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Effect of a switch in photoperiod on the reproductive development of temperate hybrids of maize

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Summary

In three phytotron experiments, the reaction of maize (*Zea mays* L.) to a switch in light phase was investigated. Number of leaves was increased by a long-day phase (20 h) before tassel initiation but was not affected thereafter. Reproductive development was delayed by long days before tassel initiation and slowed down by long days after tassel initiation, but ear development was affected more than tassel development. So the time lag between anthesis and silking increased when short days (12 h) were followed by long days. The opposite was true when long days were followed by short days. Direct responses to photoperiod, such as number of leaves and tassel branches, occurred over a rather short time. Indirect effects, such as area of leaves, height of plant and length of the ear shoot, however, were maximum when day length did not affect the number of leaves any more. One can therefore control vegetative and reproductive development separately to some extent by a day-length treatment and can desynchronize development of the male and female inflorescences, especially at higher temperature. The photoperiodic response of maize is clearly complex.

Introduction

Maize (*Zea mays* L.) is a monoecious plant with the staminate inflorescence on top (the tassel) and the pistillate ones in the axils of several lower leaves (the ears). The tassel terminates the main shoot and the ears terminate lateral branches, called shanks. There are mostly ten internodes on a shank, which normally do not elongate.

Maize is known as a (sub)tropical quantitative short-day plant, although qualitative short-day, day-neutral and long-day genotypes have been reported (Niopek, 1960; Francis et al., 1969; Francis et al., 1970; Hunter et al., 1974;

Teschemacher, 1974; Coligado & Brown, 1975; Blondon & Gallais, 1976; Aitken, 1980; Rood & Major, 1980). According to many authors (Francis et al., 1969; Rood & Major, 1980), the floral differentiation of maize can be evaluated by examining the developing tassel. In this view, the effects of photoperiod on plant development end with tassel differentiation. Because maize is determinate in growth, the rate of development is shown by the final number of leaves.

Under natural conditions, the ear is always initiated at a certain stage of tassel development, about two days after tassel initiation. The ear can only complete development if it does not lag too far behind the tassel (Fuchs, 1968).

However the female inflorescence has greater requirements for induction than the tassel (Niopek, 1960; Messiaen, 1963; Blondon & Gallais, 1976) and the gap between male and female flowering widens with a longer photoperiod (Messiaen, 1963; Moss & Heslop-Harrison, 1968; Faungfupong, 1975; Blondon & Gallais, 1976; Aitken, 1980). Because of a longer period to initiation, the number of leaves increases with longer days. The time of initiation is also longer; therefore the number of male and female florets can also be larger (Ragland et al., 1966; Moss & Heslop-Harrison, 1968; Hunter et al., 1977; Hunter, 1980).

Only a few people have worked on the effects of temporary changes in photoperiod. Faungfupong (1975) shortened the dark period after completion of tassel initiation and hardly found any effects on tassel development but a pronounced delay in silking. Scheffer (1978) accelerated reproductive development by shortening the photoperiod for some days. The moment of treatment was crucial: from the 1-leaf stage until the 9-leaf stage, there was a continuous increase in efficiency of the treatment. The effects also increased when the number of short days increased. Niopek (1960) and Kim et al. (1976) also found an acceleration of development when the photoperiod was shortened for a few days, and greater effects if the number of short photoperiods increased.

So one can influence vegetative development and the size of reproductive organs by photoperiod. However the ear and tassel differ in photoperiodic requirement for induction; they differ also in moment of initiation; the ear may develop poorly if it develops much slower than the tassel. These three aspects provide a way of uncoupling vegetative development, tassel development and ear development. Such an uncoupling by photoperiod could be useful in physiological and agricultural studies, for example on seed production or on the relevance of the ear for production pattern, productivity and quality of forage maize.

The purpose of the study was to find a method of changing the production pattern of maize without changing the rate of development of the main shoot.

Three trials were designed to influence initiation and development of the ear independently of the tassel by a different photoperiod at certain stages of growth. I used two hybrids from temperate regions (both described by Bundessortenamt, 1980), because they are almost day neutral. If these hybrids respond, photoperiod-sensitive strains will react in the same way or more sharply.

This article will be followed by a report on two trials in which some of the main treatments were imposed on a normal maize crop. Special attention will be paid then to the consequences for yield and quality.

