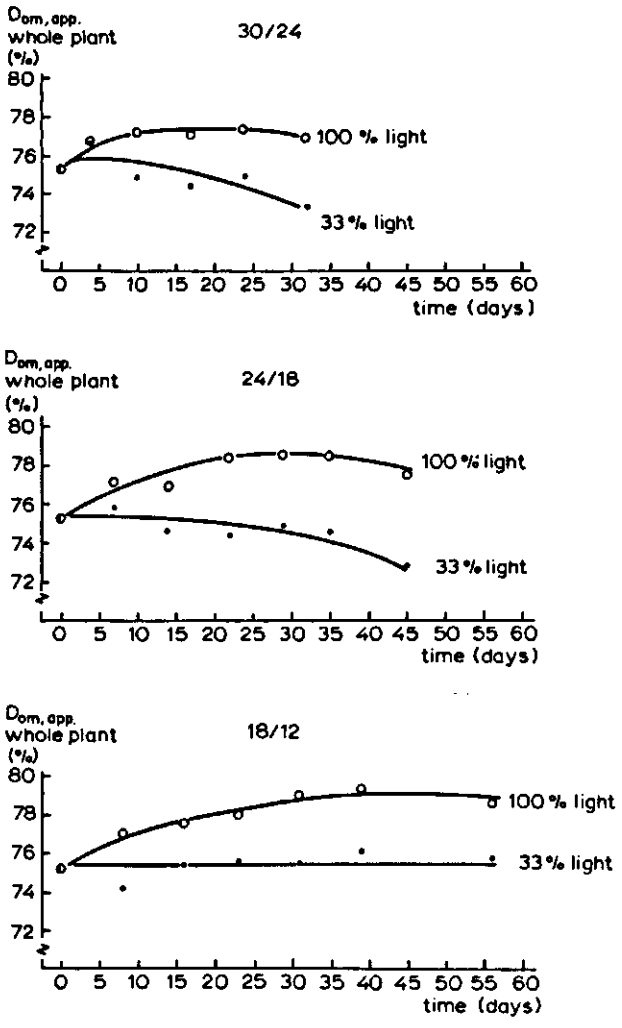

FIG. 15. Apparent digestibility of the whole plant plotted against time during period 4, for six temperature/light combinations. Day 0 = date of initiation of treatment.

tent were almost unaffected (see above). This agrees with field data obtained by STRUIK and DEINUM (1982). Shading, however, considerably reduced the proportion of organic matter in the ears.

The digestibility of husk + shank decreased during period 4. This decline was more rapid at higher temperatures but only slightly affected by radiation. In treatment 30/24 no consistent differences between shaded and unshaded plants could be identified.

In both lower temperature regimes, low light intensity initially produced lower D_{om}, but finally a much higher D_{om} was found. Also in Experiment 2 the digestibility of husk + shank in shaded crops was better: a prolonged increase in the

cell-wall content of the husks and shanks of unshaded crops caused this reversal. (This prolonged increase in cell-wall content probably occurred because redistribution from the husks to the kernels was necessary for a longer period).

Stover digestibility declined during period 4 and this decline was more rapid at higher temperature and at lower light intensity. In Experiment 2 some treatments originally showed a considerable increase in the digestibility of the stover before the decline set in. Otherwise the pattern was similar. Trends and differences in digestibility agree with the redistribution phenomena. Thus only the digestibility of vegetative parts and the proportion of ear parts were sensitive to temperature and light intensity during period 4.

These two effects of temperature and light intensity resulted in the patterns of whole-plant digestibility shown in Fig. 15. At 100% light, the increase in whole-plant digestibility continued for longer at lower temperatures, giving higher final digestibilities (Table 10). Similarly, D_{om} decreased less in shaded crops at lower temperatures. At higher temperatures, the small decline in D_{cwc} could not be compensated for by a concomitant decrease in the cell-wall content. In Experiments 2 and 3, light intensity during grain filling was relatively constant and fairly high. In practice in The Netherlands, diurnal amounts of light drop sharply during grain filling, so that a standard crop merges from the conditions experienced by the unshaded crops in these experiments to those experienced by the shaded crops. The pattern of digestibility in the unshaded crops in Experiments 2 and 3 is similar to the pattern found in Experiment 1, during the same period.

Differences in cell-wall digestibility had little effect on organic-matter digestibility. Plants had reached their maximum height before the climate shift. As Fig. 6 shows, an important differentiation in stover D_{cwc} is unlikely beyond that stage. The D_{cwc} of husk + shank was not affected by light intensity either. Its rate of decline in D_{cwc} was affected by temperature (as was plant development) but the final extent of the D_{cwc} decline (thus the D_{cwc} at the same physiological stage) was not.

