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THE EFFECTS OF SWITCHES IN PHOTOPERIOD ON CROP MORPHOLOGY, PRODUCTION PATTERN AND QUALITY OF FORAGE MAIZE (ZEA MAYS L.) UNDER FIELD CONDITIONS

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INTRODUCTION

Like all plants, maize consists of a variety of differentiated structures, each with its special form and function. These specialized organs and tissues are closely related via the distribution of photosynthates, nitrogenous compounds, nutrients and growth regulators. It is on these relations that the organization of the plant as a growing, developing and producing entity is based. The breeder and the grower, however, value certain plant parts more than others and will try to maximize their yield, even in the case of forage maize, where the whole plant is harvested.

The morphology of a forage-maize crop affects its quality as a roughage for ruminants. The digestibility of the plant parts varies greatly within a plant, because of differences in cell-wall content and in cell-wall digestibility (STRUIK, 1982a). The proportions of the various plant parts in the final crop can be affected by harvest date, cultural practice, genotype and climate, or can be artificially manipulated.

Effects stimulating the proportions of the most digestible parts of the plant in the organic matter will increase digestibility of the organic matter of the whole crop unless these stimulative effects simultaneously cause a decline in digestibility in other parts of the plant.

The most digestible part of the forage-maize plant is the kernel (BARNES et al., 1971; AERTS et al., 1978; WEAVER et al., 1978; HACKER and MINSON, 1981; STRUIK, 1982a). Numerous authors have reported that an increase in the proportion of grains or ears (grain + rachis) is accompanied by a decline in the digestibility of the non-ear parts (e.g. DEINUM and DIRVEN, 1971; DAYNARD and HUNTER, 1975; GALLAIS et al., 1976; PERRY and COMPTON, 1977; AERTS et al., 1978; WEAVER et al., 1978; PHIPPS and WELLER, 1979; GROSS and PESCHKE, 1980; HUNTER, 1981; STRUIK, 1982b). Continuous ageing of cell walls is one of the causes of this decline (STRUIK, 1982a). More important, however, is the fact that in most maize-growing regions part of the dry-matter accumulation in the grains is realized by the translocation of completely digestible cell solubles from vegetative parts to the ear. This material translocated includes minerals, nitrogenous compounds and carbohydrates (HANWAY, 1963; DAYNARD et al., 1969; BEAUCHAMP et al., 1976; STRUIK, 1982a, b); the intensity of the translocation greatly affects the final digestibility of the vegetative plant parts (STRUIK, 1982b; STRUIK and DEINUM, 1982).

The combined effects of cell-wall maturation, an increase in the proportion of ear in the crop and a decrease in stover quality mostly result in the whole-crop digestibility after grain set being approximately constant. The continuous de-

cline in quality that precedes flowering is halted in the case of maize. Because of the negative effect of grain filling on stover quality, it is questionable whether a high proportion of grain is needed to obtain a forage maize of good quality. Artificially preventing grain filling usually only induces slight decreases in whole-plant digestibility (CUMMINS and MCCULLOUGH, 1971; MARTEN and WES-TERBERG, 1972; BUNTING, 1975, 1976; DEINUM and KNOPPERS, 1979), although STRUIK (1982b) has reported larger decreases. PHIPPS et al. (1982) even reported a considerable increase in whole-plant digestibility, caused by the improbably low digestibility of the ear fraction (grains + rachis + husks) of the fertile crops. Complete removal of ear shoots before pollination causes considerable declines in crop digestibility (STRUIK, unpublished data).

Since plant organs are mutually interdependent, the rate of post-silking production may depend on the success of grain set. Barrenness, artificial sterility and ear removal reduce photosynthesis (Moss, 1962; RODE et al., 1979). BUNTING (1975, 1976), DEINUM and KNOPPERS (1979) and PHIPPS et al. (1982), however, reported that sterility hardly affected dry-matter yield in North-West Europe. In contrast, KIESSELBACH (1948) in Nebraska (U.S.A.), CAMPBELL (1964; Mississippi, U.S.A.), MARTEN and WESTERBERG (1972; Minnesota, U.S.A.) and STRUIK (1982b; Netherlands) found that the yield of sterile crops was considerably depressed. Removing the ears completely before pollination can depress yield by up to 50–60% (IREMIREN and MILBOURN, 1978; LESHEM and WERMKE, 1981; STRUIK, unpublished data). The repercussions of ear removal seem to be much greater than the repercussions of preventing grain set. In sterile plants that still bear intact husks, shanks and cobs, the storage capacity-though greatly reduced- is limited less than in plants whose ear shoots have been removed. The difference between the repercussions of removing the ears and of ear sterility is equivalent to the storage capacity of husks, shanks and cobs. Only when storage capacity in the stems, husks, shanks and cobs is insufficient (e.g. because of climate or weather conditions) grain filling is apparently required to maintain high productivity.

As well as the above-mentioned effects on digestibility, photosynthesis, production and storage capacity, grain filling has certain side effects:

- an increase in starch content. The starch content is important because starch tends to be inert during fermentation in the silage, in contrast with soluble carbohydrates, which are converted to organic acids (MCALLAN and PHIPPS, 1977).
- according to DEINUM and KNOPPERS (1979) more cell-wall material will be produced in the stover if grain filling is inhibited. The data obtained by KING et al. (1972), however, do not accord with this.
- the dry-matter content of a normal crop increases much faster than that of a grainless crop or that of a crop with a low proportion of the dry matter present in the ear. This effect of grain filling has been reported by BUNTING (1976), DEINUM and KNOPPERS (1979), PHIPPS et al. (1982), STRUIK and DEI-NUM (1982) and STRUIK (1983).
- leaf senescence may be affected by ear development; both delayed senescence

(MOSS, 1962) and advanced senescence (ALLISON and WEINMANN, 1970; CHRISTENSEN et al., 1981; THIAGARAJAH et al., 1981; STRUIK, unpublished data) may occur in sterile or earless crops. WILSON and ALLISON (1978) stated that an exceptionally large grain sink may cause the plant to die prematurely.

Removal of ears and prevention of pollination are rather drastic measures to take when investigating the effects of grain filling: these treatments are imposed at a physiological stage at which the plant is already fixed and 'programmed'. MCALLAN and PHIPPS (1977) and LESHEM and WERMKE (1981) used different plant densities to trace effects of grain filling and concluded that grain filling is not important for quality of the fresh crop. Other researchers (BEERE-POOT, 1981; DEINUM and BAKKER, 1981) have used genotypic variation to show that the proportion of ear in a crop is very positively correlated with crop digestibility, though it is not necessarily the most important factor. Earlier phytotron experiments done by the present author revealed that switches in photoperiod may alter vegetative and reproductive development after the duration of the vegetative phase has been fixed (STRUIK, 1982c). If these effects could be induced under field conditions, an elegant method would be available to measure the effects of crop structure on productivity, senescence, dry-matter content and digestibility. This report describes attempts to use this method.