Materials and methods

Maize was grown in 6-litre pots (Trial 1) or 10-litre pots (Trial 2 and 3). Four seeds were sown in each pot. After emergence, the number of seedlings was reduced to two. Final plant density was about 6 m^{-2}. The pots contained a mixture of sandy soil and peat in equal volumes. Nutrient solution, adjusted to soil type, was provided adequately. Plants were watered once or twice a day. Relative humidity was kept at about 75 %. When the plants grew taller, the volume fraction of CO_2 in air was kept at 450×10^{-6}. The pots were placed on carts, which were moved around in each growth chamber three times per week until the plants were too tall and had to be put on the floor.

Photosynthetically active irradiance in the waveband 400-700 nm was 100 W/m^2 1.20 m above the floor for 12 h. Long-day treatment of 20 h was achieved by four incandescent bulbs (100 W) over 10 m^2, which burnt for 4 h before and 4 h after the basic light period. Minimum illuminance during the supplementary photoperiod was 100 lx corresponding to an irradiance in the waveband 400-700 nm of 0.4 W/m^2, which is more than the saturation point of the photosensitivity of maize (Francis et al., 1970; Francis, 1973; Teschemacher, 1974; Faungfupong, 1975).

In Trial 1, the plants that showed anther or silk extrusion were counted daily. In the other two trials, the dates of first visible extrusion of anthers and of silks were noted for each plant separately. The plants were checked daily at the same time of day.

Maximum leaf area was calculated at anthesis by the equation length × maximum width × 0.75 (Montgomery, 1911). The maximum diameter in the middle of the second internode above the soil was estimated with a marking gauge as a measure of stem thickness. Final plant height, tassel length (measured from the axil of the top leaf) and number of leaves were measured some time after the end of flowering. Ears were measured during grain filling.

Total number of visible kernels or florets was estimated for the top ear and for all the lower ears that arose from the axils. The area of the husk laminae (normally rudimentary, but for given treatments sometimes large) was estimated with an area meter. Dry-matter yields were of little relevance in these trials. They were correlated with leaf area, so far as estimated.

The treatments in each trial are tabulated and described with the results.

Results

Trial 1: effect of photoperiod and temperature after tassel initiation on development of hybrid Blizzard

Before treatment, all plants received a light phase of 12 h at 20 °C with an equal dark phase at 15 °C.

Table 1. Growth conditions after switch in photoperiod in Trials 1 and 2.

Temperature (°C)		Photoperiod (h)
day (12 h)	night (12 h)	
18	12	12
18	12	20
30	24	12
30	24	20

Treatments with 60 plants each as in Table 1 began at the 6.5-leaf stage (i.e. 6.5 visible leaves). Because the rate of leaf appearance is constant with a certain temperature regime, time and plant age are described linearly by means of a linear scale of visible leaves. In 16 dissected plants the shoot apex showed differentiation of the tassel branches and sometimes elongation of the basal branches (i.e. Stage D-E in Fig. 2 of Bonnett, 1966).

Photoperiod after tassel initiation influenced development rate. Male flowering was retarded by only about two days for both temperature regimes, when plants were exposed to long days. Female flowering, however, was retarded more, resulting in greater desynchronization. Variation in date of female flowering increased. Effects were greater at the high temperature; at the low temperature, protogyny was found with continuance of the 12-h photoperiod (Table 2).

Table 2. Some plant characteristics indicating vegetative and reproductive development in Trial 1 for hybrid Blizzard.

	Temperature after 6.5-leaf stage (°C)			
	day 18 / night 12		day 30 / night 24	
Photoperiod regime (h) →	12 → 12	12 → 20	12 → 12	12 → 20
Desynchronization of flowering (60 plants)				
50 % ♀ – 50 % ♂ (days)	–2	1	0	4
75 % ♀ – 75 % ♂ (days)	–2	3	2	7
95 % ♀ – 95 % ♂ (days)	–2	4	7	10
Reproductive development (24 plants)				
length of top ear (cm)	16.5	18.1	15.1	18.6
number of kernels in top ear	410	492	489	514
proportion of bisexual tassels (%)	15	7½	0	0
Vegetative development (24 plants)				
number of leaves	13.2	13.3	13.2	13.1
height of plant (cm)	234.9	243.0	231.7	250.7
height of plant/number of leaves (cm)	17.8	18.3	17.6	19.1
av. leaf area of a plant (dm^2)[1]	35.1	37.8	34.5	39.1
area of husk laminae (cm^2)	0.6	6.1	0.9	22.5
proportion of tillered plants (%)	54	29	0	0

[1] Especially the leaves above the top-ear node were larger for 12 → 20 h.