Cell-wall production was affected both by temperature and light intensity and in the same direction as was dry-matter production. This limitation of cell-wall formation was very evident in husks + shanks and in ears, but was only small in the stover. In the husk + shank and in the ear fraction, the yield of cell walls from shaded plants was only approximately 70% of that of the unshaded plants, and plants in treatment 30/24 yielded about 30% fewer cell walls than plants in treatment 18/12. These reductions in the amounts of cell wall resulted in smaller effects of the treatments on the quality of ears and of husks + shanks than on the quality of stover. The most relevant factor in determining the digestibility of the vegetative parts was the extent of assimilate redistribution.

Thus in ears, dry-matter accumulation and cell-wall formation were equally affected by climatic conditions. In stover, the amounts of cell wall and their quality were barely affected, so that the necessity for redistribution was the over-

riding factor in stover quality. In the husk + shank fraction, cell-wall formation, the rate at which the cell-wall digestibility declined, and the extent and rate of translocation of metabolites all affected quality.

Since shading affected cell-wall formation in the plant organs with the best cell-wall quality, a small negative effect of shading on cell-wall digestibility of the whole plant must be expected. Table 10 confirms this supposition but also indicates that the greatest differences in cell-wall quality were found in Nicco. This hybrid showed a strong decline in D_{cwc} during the final part of the grain-filling period for shaded crops. Before this process started, the effects of shading on D_{cwc} were certainly not greater than in Ula and Dara. It is unlikely that Nicco's greater sensitivity to shading as expressed in decreasing digestibility is genetically determined.

Table 10 also presents the cell-wall contents of the whole crop at final sampling. In Experiments 2 and 3 digestibility was mainly related to this quality criterion, as is illustrated in Fig. 16 in which the whole-crop digestibility on each sampling date is plotted against the cell-wall content on the basis of the organic matter. Physiological age, temperature and light intensity all affected quality predominantly by their effects on cell-wall content. The data from the final samplings are underlined; in Ula and Dara they were equally distributed above and below the regression line, but in Nicco they were all below that line. Although also significant in both experiments, the linear correlation coefficient between D_{cwc} and D_{om} was much lower, especially in Experiment 2.

TABLE 10. Quality parameters of all treatments in Experiments 2 and 3 at final sampling (whole plant).

Day/night temperatures (°C)		30/24		24/18		18/12	
Light treatment		unshaded	shaded	unshaded	shaded	unshaded	shaded
D_{om} (%)	Ula	77.3	74.8	78.5	76.1	78.8	76.0
	Dara	76.3	74.0	78.7	75.4	77.3	76.4
	Nicco	76.9	73.3	77.5	72.8	78.5	75.6
	Mean	*76.8*	*74.0*	*78.2*	*74.8*	*78.2*	*76.0*
		75.4		*76.5*		*77.1*	
D_{cwc} (%)	Ula	68.3	64.7	66.2	66.4	68.4	67.4
	Dara	65.4	66.4	68.1	67.4	68.0	66.3
	Nicco	73.6	69.7	72.2	66.2	76.1	70.9
	Mean	*69.1*	*66.9*	*68.8*	*66.7*	*70.8*	*68.2*
		68.0		*67.8*		*69.5*	
$cwc_{\%}$ (%)	Ula	39.8	46.4	33.5	41.1	34.8	39.4
	Dara	42.3	47.3	34.8	44.3	36.4	40.2
	Nicco	43.6	51.8	38.6	47.8	37.9	46.0
	Mean	*41.9*	*48.5*	*35.6*	*44.4*	*36.4*	*41.9*
		45.2		*40.0*		*39.1*	