MATERIALS AND METHODS

Background to the method

The method is based on the following physiological facts:

- 1. Initiation of the tassel (the terminal, staminate inflorescence) stops the initiation of leaf primordia.
- 2. Initiation of the ears (pistillate inflorescences) occurs some time after tassel initiation.
- 3. The photoperiodic requirements for the induction of the female inflorescence are greater than those of the male inflorescence. Ear *development* is also more sensitive to photoperiod than tassel development.
- 4. If the ear is made to lag behind the tassel more than normal during its early development, the gap between male and female flowering can widen greatly.
- 5. The rate at which the inflorescences develop partly determines the vegetative growth (e.g. stem elongation, leaf size) and the size of the reproductive organs.

Lengthening the photoperiod shortly after tassel initiation, but before the photoperiodic requirements of the ears have been completely fulfilled will induce the following reactions:

- 1. A short delay in anthesis but a pronounced delay in silking.
- 2. A considerable desynchronization of male and female flowering.
- 3. A larger leaf area.
- It is possible to produce these effects without affecting the number of leaves



FIG. 1. Schematic representation of the effects of a photoperiod switch on number of leaves, number of tassel branches, desynchronization and leaf area as a function of the physiological stage at which the switch occurs. A, B and C indicate the stages at which 4.5, 5.5 and 6.5 leaves are visible. SD = short day; LD = long day; (based on STRUIK, 1982c).

(and thus the number of stem internodes) (Fig. 1). As well as the characteristics shown in Fig. 1, plant height, size of the reproductive organs and number of tillers may also be affected.

Shortening the photoperiod after tassel initiation will accelerate the fulfilment of the photoperiodic requirements of the ears and will therefore reduce the gap between silking and anthesis and will reduce the size of vegetative and reproductive organs.

The longer the lengthened photoperiod, the larger the effects will be.

Method of lengthening photoperiod under field conditions and treatments

In 1980 and 1981, field experiments were done in which the photoperiod was lengthened by suspending strings of incandescent bulbs (60 W) about 2.25 m above the soil level. The incandescent bulbs were distributed equally over each net plot and were capped with aluminium to increase illuminance and to decrease light dispersal to neighbouring plots. The equipment was checked daily.

Net plots were separated by large borders both between and within blocks. The average illuminance at soil level of plots receiving a lengthened photoperiod was 75.1 lx in 1980 and 77.0 lx in 1981; 95% of the measurements were above 50 lx, corresponding to an irradiance in the waveband 400–700 nm of 0.2 W.m⁻². The average illuminance at soil level of plots without photoperiod supplement was 0.2 (1980) and 0.4 (1981) lx; illuminance in these plots never exceeded values of 2.5 1x (0.01 W.m⁻²), not even with considerable wind force. Saturation of the photosensitivity of maize is obtained at illuminances above 43–65 lx (FRANCIS et al., 1970; TESCHEMACHER, 1974; FAUNGFUPONG, 1975), while no photoperiod effects are observed with illuminance below 3 lx (FAUNGFUPONG, 1975).

In 1980 the photoperiods were switched at the 5.5-leaf stage; the photoperiod treatments were:

| code photoperiod before 5.5-leaf stage | | photoperiod from 5.5-leaf stage until end of ♀ flowering | |
|---|---------|---|--|
| n →n | natural | natural | |
| n → 20 | natural | 20 h | |
| n → 24 | natural | 24 h | |
| 20 → n | 20 h | natural | |
| 20 → 20 | 20 h | 20 h | |
| 24 → n | 24 h | natural | |
| 24 → 24 | 24 h | 24 h | |

The 20 h treatment was obtained by lengthening the photoperiod both before and after the basic light period (night phase from 23.45 h to 3.45 h). In this paper the emphasis will be on the results of treatments $n \rightarrow n$, $n \rightarrow 24$, $24 \rightarrow n$ and $24 \rightarrow 24$.

In the 1981 trial the photoperiods were switched at the 4.5-leaf stage and the 6.5-leaf stage. The following treatments were applied:

| code | photoperiod before 4.5-leaf stage | photoperiod from 4.5-leaf stage until 6.5-leaf stage | photoperiod from 6.5-leaf stage until end of ♀ flower- ing | |
|----------------|--------------------------------------|---|--|--|
| n → n | natural | natural | natural | |
| n → 24a | natural | 24 h | 24 h | |
| n → 24b | natural | natural | 24 h | |
| 24 → n | 24 h | 24 h | natural | |
| <u>24 → 24</u> | 24 h | 24 h | 24 h | |

Cultural practice and technical details

The soils were amply fertilized. Rows were 75 cm wide. Herbicide had to be applied before emergence because of the installation of the equipment to lengthen the photoperiod. For optimum weed control an extra mechanical treatment was necessary in both years.

If necessary, drought was prevented by sprinkling.

In 1981 emergence was disappointing. To obtain uniform stands the density was therefore reduced to 4.4 plants per m^2 .

The two experiments differed in year, treatments, location, choice of hybrid and density. Table 1 presents some general information about the methods.

Measurements of plant growth and development

Vegetative development

The data recorded weekly included number of visible leaves, number of green leaves and height of the plant. During early development these crop descriptions were done much more frequently (sometimes twice daily) to determine the exact date for the switch in photoperiod. At silking, the leaf area of the main shoot of 16 (1980) or 20 (1981) plants per treatment was estimated by multiplying the maximum length of each leaf by its maximum width by 0.75 (MONTGOMERY, 1911).

Shortly after flowering the number of leaves above the top ear was recorded for 16 (1980) or 20 (1981) plants per treatment.

The stem thickness of the main shoot was measured by estimating the maximum diameter in the centre of the second internode above the soil level. These observations were done after stem growth had ended and also involved 16 (1980) or 20 (1981) plants per treatment.

On each sampling date in 1981, the number of tillers per row harvested was also recorded.

Reproductive development

In 1980, the percentage of plants showing anther or silk extrusion was estimated every second day by observing 80 plants per treatment (i.e. 20 plants per plot). In 1981, 25 plants per plot (i.e. 100 per treatment) were screened daily

| Year | 1980 | 1981 |
|---|--------------------|----------------------|
| Location | Wageningen | Achterberg |
| Soil type | fine-textured clay | light and moist sand |
| Hybrid | LG 11 (FAO 260) | Nicco (FAO 300) |
| Final plant density (pl.m ⁻²) | 10.05 | 4.36 |
| Sowing date | 24 April | 24 April |
| Date of 50% emergence | 16 May | 12 May |
| First date of long-day treatment | 14 May | 7 May |

TABLE 1. Cultural practice and date of application of first photoperiod extension in 1980 and 1981.

during the main period and every second day at the start or at the end of the flowering period.