Differences in ear size reflect differences in duration of floret initiation and more pronounced elongation of the cob. Sex expression in the male inflorescence was influenced by temperature and photoperiod.

As treatment started when the number of leaf primordia was already fixed, there was no difference in final number of leaves. But there were some differences in vegetative development (Table 2), indicating that long day stimulated vegetative growth.

Long days after tassel initiation apparently caused an increase in apical dominance of the tassel and depressed development of the ear-shoot buds and the proportion of tillered plants. The main shoot showed a more pronounced vegetative growth. Although high temperatures normally cause a loss of sensitivity to photoperiod (Hunter et al., 1974; Coligado & Brown, 1975), there was a greater effect of photoperiod on the vegetative growth with a cycle of 30 and 24 °C.

Trial 2: effect of photoperiod before and after tassel initiation and of temperature on development of hybrid Nicco

The trial included 8 × 30 plants, in two photoperiod treatments of 12 and 20 h in early growth and the four combinations of temperature and photoperiod shown in Table 1 from the 5.2-leaf stage.

Double ridges could not yet be seen in most growing tips but the apex had started to elongate, indicating the real start of the reproductive phase (Niopek, 1960). Bonnett (1953) called this the 'transitional stage'.

As expected, earlier treatment (5.2-leaf stage) gave greater effects with photoperiods 12 → 20 h than in Trial 1, although the hybrid used in this trial also appeared to be more sensitive than Blizzard. Again effects of photoperiod were greater at the higher temperature (Table 3).

The photoperiod treatment 20 → 12 h, absent in Trial 1, acted in the opposite way to the treatment 12 → 20 h. For example, desynchronization was less than with the treatment 12 → 12 h and the plants had shorter internodes (plant height divided by number of leaves in Table 3). With the treatment 20 → 20 h, anthesis was much later than for 12 → 20 h, but silking date was about the same, with smaller standard deviations. So anthesis date was more influenced by photoperiod after the change than in Trial 1.

Low temperature after the photoperiod switch improved synchronization in all photoperiod treatments but especially with long photoperiod after tassel initiation. Reproductive development was also less affected by photoperiod at lower temperature.

Some abnormalities occurred. Shanks were enormous for 12 → 20 h treatment (compare length of the top-ear shoot with length of the top ear), especially with the cycle of 30 and 24 °C because of excessive elongation of the internodes. Sex expression of the ear shoots was sometimes disturbed, again especially with the temperature cycle of 30 and 24 °C, and the photoperiods 12 → 20 h. Once there was a plume 13.5 cm long on an ear. Such aberrations caused a severe reduction in the number of kernels. The hybrid Nicco tends to form more than one (flowering) ear per lateral branch, as happened in the trial, but its extent was not

Table 3. Vegetative and reproductive development with two regimes of temperature and four of photoperiod. Hybrid Nicco.