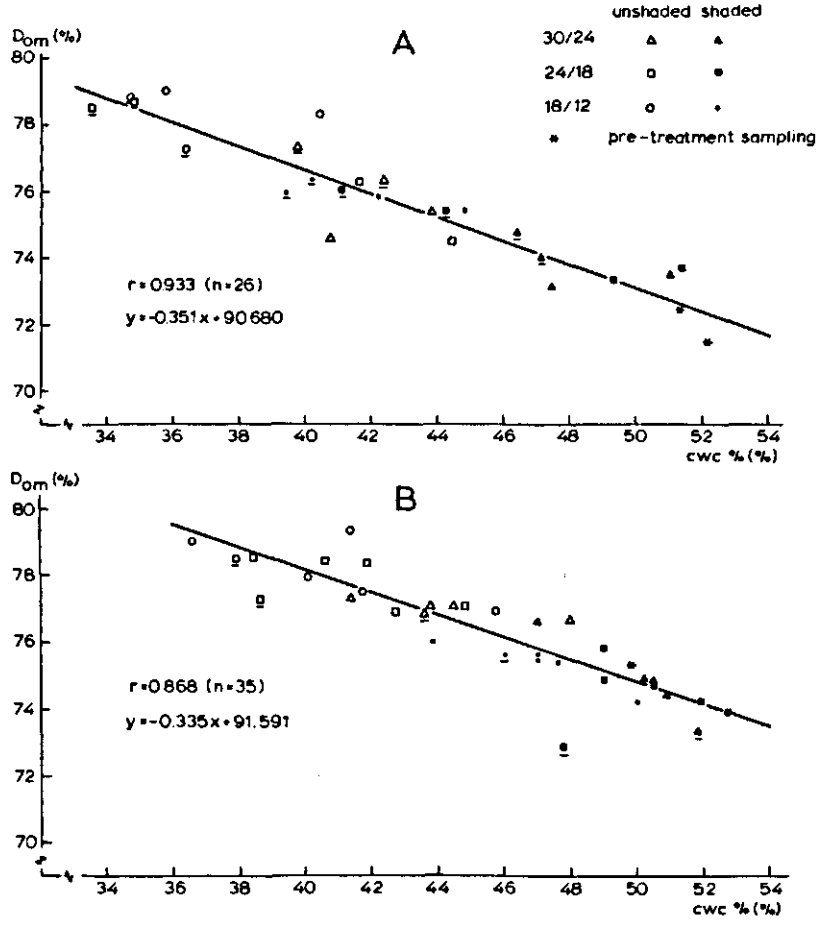

FIG. 16. Relation between cell-wall content of the organic matter (cwc%) of the whole plant and apparent digestibility of the organic matter (D_{om}) of the whole plant, in Experiment 2 (A) and Experiment 3 (B). Data from final samplings are underlined.

Résumé: *Increased temperatures during period 4 accelerated grain filling, the redistribution of certain metabolites, D_{cwc} decline and plant senescence, but curtailed the duration of grain filling and of leaf area, final ear yield, ear size and kernel activity, whole-plant yield, cell-wall yield and crop quality.*

In addition, low light intensity during period 4 stimulated the senescence of the ear and the redistribution of metabolites to the ear, and may have stimulated cell-wall maturation to some extent. Poor light conditions reduced cell-wall formation and sometimes slowed down leaf senescence.

Both temperature and light mainly affected quality by means of their effects on the proportion of ear in the whole plant and the cell-wall content of the vegetative parts, resulting in a strong correlation between crop digestibility and cell-wall content of the whole crop.

TABLE 11. Summary of effects of temperature during different stages of development on final dry-matter and cell-wall production, and on final quality parameters. Light intensity is assumed to be constant.

	Dry-matter production	Cell-wall production	Cell-wall content	Cell-wall digestibility	Organic-matter digestibility
Period 1	+ +	+ +	± or +	±	± or −
Period 2	− −	− −	±	−	−
Period 3	− −	− or ±	+	−	−
Period 4	− −	−	+	± or −	−
Entire growing season	− −	−	+	−	−

+ (+) indicates that a rise in temperature produces a (strong) positive effect.
± indicates that inconsistent or small effects are expected.
− (−) indicates that a rise in temperature produces a (strong) negative effect.

Comparisons with field data

Table 11 summarizes the findings of the above-described phytotron and desk research. It also presents the expected effects of temperature over the entire growing season. These expectations agree with data obtained by DEINUM (1976), although he did not present data on whole-crop quality.

In the years 1977, 1978, 1979, 1980 and 1981 the hybrid LG 11 was grown in the field at the same location and following the same cultural practices. Detailed data on temperature, crop development and quality were available, enabling the validity of the hypothesis to be tested. In Table 12 some relevant data are presented.

The number of leaves per plant differed significantly over the years. For example, in 1977, LG 11 had 1.5 leaves per plant more than in 1979, although the mean air temperature during the pre-tassel initiation period was almost the same. TOLLENAAR and HUNTER (1981), however, found that leaf number was determined during a short period to the tassel initiation. In the data presented in Table 12, the simple linear correlation coefficient between mean air temperature during the four days before the 6.5-leaf stage and the final number of leaves was 0.99 ($P < 0.01$). The regression coefficient was 0.28 leaves/°C, which agrees with the value of 0.2 found by TOLLENAAR et al. (1979). This temperature effect restricts the usefulness of maturity indexing systems that are based on the relationship between rate of crop development and temperature or heat unit.

The number of leaves, or rather the number of stem internodes, is crucial for final cell-wall yield and final cell-wall content. A significant linear relationship between number of leaves and cell-wall yield did indeed exist ($r = 0.97$; $n = 4$; $P < 0.05$). However, the cell-wall analysis of the 1978 crop was not available and most probably the cell-wall yield in that cool year was lower than expected on the basis of this relation. This supposition is supported by the good digestibility compared with the 1977 crop. The low height of the plant given the large number of stem internodes may be connected with this deviation. Climatic conditions during periods 2, 3 and 4 of the 1978 growing season were

TABLE 12. Crop descriptions of LG 11, grown at the same location for five years, together with the mean temperatures during different stages of growth for each year.