The number of tassel branches per plant was estimated on 20 plants per treatment in the 1981 experiment.

The length and number of kernels of the top ear were measured on 40 plants per treatment at the final sampling of both experiments. In 1981 maximum ear thickness was also measured.

The number of lower ears (i.e. all ears emerging from the axils of the leaves below the ear leaf of the main shoot) was measured on each sampling date. In 1981 the number of axillary ears (i.e. small ear shoots developed from the reproductive axillary buds in the axils of the husks of the top ear and large enough to extrude from the husks) was also recorded.

Plot size and sampling technique

The plots occupied an area of $10 \times 9 \text{ m}^2$ (1980) or $10 \times 7.5 \text{ m}^2$ (1981) with two border rows on either side of the plot and one row separating the rows intended for sampling. One extra net row was available for possible additional observations at final sampling. Both experiments were laid down as a completely randomized block design with four replicates. The plots were sampled 23 days after midsilk of the control (approximately at the onset of the rapid dry-matter accumulation in the kernels) and twice thereafter. In 1980 the dry-matter yields at the 5.5-leaf stage were estimated as well.

One row 6 m long (4.5 m^2) was harvested. The plants were cut off at soil level, counted and stored in a cold chamber during further processing. The plants were separated into stover (stem + leaves + tassel), husk + shank, top ear and lower ears. In 1981, tillers were treated as the fifth fraction. After recording the fresh weight, the fractions were chopped. Husk + shank and stover were chopped with a stationary 1-row FAHR MH 70 chopper. The chopped material was transported directly into an operating concrete mixer by means of a jet of air and a conveyor belt. Subsamples were taken from the stream of material while emptying the mixer. Top ears, lower ears and tillers were chopped with a vegetable cutter.

Subsamples were dried to constant weight in forced ventilated ovens at a maximum temperature of 70 °C.

After dry weighing, samples were bulked per plant part and per treatment, ground in hammer mills with sieves of 1 mm and subsampled again.

Chemical analyses

Although an extensive chemical analysis was carried out, only the results of the in vitro digestibility and cell-wall analysis will be presented, since these two criteria adequately describe quality dynamics. True digestibility in vitro of organic matter (D_{true}) was estimated according to the method of VAN SOEST et al. (1966). A series of standard maize samples of known in vivo digestibility for sheep, analysed in each run, made it possible to convert the data to apparent digestibility (D_{om}). The cell-wall content of dry matter (after dissolving the

starch) was estimated using the method described by VAN SOEST (1977). Cell-wall digestibility (D_{cwc}) was calculated from true digestibility (D_{true}), cell-wall content (cwc%) and ash content (ash%) by means of the formula

$$D_{cwc} = 100 - \frac{(100 - D_{true}) \times (100 - ash_{o})}{cwc_{o}^{o}}$$

RESULTS AND DISCUSSION

1. Climatic data

Table 2 shows the mean temperature, amounts of radiation and precipitation for 1980 and 1981 at Wageningen. The most relevant differences in weather between these two years were:

- a. May 1980 was cold, but sunny and dry; in contrast May 1981 was much warmer, with sufficient precipitation but less irradiance.
- b. July was cool and extremely wet in 1980, especially in the first three weeks.
- c. The period between 10% and 90% silking was much warmer in 1980 (mean temperature 19.6°C) than in 1981 (mean temperature 15.4°C).

These climatic patterns affected the way that the physiological effects induced

| Month | | Average temperature (°C) | | Solar irradiance (MJ.m ⁻²) | | Rainfall (mm) | |
|-----------|------|--------------------------|------|--|------|---------------|---------------------|
| | Year | 1980 | 1981 | 1980 | 1981 | 1980 | 1981 |
| Мау | | 12.0 | 13.4 | 649 | 496 | 9.3 | 64.3 |
| June | | 14.8 | 14.4 | 488 | 419 | 66.5 | 64.3 |
| July | | 15.6 | 16.3 | 425 | 441 | 145.7 | 49.4 |
| August | | 16.9 | 16.5 | 422 | 406 | 46.4 | 19.8 ¹) |
| September | | 15.2 | 14.7 | 333 | 311 | 27.4 | 57.91 |
| October | | 8.7 | 8.8 | ? | 144 | 67.4 | 137.2 |

TABLE 2. Climatic data for Wageningen for 1980 and 1981.

1) Drought prevented by sprinkling.

TABLE 3. Time required to reach specific developmental stages, expressed in days after sowing (24 April in 1980 and 1981).

| | 1980 | 1981 |
|--------------------------------|------|------|
| 50% emergence | 22 | 19 |
| 4.5-leaf stage | 38 | 31* |
| 5.5-leaf stage | 43* | 35 |
| 6.5-leaf stage | 48 | 39* |
| 50% & flowering ¹) | 102 | 91 |
| 50% ♀ flowering ¹) | 100 | 92 |

1) of the control.

* time of change in photoperiod in some treatments.

by manipulating the photoperiod were manifested. The cool weather during early growth in 1980 delayed development and consequently the time of the photoperiod switch was later (Table 3). Therefore in 1980 the switch was done at a time when natural daylength was somewhat longer than in 1981. As well, dense cloud cover around the time of sunrise and sunset may shorten natural daylength considerably (FRANCIS, 1970). In 1980 the amounts of irradiance and the relative duration of sunshine during May and June were much higher than in 1981. The data on hourly recorded light intensity also suggest that photoperiods were longer in 1980. It must therefore be concluded that lengthening the photoperiod was less effective in 1980. Cool weather during the pre-silking period decreases apical dominance and will thus limit the effects of photoperiod on desynchronization (STRUIK, 1982c). Low temperatures also cause protandry to revert to protogyny (Table 3; cf. STRUIK, 1982c). High temperatures during the flowering period shorten the anthesis-to-silking interval of each individual plant and will therefore reduce the effects of photoperiod treatments.

2. Vegetative development

2.1. Leaf appearance

The rate of leaf appearance was not affected by photoperiod. This agrees with data presented by BROUWER et al. (1973), GMELIG MEYLING (1973) and HUNTER et al. (1977). Because of differences in the duration of leaf initiation, the numbers of leaves ultimately produced per plant differed (Table 4). The data fitted in the expected pattern shown in Fig. 1. Only the photoperiods before the photoperiod switch influenced the number of leaves, except in the case of treatment $n \rightarrow 24a$, where the switch took place at the 4.5-leaf stage.

However, the differences between the number of leaves in the different treatments were small in both years.