	Temperature after 5.2-leaf stage (°C)							
	day 18 / night 12				day 30 / night 24			
Photoperiod before → after 5.2-leaf stage (h) →	12 → 12	12 → 20	20 → 12	20 → 20	12 → 12	12 → 20	20 → 12	20 → 20
Flowering (30 plants)								
anthesis date (days after 50 % emergence) av.	74.8	82.9	82.3	87.0	43.6	45.5	46.0	50.0
s.d.	*4.3*	*4.4*	*2.9*	*3.2*	*2.0*	*2.3*	*1.9*	*3.8*
silking date (days after 50 % emergence) av.	76.1	90.3	81.6	89.9	48.2	57.5	48.7	58.1
s.d.	*4.3*	*5.3*	*2.2*	*3.7*	*3.7*	*5.7*	*2.2*	*3.2*
av. desynchronization (♀ – ♂; days)	1.3	7.4	–0.7	2.9	4.5	12.0	2.7	8.1
Reproductive development (12 plants)								
number of tassel branches	13.4	13.7	14.4	18.7	9.1	11.9	13.3	17.0
length of tassel (cm)	40.0	44.5	35.6	37.6	45.4	49.3	38.0	42.2
length of top-ear shoot (cm)	36.7	43.5	32.6	39.1	37.4	57.3	34.1	43.8
length of top ear (cm)	16.2	14.4	14.3	13.1	17.7	15.4	18.9	18.4
number of kernels, top ear	445	498	422	473	473	373	502	481
proportion of bisexual ears (%)	0	0	0	0	8	67	8	25
Vegetative development (12 plants)								
number of leaves	13.5	13.5	15.5	15.8	13.5	13.9	15.9	16.4
height of plant (cm)	197	223	211	236	224	244	233	252
height of plant/number of leaves (cm)	14.6	16.5	13.6	14.9	16.6	17.6	14.7	15.4
thickness of stem (cm)	2.74	2.83	2.78	2.69	2.26	2.50	2.16	2.19
av. leaf area of a plant (dm^2)	46.1	46.7	46.8	57.3	36.8	46.5	45.5	55.0
area of husk laminae (cm^2)	4.8	35.0	<0.5	2.1	12.9	256.1	2.0	64.9
number of tillers per plant	1.6	0.9	1.7	0.4	0.1	0.2	0.1	0.1

affected by treatment.

Vegetative development showed the same pattern for both temperature regimes, although the high leaf area for the temperature cycle of 18 and 12 °C, with a photoperiod of 12 → 12 h was conspicuous.

Numbers of leaves depended only on photoperiod before the 5.2-leaf stage.

So in Trial 1 and 2 with different hybrids, male and female flowering could be synchronized or desynchronized by temperature and photoperiodic treatments. These two climatic factors interacted. Desynchronization was linked to reproductive and vegetative development, possibly because of a change in apical dominance for hormones, carbohydrates and nutrients.

Trial 3: effect of a photoperiodic switch at different leaf stages on subsequent development of hybrid Nicco

In Trials 1 and 2 we found a shift from reproductive to vegetative growth if the development of the ear was retarded by long days after tassel initiation. In Trial 3, I tried to trace the most sensitive moment for the photoperiodic switch and to analyse the processes by making a continuous series of photoperiodic switches.

Growth conditions: day temperature (12 h) 24 °C; night temperature 18 °C; photoperiod 12 or 20 h.

Treatments: 12 plants were transferred from the short days (12 h) to the long days (20 h) in each of the following leaf stages: 3.5, 4.0, 4.5, 5.0, 5.5, 6.0, 6.5, 7.1 and 7.5. Also 12 plants were transferred from the long days to the short days in the leaf stages 3.5, 4.0, 4.5, 5.0, 5.5, 6.0, 7.0 and 7.6. Besides, 12 plants were kept at short days or long days during their development as 12 → 12 h or 20 → 20 h control treatments, respectively.

Long days retarded induction, so the periods till anthesis and silking increased for 20 → 12 h, when the plants were transferred later. Periods till anthesis and silking decreased, however, for 12 → 20 h, when the plants were older at the photoperiodic switch. Maximum difference in anthesis date was 7 days; maximum difference in date of silk extrusion was 13 days. More significant than these differences were the effects on desynchronization (Fig. 1).

Number of leaves was influenced by photoperiod during a short time (less than 1 week; Fig. 1).

However photoperiod was effective on vegetative and reproductive development for a longer time than is spanned in this trial. Greatest effects on desynchronization were found in the middle of the period in which the number of leaves also changed but effects remained large beyond that range of time.

The number of tassel branches showed the same pattern as the number of leaves but the increase or decrease continued for a longer period (Fig. 2). The number of kernels in the top ear appeared to be rather constant for 20 → 12 h, but is was in all cases lower than for the 12 → 12 h or 20 → 20 h control. For 12 → 20 h the number of kernels was mostly higher than for both controls. Moreover, there were two peaks, one at the 4.0-leaf stage and one at the 6.5-leaf stage. Careful examination of Fig. 2 for 20 → 12 h shows a similar pattern, although it is not significant.