Year	1977	1978	1979	1980	1981
number of leaves per plant	15.3	15.7	13.8	14.2	14.9
height of plant (cm)	261	226	214	215	235
dry-matter yield ($Mg.ha^{-1}$)	15.4	13.4	12.8	14.1	17.0
cell-wall yield ($Mg.ha^{-1}$)	7.1	–	5.2	6.1	7.0
cell-wall content (% of organic matter)	49.3	–	42.2	44.8	42.4
digestibility (% of organic matter)	71.5	74.1[1])	74.8	73.6	74.3
cell-wall digestibility (%) after standardization of the true digestibility	61	–	61	61	61
T_1 (°C)	12.1	12.9	12.0	11.7	12.5
T_f (°C)	19.8	20.6	13.8	15.9	17.6
T_2 (°C)	16.2	14.7	15.3	15.5	15.2
T_3 (°C)	16.4	15.5	16.0	17.8	19.0
T_4 (°C)	13.0	12.8	13.7	14.5	14.9
T_m (°C)	14.1	13.8	14.0	14.4	14.8

T_1 = mean temperature during period 1.
T_f = mean temperature during 4 days prior to the 6.5-leaf stage.
T_2 = mean temperature during period 2.
T_3 = mean temperature during period 3.
T_4 = mean temperature during period 4.
T_m = mean temperature during the entire growing season.
[1]) Ear samples were not analysed in this year. Digestibility was calculated assuming that the digestibility and ash content of the ear were equal to the means of the years 1977, 1979, 1980 and 1981.

clearly unfavourable for dry-matter production and cell-wall formation.

Thus, the annual variation in cell-wall yield can largely be explained by variation in air temperature just prior to the 6.5-leaf stage. Extreme climatic conditions during the post-tassel initiation period, however, may cause deviations from this general pattern.

The cell-wall content also depends on the dilution of the cell walls with non-structural carbohydrates after silking. During the autumn in The Netherlands, prevailing temperatures are mostly below the optimum for dry-matter production. Therefore, an increase in temperature during period 4 will mostly benefit dry-matter production and thus crop quality. This means that the 1981 crop diluted its amounts of cell wall much more than the 1977 crop, although the cell-wall yields were approximately the same. The light intensity also plays an important role during this stage and is closely correlated with temperature under uncontrolled conditions.

Mean air temperatures during periods 2 and 3 varied considerably between years, but the mean temperatures during the period from 6.5-leaf stage until the grain-filling period ranged between 14.8–16.2 C only. This range is much too small to induce differences in cell-wall digestibility. The D_{cwc} of all crops

for which the cell-wall analysis was available, was the same, resulting in a significant linear correlation between cell-wall content and digestibility of organic matter ($r = -0.99$; $n = 4$; $P < 0.01$).

High temperatures during grain filling make the crop suitable for ensiling at an earlier date or cause higher dry-matter contents at harvest if the harvest date is not advanced. This aspect of suitability for ensiling has not been taken into account in this analysis, but certainly plays an important role in areas at the limits of the range of maize.

The practical implications of the results obtained will be discussed in the author's doctoral thesis.

Summary

The effects of temperature on the growth, development, dry-matter production, dry-matter distribution and digestibility of forage maize were analysed.

Higher temperatures during the *period before tassel initiation* stimulated whole-crop yield without affecting its quality. During this period, however, temperature may affect the number of stem internodes and thus the plant's ability to form cell walls. High temperatures during early growth may therefore reduce crop quality, especially when the digestibility of cell walls is poor.

Higher temperatures during the *period from tassel initiation to anthesis* greatly accelerates plant development, without affecting leaf number. Stem diameter decreased as temperature rose but the final plant height in the various temperature treatments was similar. The interval between anthesis and silking was dramatically lengthened by high temperatures during this period. Initially, dry-matter production was more rapid at higher temperatures, but total dry matter at anthesis and productivity after anthesis decreased as temperatures rose. The digestibility of organic matter and of cell walls before anthesis declined more rapidly at higher temperatures, because temperature affected the rate of development, the cell-wall content, the encrustation of lignin and of silica and other physical/chemical processes. The latter were ascertained by estimating potential cell-wall digestibility and the rate of digestion of potentially digestible cell walls. Differences disappeared during the post-anthesis period, during which the temperature was the same for all treatments in this experiment.

The temperature *during flowering* may affect production and quality by its influence on anther emergence, pollen viability, silk emergence and grain set. In addition, temperature may affect the intensity of the ongoing cell-wall formation and the quality of the cell walls.

High temperatures *during grain fill* not only accelerated grain filling but also leaf senescence: they also reduced kernel viability, the duration of grain filling, and final plant yield. Crop quality was affected because temperature influenced the proportion of ear in the whole plant and the cell-wall content of the stover. Low light during this period influenced crop quality in the same way as high

temperature. Leaf senescence, however, was sometimes retarded by shading.