2.2. Plant height and stem diameter

Photoperiod affects plant height by affecting the number of internodes and internode length (AITKEN, 1980; STRUIK, 1982c). Differences in plant height arose when differences in leaf number became apparent. Final plant heights are listed in Table 4 together with the mean internode length (estimated by dividing final plant height by final number of leaves) and stem diameter.

In 1980, the photoperiod before the switch affected plant height by means of its effect on the number of phytomeres. The photoperiod after the 5.5-leaf stage affected plant height through its effect on internode length, sometimes at the expense of the radial growth of the stem. Internode elongation correlated significantly with the anthesis-to-silking interval (simple linear correlation coefficient r = 0.899, P<0.01) mentioned below. In 1981, differences were smaller than in 1980, and the internodes of plants grown under long days elongated less than in 1980. The linear correlation between desynchronization and internode elongation was again significant (r = 0.936, P<0.05). Stem thickness was not affected in this experiment. Since the correlation between elongation and

desynchronization was significant in both years and since photoperiod itself is not the only factor determining internode elongation, these two correlated phenomena might have a common physiological basis. Perhaps the size of the tassel influences its production of auxins and gibberellins; these growth regulators are necessary for the suppression of axillary buds, cell elongation and cell division (cf. MESSIAEN, 1963; STRUIK, 1982c). The production of these growth regulators is probably not only affected by the duration of the light phase but also by the quality and intensity of the light during the extension of the photoperiod.

2.3. Leaf area and leaf senescence

Leaf area increases with longer photoperiods, not only because more leaves are produced but also because the individual leaves are larger (AITKEN, 1980; HUNTER, 1980; STRUIK, 1982c; see also Fig. 1). Leaf areas at silking are listed in Table 4. Data of individual plants suggest that $20 \rightarrow 20$ and $24 \rightarrow 24$ (1980) were somewhat underestimated. Otherwise the data agree with the trends anticipated in Fig. 1. Differences in light interception were not large enough to induce significant differences in dry-matter production.

The number of dead leaves in all photoperiod treatments showed a similar development over time. In 1980, however, $24 \rightarrow n$ tended to senesce faster.

2.4. Other data on vegetative development

The number of above-car leaves in 1980 was independent of photoperiod treatment. Thus, differences in final number of leaves were caused by differences in the number of leaves below the top ear. The ratio of leaf area above the ear to total leaf area was therefore smaller in treatments receiving longer photoperiods before the switch, especially when a long-day treatment was followed by a short-day treatment.

In the 1981 experiment, both the number of leaves below the ear and the number of leaves above the ear differed between treatments, resulting in relatively more leaf area above the ear in $n \rightarrow 24a$ and $n \rightarrow 24b$ than in the other treatments. These differences in distribution of leaf area might induce differences in dry-matter distribution.

The number of tillers will be discussed in section 3.2, together with other phenomena related to apical dominance.

Résumé:

The data on vegetative development agreed with those presented in an earlier paper (STRUIK, 1982c). Differences between the treatments in these field experiments, however, were small. The main differences were in leaf area per plant and in plant height.

| Treatment | Mean number of leaves/pl | Mean plant height (cm) | Mean internode length (cm)† | Mean stem diameter (cm) | Mean leaf area/pl (dm²) |
|-----------------------|--------------------------------|------------------------------|-----------------------------------|-------------------------------|-------------------------------|
| | | 19 |) 80 | | |
| $n \rightarrow n$ | 14.1 a§ | 195 a | 13.8 | 2.43 b | 35.7 ab |
| $n \rightarrow 20$ | 14.0 a | 207 ab | 14.8 | 2.22 ab | 38.9 ab |
| $n \rightarrow 24$ | 14.2 a | 221 bc | 15.5 | 2.02 a | 41.6 b |
| 20 → n | 14.5 ab | 207 ab | 14.3 | 2.21 ab | 36.5 ab |
| 20 → 20 | 14.5 ab | 204 ab | 14.0 | 2.12 ab | 35.2 a |
| 24 → n | 15.1 b | 213 abc | 14.1 | 2.10 ab | 38.3 ab |
| 24 → 24 | 15.2 b | 231 c | 15.2 | 2.32 ab | 39.9 ab |
| | | 19 | 981 | | |
| n → n | 15.1 ab | 212 a | 14.0 | 3.21 | 65.3 a |
| n → 24a | 15.6 bc | 224 b | 14.3 | 3.43 | 70.1 ab |
| n → 24b | 14.9 a | 222 b | 14.9 | 3.30 | 71.0 abc |
| 24 → n | 16.3 d | 219 ab | 13.4 | 3.31 | 71.7 bc |
| <u>24 → 24</u> | 16.2 cd | 226 b | 13.9 | 3.31 | 76.2 c |

TABLE 4. Data on vegetative development of all treatments in both experiments.

† Statistical analysis is not possible for this parameter.

§ Means with a letter in common are not significantly different at the 0.05 probability level, according to Tukey's studentized range test.

3. Reproductive development

3.1. Flowering dates and desynchronization

Fig. 2 illustrates the development over time of the proportion of plants showing pollen shed and silk extrusion for the $n \rightarrow n$ treatments of both experiments. The way of estimating desynchronization (i.e. number of days required to reach 50% silking minus number of days required to reach 50% pollen shed) is also illustrated.

Estimates of 50% flowering dates and desynchronization values are presented in Table 5. To simplify the discussion, the desynchronization data have been modified by subtracting the desynchronization value of the control. In this way the direct effect of temperature on desynchronization is neutralized.

The flowering dates differed in the same way in 1980 and in 1981. However, in 1981 the differences were much more pronounced. Long days before and after the photoperiod switch retarded both pollen shed and silking. However, the photoperiod before tassel initiation affected anthesis more than silking, whereas the opposite was true for photoperiod after tassel initiation. Each treatment therefore showed a characteristic desynchronization value.

Long photoperiods during the entire growing season increase the desynchronization because silking is delayed more than anthesis. This has already been



FIG. 2. Course of proportion of flowering plants in untreated plots of both experiments. *a* indicates the desynchronization (Q-d).

reported by FAUNGFUPONG (1975), BLONDON and GALLAIS (1976), AITKEN (1980), STRUIK (1982c) and other researchers (see also Fig. 1). Although the difference between $n \rightarrow n$ and $24 \rightarrow 24$ was similar in both years, Nicco seems to react more sharply to photoperiod switches than LG 11, certainly if the later stage of the switch is taken into account.

Again, the differences between treatments were rather small but agreed with expectations based on phytotron experiments. Similar effects resulting from photoperiod switches were also obtained by FAUNGFUPONG (1975).