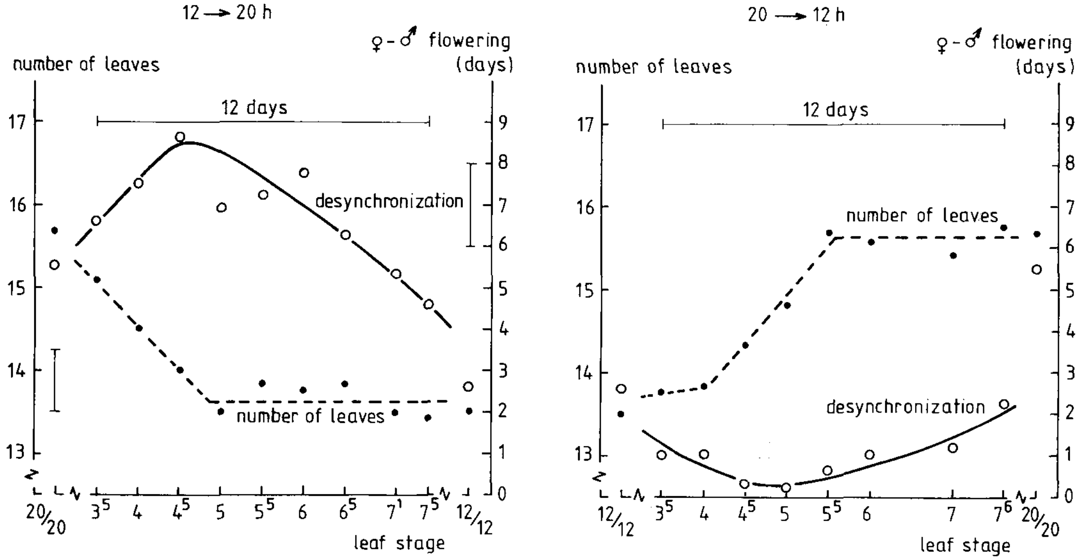

Fig. 1. Number of leaves (— — — ● — — —) and desynchronization of silking and anthesis (—— O ——) in relation to leaf stage at time of photoperiodic switch.
Vertical bars in all figures indicate the least-significant difference for 19 treatments, according to Tukey's range test ($P < 0.10$).

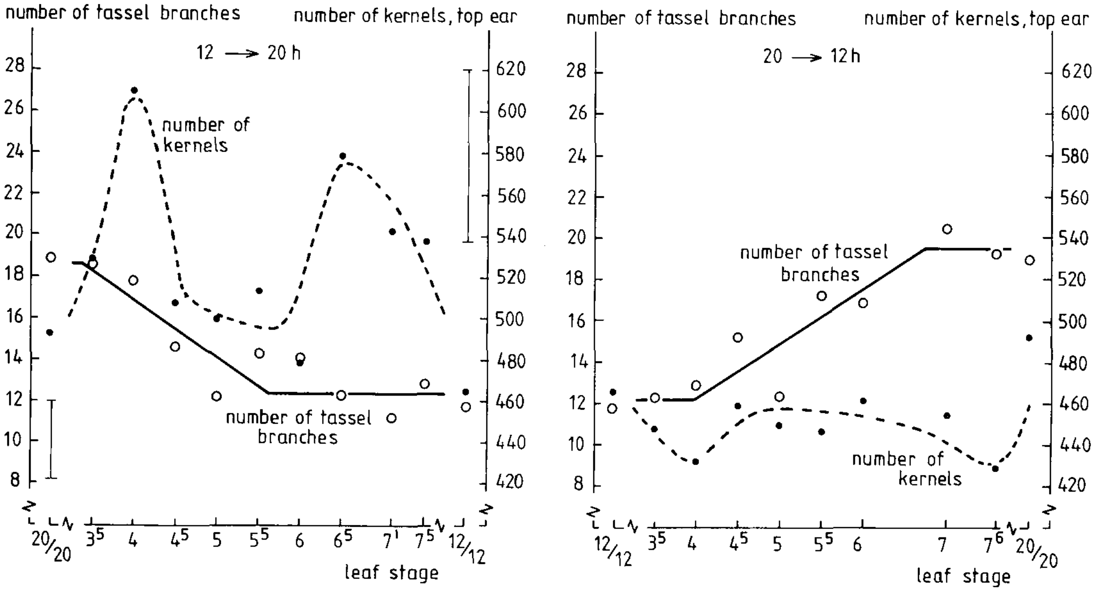

Fig. 2. Number of tassel branches (—— O ——) and number of kernels in the top ear (— — ● — —) in relation to leaf stage at time of photoperiodic switch.