When these results were compared with field data it appeared that in practice it is mainly the temperature just prior to tassel initiation that is critical for crop quality.

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References

Adelana, B. O. and G. M. Milbourn: 1972. The growth of maize. II. Dry-matter partition in three maize hybrids. J. agric. Sci., Camb., **78**: 73–78.

Aerts, J. V., B. G. Cottyn, D. L. De Brabander, Ch. V. Boucqué and F. X. Buysse: 1978. Digestibility and feeding value of maize. Proc. European Maize Meeting, Louvain-La-Neuve (Belgium), (ed.) J.-F. Ledent, pp. 106–128.

Akin, D. and D. Burdick: 1981. Relationships of different histochemical types of lignified cell walls to forage digestibility. Crop Sci., **21**: 577–581.

Allison, J. C. S. and T. B. Daynard: 1979. Effect of a change in time of flowering, induced by altering photoperiod or temperature on attributes related to yield in maize. Crop Sci., **19**: 1–4.

Allison, J. C. S. and D. J. Watson: 1966. The production and distribution of dry matter in maize after flowering. Ann. Bot. N.S., **30**: 365–381.

Andrieu, J.: 1976. Factors influencing the composition and nutritive value of ensiled whole-crop maize. Animal Feed Science and Technology, **1**: 381–392.

Bailey, R. W., J. A. Monro, S. E. Pickmere and A. Chesson: 1976. Herbage hemicellulose and its digestion by the ruminant. In: Carbohydrate research in plants and animals. Misc. Papers nr. 12, Agric. Univ. Wageningen, pp. 1–15.

Beauchamp, E. G., L. W. Kannenberg and R. B. Hunter: 1976. Nitrogen accumulation and translocation in corn genotypes following silking. Agron. J., **68**: 418–422.

Below, F. E., L. E. Christensen, A. J. Reed and R. H. Hageman: 1981. Availability of reduced N and carbohydrates for ear development of maize. Plant Physiol., **68**: 1186–1190.

Blacklow, W. M.: 1972a. Mathematical description of the influence of temperature and seed quality on imbibition by seeds of corn (*Zea mays* L.). Crop Sci., **12**: 643–646.

Blacklow, W. M.: 1972b. Influence of temperature on germination and elongation of the radicle and shoot of corn (*Zea mays* L.). Crop Sci., **12**: 647–650.

Blondon, F. and A. Gallais: 1976. Influence de la température, de la valeur de l'éclairement et de la photopériode sur le développement floral de quatre génotypes de maïs. Ann. Amélior. Plantes, **26**: 195–213.

Breuer, C. M., R. B. Hunter and L. W. Kannenberg: 1976. Effects of 10- and 20-hour photoperiod treatments at 20 and 30 C on rate of development of a single-cross maize (*Zea mays*) hybrid. Can. J. Plant Sci., **56**: 795–798.

BROUWER, R., A. KLEINENDORST and J. TH. LOCHER: 1973. Growth responses of maize plants to temperature. In: Plant response to climatic factors. Proc. Uppsala Symp., 1970. UNESCO, Paris, pp. 169–174.

BUNTING, E. S.: 1975. The question of grain content and forage quality in maize: comparisons between isogenic fertile and sterile plants. J. agric. Sci., Camb., **85**: 455–463.

BUNTING, E. S.: 1976. Effects of grain formation on dry matter distribution and forage quality in maize. Expl Agric., **12**: 417–428.

BUREN, L. L., J. J. MOCK and I. C. ANDERSON: 1974. Morphological and physiological traits in maize associated with tolerance to high plant density. Crop Sci., **14**: 426–429.

CHESSON, A.: 1982. Degradation of plant cell walls by rumen organisms. Livestock Prod. Sci. (in press).

CHOWDHURY, S. I. and I. F. WARDLAW: 1978. The effect of temperature on kernel development in cereals. Aust. J. agric. Res., **29**: 205–223.

COLIGADO, M. C. and D. M. BROWN: 1975a. A bio-photo-thermal model to predict tassel-initiation time in corn (*Zea mays* L.). Agric. Met., **15**: 11–31.

COLIGADO, M. C. and D. M. BROWN: 1975b. Response of corn (*Zea mays* L.) in the pre-tassel initiation period to temperature and photoperiod. Agric. Met., **14**: 357–367.

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.

DAYNARD, T. B. and L. W. KANNENBERG: 1976. Relationships between length of the actual and effective grain filling periods and the grain yield of corn. Can. J. Plant Sci., **56**: 237–242.

DAYNARD, T. B., J. W. TANNER and D. J. HUME: 1969. Contribution of stalk soluble carbohydrates to grain yield in corn (*Zea mays* L.). Crop Sci., **9**: 831–834.