In all cases desynchronization was too short to affect the extent of pollination.

| | 50% anthesis (days after sowing) | 50% silking (days after sowing) | Desynchroni- zation (days) | Modified ¹) desynchroni- zation (days) |
|---------------------|--|---------------------------------------|----------------------------------|--|
| | | 1 | 980 | |
| n → n | 103 | 100 | -2.2 | 0 |
| $n \rightarrow 20$ | 103 | 101 | -1.6 | +0.6 |
| $n \rightarrow 24$ | 103 | 102 | -0.7 | +1.5 |
| $20 \rightarrow n$ | 103 | 100 | -2.4 | -0.2 |
| $20 \rightarrow 20$ | 103 | 101 | 1.8 | +0.4 |
| 24 → n | 103 | 100 | -2.2 | +0.0 |
| 24 → 24 | 104 | 103 | -1.1 | +1.1 |
| | | 1 | 981 | |
| n → n | 91 | 92 | +0.7 | 0 |
| n → 24a | 95 | 97 | +2.8 | +2.1 |
| $n \rightarrow 24b$ | 93 | 97 | +3.4 | + 2.7 |
| 24 → n | 94 | 93 | -1.0 | -1.7 |
| 24 → 24 | 95 | 96 | +1.5 | +0.8 |

Table 5. Number of days after sowing required to reach 50% anthesis and 50% silking (rounded off), together with the estimated desynchronization between Q and d flowering before and after modification¹).

1) See text for explanation.

3.2. Size of the reproductive organs

Table 6 gives data on number of tassel branches, ear sizes and number of kernels.

The data on number of tassel branches agree with Fig. 1 and are comparable with data on number of leaves. They indicate that tassel-branch initiation was complete at the 6.5-leaf stage. In these experiments, tassel initiation apparently occurred at a much earlier physiological stage than has been reported for genotypes most frequently used in American and Canadian research.

Ear elongation was affected by photoperiod after ear initiation but was almost independent of photoperiod before ear initiation. Although not significantly different, ear width correlated negatively with ear length (r = -0.964, P < 0.01) in 1981.

The way ear elongation reacted to a switch in photoperiod was similar to the reaction of internode elongation.

The number of kernels on the top ear was significantly affected by treatments in 1981 but not (at P < 0.05) in 1980, although the trend was the same. An increase in the number of kernel primordia resulting from a longer photoperiod has also been reported by RAGLAND et al. (1966), HUNTER et al. (1977) and HUNTER (1980).

| TABLE 6. | Size of | the re | productive | organs. |
|----------|---------|--------|------------|---------|
|----------|---------|--------|------------|---------|

| | Number of primary tassel branches per plant | Number of secondary tassel branches per plant | Mean length of top ear (cm) | Mean maximum width top ear (cm) | Mean number of kernels on top ear |
|---------------------|--|--|-----------------------------------|---------------------------------------|---|
| | | 19 | 30 | | |
| n → n | -1) | - | 14.6 a ²) | _ | 411 |
| n → 20 | _ | - | 15.3 ab | - | 417 |
| $n \rightarrow 24$ | | - | 15.8 Б | - | 438 |
| 20 → n | _ | _ | 14.4 a | - | 406 |
| $20 \rightarrow 20$ | - | - | 15.1 ab | - | 418 |
| 24 → n | _ | _ | 15.1 ab | _ | 415 |
| $24 \rightarrow 24$ | - | _ | 16.0 b | - | 444 |
| | | 19 | 81 | | |
| $n \rightarrow n$ | 11.9 ab | 1.8 ab | 18.4 a | 5.60 | 422 ab |
| n → 24a | 13.8 bc | 1.4 ab | 20.3 b | 5.45 | 439 Ъс |
| n → 24b | 11.5 a | 1.1 a | 20.0 b | 5.52 | 435 abc |
| 24 → n | 13.9 bc | 2.0 ab | 18.2 a | 5.62 | 398 a |
| 24 → 24 | 14.1 c | 2.2 Ь | 19.9 b | 5.48 | 460 c |

 $^{1}) - =$ not estimated.

²) Means with a letter in common are not significantly different at the 0.05 level of probability (Tukey's range test).

Both the rate of floret initiation (ALLISON and DAYNARD, 1979) and the rate of leaf appearance are independent of photoperiod. The number of visible kernels therefore reflects the duration of floret initiation and the number of leaves reflects the duration of leaf initiation and also the duration of the period before tassel emergence. Thus, dividing the final number of visible kernels by the final number of leaves gives an estimate of the duration of ear-shoot development relative to the duration of vegetative development. These estimates correlated significantly with desynchronization both in 1980 (r = 0.825, P < 0.05) and in 1981 (r = 0.879, P < 0.05). Desynchronization gives an estimate of the final gap between ear development and tassel development irrespective of differences in the time at which both inflorescences were initiated. The significance of the correlations between desynchronization and duration of ear development suggests that the time lag between tassel initiation and ear initiation was fairly constant. Ear development was the most sensitive to the photoperiod switch.

There are three types of shoot in the maize plant: main shoots terminated by a tassel, ear shoots terminated by ears, and tillers terminated bij an inflorescence that is usually hermaphroditic. The apical dominance of the main shoot over the other shoots can be assessed by the number of lower ears and the number of tillers. Apical dominance within the ear shoot can be assessed by the number of axillary ears. Table 7 lists the results for the main treatments. Trends were the same for all parameters: apical dominance was greatest for $n \rightarrow 24$ treatments and least for $24 \rightarrow n$ treatments.

| 1980 | Number of lower ears per m ² | 1981 | Number of tillers (m ⁻²) | Number of lower ears (m ⁻²) | Number of axillary ears (m ⁻²) |
|---------|---|--|--|---|--|
| n → n | 10.8 ab† | n → n | 3.1 | 6.9 b | 0.8 ab |
| n → 24 | 8.6 a | n → 24a | 2.7 | 5.8 a | 0.6 a |
| 24 → n | 12.9 b | n → 24b | 2.9 | 6.0 a | 0.2 a |
| 24 → 24 | 9.2 a | $\begin{array}{l} 24 \rightarrow n \\ 24 \rightarrow 24 \end{array}$ | 3.3 3.1 | 8.2 с 6.8 b | 1.8 с 1.4 bc |

TABLE 7. Number of tillers, lower ears and axillary ears, indicating the extent of apical dominance.

[†] Means with a letter in common are not significantly different at the 0.05 probability level (Tukey's range test).

Résumé:

In relation to the control, $n \rightarrow 24$ showed more pronounced vegetative growth (taller plants, larger leaf area) and delayed ear development (suppression of ear shoots) but nevertheless had large ears.

 $24 \rightarrow n$ showed less pronounced vegetative growth than $24 \rightarrow 24$ (shorter plants, smaller leaf area), and advanced ear development but, ultimately, had small ears.

4. Dry-matter production

In sections 4, 5 and 6, the consequences of the differences in development on production, dry-matter content and quality are presented and discussed.