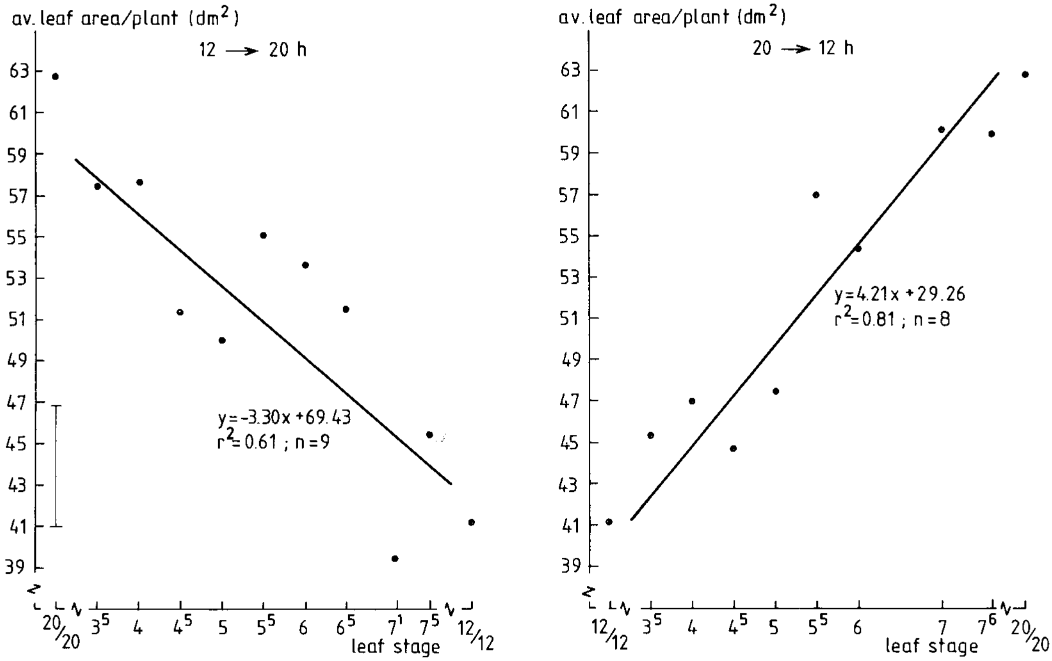

Fig. 3. Average leaf area per plant in relation to leaf stage at time of photoperiodic switch.

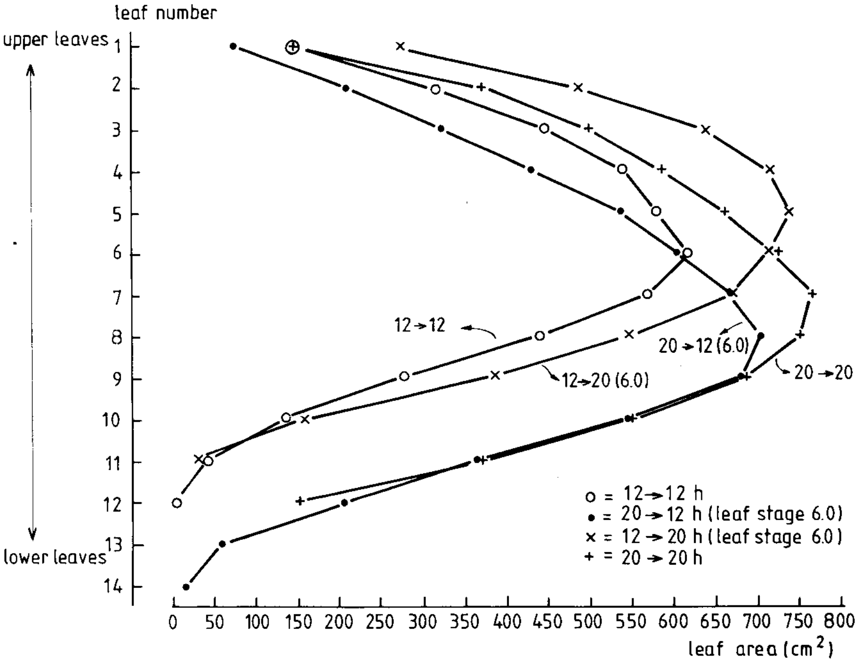

Fig. 4. Leaf area in relation to leaf number for four treatments.