DEINUM, B.: 1974. Structural inhibitors of quality in forage. Proc. Eur. Grassl. Fed. 5th Gen. Meeting, Växtodling, 1973, pp. 42–52.

DEINUM, B.: 1976. Effect of age, leaf number and temperature on cell wall and digestibility of maize. In: Carbohydrate research in plants and animals. Misc. Papers nr. 12, Agric. Univ. Wageningen, pp. 29–41.

DEINUM, B.: 1979. Invloed van uitwendige omstandigheden op produktie en celwandsamenstelling van gras. Proc. Symp. 'Ruwe celstof of voedingsvezel?', organized by Contactcommissie Celwand en celwandvertering, NRLO, Wageningen, pp. 27–33.

DEINUM, B.: 1981. The influence of physical factors on the nutrient content of forages. Mededelingen Landbouwhogeschool Wageningen **81-5**, pp. 1–18.

DEINUM, B. and J. G. P. DIRVEN: 1971. Climate, nitrogen and grass. 4. The influence of age on chemical composition and in vitro digestibility of maize (*Zea mays* L.) and tall fescue (*Festuca arundinacea* Schreb.). Neth. J. agric. Sci., **19**: 264–272.

DEINUM, B. and J. G. P. DIRVEN: 1975. Climate, nitrogen and grass. 6. Comparison of yield and chemical composition of some temperate and tropical grass species grown at different temperatures. Neth. J. agric. Sci., **23**: 69–82.

DEINUM, B. and J. G. P. DIRVEN: 1976. Climate, nitrogen and grass. 7. Comparison of production and chemical composition of *Brachiaria ruziziensis* and *Setaria sphacelata* grown at different temperatures. Neth. J. agric. Sci., **24**: 67–78.

DEINUM, B. and J. KNOPPERS: 1979. The growth of maize in the cool temperate climate of the Netherlands: Effect of grain filling on production of dry matter and on chemical composition and nutritive value. Neth. J. agric. Sci., **27**: 116–130.

DIRVEN, J. G. P. and B. DEINUM: 1977. The effect of temperature on the digestibility of grasses. An analysis. Forage Res., **3**: 1–17.

DONSELAAR, B. van and A. STEG: 1980. Voederwaardebepaling en voederwaardeberekening van mengvoer voor melkvee. Rapport no. **132**, Instituut voor Veevoedings Onderzoek 'Hoorn', Lelystad, pp. 1–12.

DUNCAN, W. G.: 1975. Maize. In: Crop physiology. Some case histories. (ed.) L. T. EVANS, Cambridge University Press, London, pp. 23–50.

DUNCAN, W. G. and J. D. HESKETH: 1968. Net photosynthetic rates, relative leaf growth rates and leaf numbers of 22 races of maize grown at eight temperatures. Crop Sci., **8**: 670–674.

EDMEADES, G. O. and T. B. DAYNARD: 1979. The development of plant-to-plant variability in maize at different planting densities. Can. J. Plant Sci., **59**: 561–576.

FRIEND, D. J. C. and Marion E. POMEROY: 1970. Changes in cell size and number associated with the effects of light intensity and temperature on the leaf morphology of wheat. Can J. Bot., **48**: 85–90.

GENTER, C. F., G. D. JONES and M. T. CARTER: 1970. Dry matter accumulation and depletion in leaves, stems, and ears of maturing maize. Agron. J., **62**: 535–537.

GMELIG MEYLING, H. D.: 1973. Effect of light intensity, temperature and daylength on the rate of leaf appearance of maize. Neth. J. agric. Sci., **21**: 68–76.

GOERING, H. K. and P. J. VAN SOEST: 1970. Forage fiber analysis; apparatus, reagents, procedures and some applications. USDA Agric. Handbook No. **359**.

GOODRICH, R. D. and J. C. MEISKE: 1979. Rate and extent of digestion. Aids for explaining some nutritional observations. Proc. 1979 Minnesota Nutrition Conference: 51–64.

GROBBELAAR, W. P.: 1963. Responses of young maize plants to root temperatures. Mededelingen Landbouwhogeschool **63-5**, Agric. Univ. Wageningen, pp. 1–71.

GRZESIAK, S., S. B. ROOD, S. FREYMAN and D. J. MAJOR: 1981. Growth of corn seedlings: Effects of night temperature under optimum soil moisture or under drought conditions. Can. J. Plant Sci., **61**: 871–877.

HACKER, J. B. and D. J. MINSON: 1981. The digestibility of plant parts. Herbage Abstracts, **51**: 459–482.

HANWAY, J. J.: 1963. Growth stages of corn (*Zea mays* L.). Agron. J., **55**: 487–492.

HARTLEY, R. D.: 1981. Chemical constitution, properties and processing of lignocellulosic wastes in relation to nutritional quality for animals. Agric. Environm., **6**: 91–113.