4.1. Ear yield and proportion of ear in the dry matter

Ear yields were significantly different between treatments at 23 days after midsilk of the control in 1980 and at 23 and 51 days after midsilk of the control in 1981. Treatments with short days after the photoperiod switch $(n \rightarrow n \text{ and }$ $24 \rightarrow n$) yielded more on the same date than $n \rightarrow 24$ or $24 \rightarrow 24$ treatments (Fig. 3). These differences were at least partly caused by differences in the onset of the linear dry-matter accumulation in the kernels: they decreased during the latter part of the growing season, especially in 1981, when ear maturity was probably more advanced. Parallel sigmoid curves can be drawn through the ear yields recorded for each treatment. These hypothetical curves explain the development over time of the differences in ear yield between treatments in both years. The distances between these curves, however, do not always correspond with the differences in flowering dates. Since dry-matter content and ear size were different, it is reasonable to expect that ear yields at physiological maturity in treatments with long days after tassel initiation would be higher, at least in the 1981 experiment, because the duration of ear filling was longer. FAUNGFU-PONG (1975) reported dramatic reductions in grain yield as a consequence of night lighting started shortly after planting (compare with treatment $24 \rightarrow 24$). At least some of this reduction was caused by increased barrenness and by a delay in flowering. However, HUNTER (1980) found that a long photoperiod before tassel initiation had significant positive effects on ear yield. The ear yields

of the long-day treatments were higher because there were more kernels and because the kernels were heavier. HUNTER actually compared the photoperiod switches short day \rightarrow intermediate day and long day \rightarrow intermediate day (comparable with treatments $n \rightarrow 24$ and $24 \rightarrow n$). Since in his experiments the switch occurred late (probably long after stage C in Fig. 1), the results would have been similar if continuously short and continuously long photoperiods had been applied.

RAGLAND et al. (1966) conducted experiments in which night lighting was applied to crops sown on different dates. For the April sowing the night lighting started 11 days after emergence (comparable with treatment $n \rightarrow 24a$) and for the June sowing the photoperiod treatment started before emergence (comparable with treatment $24 \rightarrow 24$). In both sowings a significant reduction in grain yield was observed as a result of the lengthening of the photoperiod. The effect was greater in the later sowing and was caused by an increased number of aborted kernels and a lower 1000-kernel weight. The results described in the present paper tend to agree with HUNTER's (1980) findings but disagree with those of FAUNGFUPONG (1975) and of RAGLAND et al. (1966). HUNTER et al. (1977), however, found a significant interaction between photoperiod and temperature under phytotron conditions which was expressed in the length of the grain-filling period, the kernel number and the grain yield. BREUER et al. (1976) reported that there was an interaction between photoperiod and temperature that affected the duration of grain filling. Both reports suggest that lengthening the photoperiod causes a reduction in grain yield at high temperatures but an increase in grain yield at low temperatures. Light conditions and the length of the frost-free period also determine whether crops grown under long photoperiods are able to profit from the potentially larger sink. As well as climatic differences, genotypic differences might also be responsible for some of the abovementioned discrepancies.

KIM et al. (1976) and SCHEFFER (1978) reported reductions in grain yield when plant development was accelerated by shortening the photoperiod during early stages of growth. These researchers compared the photoperiod sequence natural \rightarrow short day \rightarrow natural with continuously natural photoperiods. (Note: natural daylength thus represents the long photoperiod.) These treatments are not exactly comparable with treatments used in our experiments, because the timing and duration of the short-day treatment determine which of the two switches will dominate. Since both papers report an acceleration of plant development it is probable that the comparison made in the trials done by KIM et al. and SCHEFFER is equivalent to the comparison between treatments 24 \rightarrow n and 24 \rightarrow 24 in the present study. If so, the results presented in this paper agree with the results obtained by KIM et al. (1976) and SCHEFFER (1978).

SCHEFFER (1982a, b) applied different photoperiod treatments by sowing maize in a glasshouse on different dates with and without artificial lengthening of the photoperiod before transplantation into the field. The effects observed, however, are probably strongly confounded with the effects of light intensity, growing-point temperature and other uncontrolled environmental factors.



FIG. 3. Development over time of ear yield and of the proportion of dry matter in the main shoot that is contained in the ear, for main treatments of both experiments.

These results are therefore not discussed in this paper.

The proportion of dry matter in the main shoot that was accounted for by the ears remained significantly different during the entire grain-filling period in 1980 (P<0.01; Fig. 3) but in 1981 the differences vanished as the grain filling progressed. The relevance of the differences between treatments in proportion of ear will be discussed in conjunction with quality parameters (see section 6).

The yields of husks + shanks were always similar for all treatments. The maximum differences were 100 kg.ha⁻¹ (1980) and 150 kg.ha⁻¹ (1981) at final sampling.

4.2. Stover and tiller yield; whole-crop yield

Although the effects of photoperiod treatment on stover yield were never significant on any sampling date, differences between treatments in 1980 were consistent and in agreement with expectations. On all sampling dates (except for the one at the 5.5-leaf stage) the control crop showed the lowest stover yields. Lengthening the photoperiod stimulated stover yield whether it was done before or after the switch. This means that delaying ear initiation and delaying ear development both stimulate the production of vegetative parts. Long days after the 5.5-leaf stage, however, produced a consistently greater effect than long days before this stage, resulting in the yield sequence $n \rightarrow n < 24 \rightarrow n < n \rightarrow 24 < 24 \rightarrow 24$. Even the intermediate treatments $n \rightarrow 20$, $20 \rightarrow n$ and $20 \rightarrow 20$ fitted the pattern quite well.

In 1981 the same tendency was apparent 23 days after midsilk of the control. As was the case for differences in ear yield, differences in stover yield vanished during grain filling. The control, however, always gave the lowest stover yield.

No clear trends were observed for tiller yield in 1981; the variation coefficients were too high.

Table 8 gives the whole-crop yields at final sampling. Yields were somewhat higher in 1981 than in 1980: the favourable weather in May and the genotypic differences compensated for the loss that was expected to result from the low plant density in 1981. Photoperiod treatments did not significantly affect whole crop dry-matter yield. In 1981 the amount of dry matter in the main shoot (i.e. whole crop minus tiller) produced after the first sampling (17 August) correlated significantly with the silking date (r = 0.965; P < 0.01) and not with maximum leaf area or leaf-area duration. In this particular experiment, later silking was accompanied by a larger dry-matter production after silking.

It is striking that the reaction of Nicco in 1981 shown by leaf area, reproductive development and dry-matter production was more pronounced than the reaction of LG 11 in 1981. Conversely differences in stem growth and dry-matter distribution were more pronounced in LG 11 in 1980 than in Nicco in 1981. Differences in climatic conditions, location, plant density and genotype probably all contributed to this discrepancy.

Although the rate of development of the main shoot was almost the same, comparing the dry-matter production and dry-matter distribution of treatment $n \rightarrow 24$ with the control is like comparing a late hybrid and an early hybrid. In contrast, $24 \rightarrow n$ shows the characteristics of an early genotype by comparison with $24 \rightarrow 24$.

Résumé:

Although crop development was affected by photoperiod switches, the effects were too small to produce relevant differences in yield. The proportion of dry matter in the ears was considerably affected, making it possible to analyse to what extent ear proportion in itself affected the digestibility of the whole crop.

5. Dry-matter content

The proportions of dry matter in fresh material ('dry-matter content') are listed in Table 8 for certain fractions at final sampling. The dry-matter content of top ear, husk + shank and of the whole crop was significantly different at all samplings in both experiments. In all cases trends were similar: dry-matter content was approximately the same for $n \rightarrow n$ and $24 \rightarrow n$ and much higher than for $n \rightarrow 24$ and $24 \rightarrow 24$.

There were no clear differences in the dry-matter content of stover, or lower ears, or tillers, although the trends were often the same as those in the top ear, husk + shank and whole crop in 1981 (Table 8). Whole crop dry-matter content was calculated from the dry-matter content of the individual fractions and their proportions of fresh matter. During the grain-filling period the dry-matter content and the ear proportion both increase very rapidly; the proportion of husk + shank is small and the dry-matter content in the stover increases only slightly before complete senescence or frost damage. In these trials therefore, the drymatter content of the whole crop was mainly determined by the proportion of ear in the fresh material and its dry-matter content (see Fig. 4). Any differences between treatments in the proportion of ears decreased during grain filling, whereas differences in the dry-matter content of the ears did not alter very much. Differences in the dry-matter content of the whole crop increased during the post-silking period because the fraction that exhibited the greatest differences

| | Dry-matter yield (Mg.ha ⁻¹) | Proportion of dry matter in fresh material $(%)$ | | | |
|--------------------|--|--|--------------|---------|--------------------------------|
| | wholecrop | stover | husk + shank | top ear | whole plant (incl. tillers) |
| | | | 980 | | |
| $n \rightarrow n$ | 14.36 | 18.5 | 24.7 | 51.3 | 29.3 |
| $n \rightarrow 24$ | 14.79 | 18.7 | 23.0 | 47.9 | 27.3 |
| 24 → n | 15.03 | 19.3 | 24.7 | 51.4 | 29.6 |
| 24 → 24 | 14.47 | 18.5 | 21.9 | 47.0 | 26.7 |
| Р | ns* | ns | 0.051 | 0.011 | 0.005 |
| | | 19 | 81 | | |
| n → n | 15.29 | 20.2 | 27.1 | 55.9 | 31.3 |
| n → 24a | 15.21 | 18.2 | 24.5 | 53.7 | 28.7 |
| n → 24b | 15.93 | 18.3 | 23.4 | 53.8 | 28.8 |
| 24 → n | 15.45 | 19.5 | 27.9 | 55.5 | 30.6 |
| 24 → 24 | 15.39 | 18.9 | 24.2 | 53.6 | 29.1 |
| Р | ns | ns | 0.013 | 0.004 | 0.039 |

TABLE 8. Whole-crop yield and dry-matter content of stover, hus + shank, top ear and whole crop at final sampling.

* ns = not significant.



FIG. 4. Development over time of dry-matter content of the whole crop (---) and of the top ear (----) together with the proportion of whole crop fresh material that is accounted for by the ears (...).

between treatments (i.e. the ear) became increasingly important. Since ear drymatter content correlated with silking date, the dry-matter content of the whole crop also closely correlated with silking date. The linear correlation coefficients at final sampling were -0.943 (P<0.01; n = 7) and -0.998 (P<0.01; n = 5) for 1980 and 1981, respectively.

Thus the rate of the ear development and not the rate of development of the main shoot determined the course of the dry-matter content of the whole crop. At final sampling the dry-matter content of the whole crop decreased by 1.1% (1980) or 0.5% (1981) for every day the silking was delayed. These high regression coefficients emphasize the relevance of good ear development for the maturation of maize as a forage crop.

Résumé:

The dry-matter content of the whole crop was mainly affected by the dry-matter content of the ear and the proportion of ear in the fresh material. Dry-matter content was closely correlated with silking date.

6. Cell-wall content and in vitro digestibility

A plant is composed of cell walls and cell contents. Cell contents are almost completely digestible for ruminants but cell walls are only digestible to a certainvariable-extent. The digestibility of a forage-maize crop as roughage for ruminants is therefore determined by the cell-wall content and the digestibility of the cell walls. Vegetative parts contain a considerable amount of poorly digestible cell-wall constituents. By contrast, ear parts are mainly composed of cell contents and highly digestible cell walls.

Since whole-crop yields were fairly constant and dry-matter distribution was variable, the cell-wall content, cell-wall yield, cell-wall digestibility and in vitro digestibility of organic matter may vary. Table 9 presents the data from the most relevant treatments and fractions at final sampling.

The cell-wall yield at first post-anthesis sampling (23 days after midsilk of the control) showed only a small variation between treatments. The amounts of cell wall in the stover, however, were much greater if long days were applied after tassel initiation. In both years these differences were still present at final sampling (Table 9), although in 1980 the 20 h treatments did not conform to the pattern very well: at first the smaller amounts of cell wall in the stover were compensated for by larger amounts of cell wall present in the ear parts. At the first sampling after silking the ears in treatments $n \rightarrow n$ and $24 \rightarrow n$ were more developed. Final ear size was stimulated by a photoperiod-induced deceleration of ear development, resulting in considerably high cell-wall production during September and high yields of cell wall in the ear (Table 9). No important differences were induced in cell-wall formation in husks + shanks. The combined effects of photoperiod treatment on cell-wall formation in different plant fractions resulted in final cell-wall yields of the whole crop shown in Table 9. Wholecrop data of the 1981 experiment were somewhat distorted by tiller development. Therefore data for the crops without tillers are given. Total cell-wall yield was affected by the extent of vegetative development, delay of reproductive development and ear size.

The effects of photoperiod switches on the cell-wall content in the stover were much greater in 1981 than in 1980, but cell-wall content in the ear differed considerably in both experiments because of differences in physiological stage and shelling percentage. In the 1981 experiment the cell-wall content of the top ear of $24 \rightarrow 24$ was lower than expected on the basis of data from other treatments and earlier samplings. Because of these effects on cell-wall content of the top ear and because of the effects of photoperiod mentioned above on the proportion of the ear, the cell-wall content of the whole crop showed clear differences between treatments, especially in the 1980 experiment. In this experiment, the cell-

wall content of the whole crop correlated significantly with silking date (P < 0.05).