HAY, R. E., E. B. EARLY and E. E. DETURK: 1953. Concentration and translocation of nitrogen compounds in the corn plant (*Zea mays*) during grain development. Plant Physiol., **28**: 606–621.

HERRERO, M. P. and R. R. JOHNSON: 1980. High temperature stress and pollen viability of maize. Crop Sci., **20**: 796–800.

HUNTER, R. B., M. TOLLENAAR and C. M. BREUER: 1977. Effects of photoperiod and temperature on vegetative and reproductive growth of a maize (*Zea mays*) hybrid. Can. J. Plant Sci., **57**: 1127–1133.

INGLE, J., D. BEITZ and R. H. HAGEMAN: 1965. Changes in composition during development and maturation of maize seeds. Plant Physiol., **40**: 835–839.

JOANNING, S. W., D. E. JOHNSON and B. P. BARRY: 1981. Nutrient digestibility depressions in corn silage-corn grain mixtures fed to steers. J. Anim. Sci., **53**: 1095–1103.

JOHNSON, D. R. and J. W. TANNER: 1972. Calculation of the rate and duration of grain filling in corn (*Zea mays* L.). Crop Sci., **12**: 485–486.

JONES, R. J., B. G. GENGENBACH and V. B. CARDWELL: 1981. Temperature effects on in vitro kernel development of maize. Crop Sci., **21**: 761–766.

JOVANOVIĆ, B. and Ż. JOVANOVIĆ: 1963. The effect of temperature and relative air humidity on corn fertilization. Review of research work at the Faculty of Agriculture, Univ. of Belgrade, Yugoslavia. Year 11 no. 355, pp. 1–11.

LUCAS, E. O.: 1981. Remobilization of stem assimilates in maize varieties grown under tropical conditions, Maydica, **26**: 287–292.

MERTENS, D. R.: 1977. Dietary fiber components: relationship to the rate and extent of ruminal digestion. Federation Proc., **36**: 187–192.

MERTENS, D. R. and P. J. VAN SOEST: 1972. Estimation of the maximum extent of digestion. J. Anim. Sci., **35**: 286 (Abstr.).

MINSON, D. J.: 1973. Effect of fertilizer nitrogen on digestibility and voluntary intake of *Chloris gayana*, *Digataria decumbens* and *Pennisetum clandestinum*. Austr. J. Exp. Agric. and Anim. Husbandry, **13**: 153–157.

MINSON, D. J.: 1976. Relation between digestibility and composition of feed. A review. In: Carbohydrate research in plants and animals. Misc. Papers nr. 12, Agric. Univ. Wageningen, pp. 101–114.

MINSON, D. J. and M. N. MCLEOD: 1970. The digestibility of temperate and tropical grasses. Proc. XI. Int. Grassl. Congress, Queensland, Australia, (ed.) M. J. T. NORMAN, pp. 719–722.