Estimates of cell-wall digestibility are more inaccurate than estimates of cellwall content or organic-matter digestibility, especially in ear samples where the cell-wall residue after in vitro digestion is only small. Differences in cell-wall digestibility were small and inconsistent; whole crop cell-wall digestibility at final sampling should therefore be regarded as being unaffected by photoperiod treatments. Thus the continuous decrease in cell-wall digestibility was similarly not affected by the physiological stage of the crop. Photoperiod treatments seemed to have disturbed the synchronization between crop maturity and cell-wall maturation.

In vitro digestibility of the fractions differed only slightly in both experiments (Table 9). Differences in whole-crop digestibility therefore depended mainly on differences in the proportions of the different fractions in the organic matter. Only in the 1980 experiment did these proportions still differ at final sampling.

Résumé:

Long days before and after tassel initiation stimulated cell-wall formation in vegetative parts. Long days after tassel initiation stimulated cell-well formation in the ears. Both cell-wall yield and cell-wall content were therefore affected by photoperiod treatment. The consequences of this on whole-crop digestibility were small.

OVERVIEW

The reaction of the plants to photoperiod switches, as expressed in the number of leaves, number of tassel branches, desynchronization and leaf area was as postulated in Fig. 1.

| TABLE 9. Cell-wall yield (cwc yield), cell-wall content (cwc%), cell-wall digestibility (D_{cwc}) and in v | itro digestibility |
|--|--------------------|
| of organic matter (Dom) of stover, top ear and whole crop, excluding tillers, at final sampling. | |

| | Stover | | | | Topear | | | | Wholecrop | | | |
|---------------------|-------------------------------------|--------------|-------------------------|------------------------|-------------------------------------|--------------|-------------------------|------------------------|-------------------------------------|-------------|-------------------------|------------------------|
| | cwc yield (Mg.ha ⁻¹) | cwc% (%) | D _{cwc} (%) | D _{om} (%) | cwc yield (Mg.ha ⁻¹) | cwc % (%) | D _{cwc} (%) | D _{om} (%) | cwc yield (Mg.ha ⁻¹) | cwc% (%) | D _{cwc} (%) | D _{om} (%) |
| | | | | | 19 | 80 | | | | | | |
| n → n | 3.19 | 60.5 | 62.0 | 61.2 | 1.18 | 15.4 | 73.1 | 83.6 | 5.33 | 37.1 | 65.6 | 74.0 |
| n → 24 | 3.70 | 61.1 | 62.1 | 61.3 | 1.40 | 19.3 | 80.4 | 84.0 | 6.04 | 40.8 | 67.2 | 73.3 |
| 24 → n | 3.51 | 62.1 | 62.3 | 61.1 | 1.38 | 17.4 | 78.3 | 84.0 | 5.88 | 39.1 | 67.0 | 74.0 |
| 24 → 24 | 3.70 | 61.3 | 62.5 | 61.7 | 1.52 | 21.6 | 76.4 | 82.5 | 6.16 | 42.6 | 67.1 | 72.7 |
| | | | | | 19 | 81 | | | | | | |
| $n \rightarrow n$ | 2.58 | 58.2 | 57.1 | 62.9 | 1.12 | 16.1 | 75.0 | 86.8 | 5.17 | 37.7 | 63.8 | 76.2 |
| $n \rightarrow 24a$ | 2.82 | 60.5 | 58.8 | 62.8 | 1.33 | 19.5 | 75.4 | 86.1 | 5.66 | 40.1 | 65.8 | 76.2 |
| $n \rightarrow 24b$ | 2.95 | 60.6 | 58.3 | 62.3 | 1.40 | 19.2 | 72.1 | 85.5 | 5.79 | 39.9 | 64.0 | 75.5 |
| 24 → n | 2.61 | 57.0 | 58.1 | 63.9 | 1.23 | 18.2 | 78.3 | 86.9 | 5.43 | 38.8 | 65.3 | 76.5 |
| $24 \rightarrow 24$ | 2.91 | 59 .7 | 58.6 | 63.0 | 1.29 | 18.1 | 74.6 | 85.6 | 5.61 | 39.1 | 64.1 | 75.9 |

The following parameters correlated significantly with desynchronization: mean internode length, number of tillers, length of top ear, number of lower ears, dry-matter production after grain set, proportion of ear in the crop, ear yield, dry-matter content of top ear and dry-matter content of whole crop. Significantly correlated with silking date were: length of top ear, width of top ear, cell-wall content, dry-matter production after grain set, proportion of ear in the crop, ear yield and dry-matter content of whole crop and of top ear. The parameters that correlated significantly with silking date and with desynchronization always correlated better with silking date than with desynchronization. This means that desynchronization mainly influenced elongation of the main shoot and apical dominance. Silking date mainly affected the success of ear development and the distribution of fresh and dry matter. Since silking was more sensitive to a switch in photoperiod than anthesis, the variation in silking date was greater than the variation in anthesis date.

In the introduction, a number of effects ear development could have on crop parameters were listed. Only the effects of ear development on cell-wall production and crop drying became apparent in these experiments. The results would have been more pronounced if an early, photoperiod-sensitive genotype had been sown at a low density and at a later date or at a lower latitude (e.g. Hawaii or Kenya). Source limitation, high temperatures, short natural photoperiod and genotypic sensitivity to photoperiod switches would ensure great effects.

Nevertheless the present data illustrate that slight alterations in the relative rate of ear development within one genotype may produce noticeable effects in cell-wall content, without affecting cell-wall digestibility. These effects may result in differences in whole-crop digestibility when the digestibility of cell walls is poor.

A high proportion of ear in the crop may therefore be desirable in forage maize, unless the ear sink is so strong that leaf senescence is accelerated.

SUMMARY

In order to ascertain the relevance of crop morphology to production, quality and dry-matter content, attempts were made to induce differences in dry-matter distribution by switching the photoperiod during the early development of forage maize.

The different types of photoperiod switches applied effected small, significant differences in vegetative and reproductive development but no differences in the dry-matter yield of the whole crop. Differences between silking dates were greater than differences between anthesis dates. The experimental method used enabled ear maturity and the proportion of ear in the crop to be varied almost independently of leaf number and main-shoot development.

The results indicate that silking date is closely correlated with ear yield, ear proportion, ear maturity, dry-matter content of the whole crop and cell-wall content.

Differences in crop quality (measured as in vitro digestibility) were small but not insignificant in one of the two years.

Although the effects induced were small, they underline the importance of good ear development for the dry-down of the whole plant and also for the digestibility of the crop.

The effects would have been greater if the experiments had been done in tropical regions with tropical genotypes grown at lower plant densities.

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1