MONTGOMERY, F. G.: 1911. Correlation studies of corn. Nebr. agric. Exp. Stn ann. Rep., **24**: 108–159.
NELSON, C. J. and K. J. TREHARNE: 1973. Temperature adaptation in *Festuca arundinacea*. Report Welsh Breeding Station for 1973, University College of Wales, Aberystwyth, p. 11.
PAIN, B. F.: 1978. Nutritional requirements of forage maize. In: Forage maize. (eds) E. S. BUNTING, B. F. PAIN, R. H. PHIPPS, J. M. WILKINSON and R. E. GUNN, Agricultural Research Council, London, pp. 87–116.
PERRY, L. J. JR. and W. A. COMPTON: 1977. Serial measures of dry matter accumulation and forage quality of leaves, stalks and ears of three corn hybrids. Agron. J., **69**: 751–755.
PHIPPS, R. H. and R. F. WELLER: 1979. The development of plant components and their effects on the composition of fresh and ensiled forage maize. I. The accumulation of dry matter, chemical composition and nutritive value of fresh maize. J. agric. Sci., Camb., **92**: 471–483.
PITMAN, W. D., D. M. VIETOR and E. C. HOLT: 1981. Digestibility of kleingrass forage grown under moisture stress. Crop Sci., **21**: 951–953.
PRINS, R. A., W. C. CLINÉ-THEIL and A. TH. VAN 'T KLOOSTER: 1981. An in vitro procedure for the estimation of in vivo digestibility of roughage plant cell wall components in herbivores using mixed rumen microorganisms. Agric. Environm., **6**: 183–194.
RICHARDS, G. N.: 1976. Search for factors other than 'lignin-shielding' in protection of cell-wall polysaccharides from digestion in the rumen. In: Carbohydrate research in plants and animals. Misc. Papers nr. 12, Agric. Univ. Wageningen, pp. 129–135.
SMITH, L. W., H. K. GOERING and C. H. GORDON: 1972. Relationships of forage composition with rates of cell wall digestion and indigestibility of cell walls. J. Dairy Sci., **55**: 1140–1147.
SMITH, L. W., H. K. GOERING, D. R. WALDO and C. H. GORDON: 1971. In vitro digestion rate of forage cell wall components. J. Dairy Sci., **54**: 71–76.
SOFIELD, I., L. T. EVANS and I. F. WARDLAW: 1974. The effect of temperature and light on grain filling in wheat. In: Mechanisms of regulation of plant growth. Bull. Royal Soc. N.Z. **12**: 909–915.
SPIERTZ, J. H. J.: 1974. Grain growth and distribution of dry matter in the wheat plant as influenced by temperature, light energy and ear size. Neth. J. agric. Sci., **22**: 207–220.
SPIERTZ, J. H. J.: 1977. The influence of temperature and light intensity on grain growth in relation to the carbohydrate and nitrogen economy of the wheat plant. Neth. J. agric. Sci., **25**: 182–197.
STRUIK, P. C.: 1982a. Effect of a switch in photoperiod on the reproductive development of temperate hybrids of maize. Neth. J. agric. Sci., **30**: 69–83.
STRUIK, P. C.: 1982b. Production pattern, chemical composition and digestibility of forage maize (*Zea mays* L.). Mededeling no. **64**, Vakgroep Landbouwplantenteelt en Graslandkunde, Agric. Univ. Wageningen, pp. 1–28.
STRUIK, P. C. and B. DEINUM: 1982. Effects of light intensity after flowering on the productivity and quality of silage maize. Neth. J. agric. Sci., **30**: 297–316.
TOLLENAAR, M. and T. B. DAYNARD: 1978. Kernel growth and development at two positions on the ear of maize (*Zea mays*). Can. J. Plant Sci., **58**: 189–197.
TOLLENAAR, M., T. B. DAYNARD and R. B. HUNTER: 1979. Effect of temperature on rate of leaf appearance and flowering date in maize. Crop Sci., **19**: 363–366.
TOLLENAAR, M. and R. B. HUNTER: 1981. Quantification of the effects of temperature and photoperiod on maize development. Agronomy Abstracts 1981, Amer. Soc. of Agronomy, p. 14.
VAN SOEST, P. J.: 1965. Comparison of two different equations for the prediction of digestibility from cell contents, cell wall constituents and the lignin content of acid detergent fiber. Paper **118**, Ann. Meeting Amer. Dairy Sci. Ass., Lexington, Kentucky, 1965, pp. 1–7.
VAN SOEST, P. J.: 1967. Development of a comprehensive system of feed analyses and its application to forages. J. anim. Sci., **26**: 119–128.
VAN SOEST, P. J.: 1977. Modified procedure for determining plant cell wall by the neutral detergent procedure. Paper presented at the 69th Ann. Meeting Amer. Soc. of Animal Sci., Madison, Wisconsin, 1977.
VAN SOEST, P. J. and L. H. P. JONES: 1968. Effect of silica in forage upon digestibility. J. Dairy Sci., **51**: 1644–1648.

VAN SOEST, P. J., R. H. WINE and L. A. MOORE: 1966. Estimation of the true digestibility of forages by the in vitro digestion of cell walls. Proc. X Int. Grassl. Congress, Helsinki, Finland, (ed.) A.G.G. HILL, pp. 438–441.

VOS, J.: 1981. Effect of temperature and nitrogen supply on post floral growth of wheat; measurements and simulations. Centre for agricultural Publishing and Documentation PUDOC, Wageningen, pp. 1–164.

WALDO, D. R., L. W. SMITH and E. L. COX: 1972. Model of cellulose disappearance from the rumen. J. Dairy Sci., **55**: 125–129.

WHIGHAM, D. K. and D. G. WOOLLEY: 1974. Effect of leaf orientation, leaf area and plant densities on corn production. Agron. J., **66**: 482–486.

WIEGAND, C. L. and J. A. CUELLAR: 1981. Duration of grain filling and kernel weight of wheat as affected by temperature. Crop Sci., **21**: 95–101.

WILKINS, R. J.: 1969. The potential digestibility of cellulose in forage and faeces. J. agric. Sci., Camb., **73**: 57–64.

WILSON, J. R.: 1982. Environmental and nutritional factors affecting herbage quality. In: Nutritional limits to animal production from pastures. (ed.) J. B. HACKER. Farnham Royal, U.K., Commonwealth Agricultural Bureaux, pp. 111–131.

WILSON, J. R. and T. T. NG: 1975. Influence of water stress on parameters associated with herbage quality of *Panicum maximum* var. *trichoglume*. Austr. J. agric. Res., **26**: 127–136.

WILSON, J. R., A. O. TAYLOR and G. R. DOLBY: 1976. Temperature and atmospheric humidity effects on cell wall content and dry matter digestibility of some tropical and temperate grasses. N.Z. J. agric. Res., **19**: 41–46.