Average leaf area per plant showed a linear relation with the moment of switch until the latest treatments (Fig. 3). This relation is hardly influenced by the number of leaves, but mainly by the area of the upper leaves.

In Fig. 4 the leaf areas for four treatments are given as an example. 12 → 20 h had larger upper leaves than 12 → 12 h, while 20 → 12 h had smaller ones than 20 → 20 h. The effect of a long photoperiod on leaf enlargement was dependent on the number of long days during the early development of the leaf.

In Fig. 5 the length of the tassel and of the complete top-ear shoot are related to the time of photoperiodic switch. These curves look like the desynchronization curves, but the minima or maxima are shifted to later stages. Similar curves can be drawn for stem thickness, length of the top ear, area of the husk laminae, height of the plant divided by number of leaves and individual leaf area if the leaves are counted form above; if leaves are counted from below, the relations are linear like for the total leaf area. For the ear shoot the correlation is not as high as for the tassel length, connected with the differences in number of kernels (compare Fig. 2 and 5).

Length of the top ear ranged from 16.4 cm for the 12 → 12 h control till 22.2 cm for 12 → 20 h, 6.5-leaf stage. The areas of the husk laminae were very small for 20 → 12 h (less than 20 cm^2/plant), but very large for 12 → 20 h (till almost 200 cm^2/plant), as in Trial 2.

From Trial 3, it is clear that different plant characteristics show different patterns of photoperiod response. With regard to number of leaves, for example, plants were only photosensitive during a short time but tassel length, among other things, was influenced during a long period and reached its extreme, when number of leaves was not changeable any more. Because of the

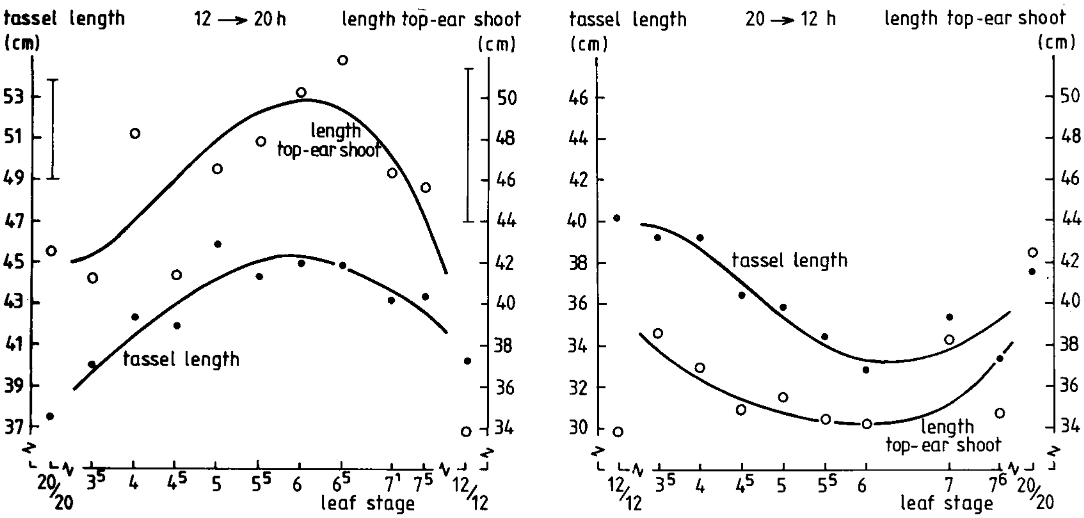

Fig. 5. Tassel length (——●——) and length of the top-ear shoot (——○——) in relation to leaf stage at time of photoperiodic switch.

complexity of the processes involved, even curves with more than one maximum or minimum can be obtained. In these trials, it has been demonstrated that photoperiod sensitivity in maize is not confined to the time from emergence to tassel initiation.

The results of the three trials are in agreement with each other, although there is an interaction with temperature and hybrid. The sexual abnormalities in Trial 2, however, caused some disturbance.

Discussion

Flowering. Rate of development of the reproductive organs of maize was retarded with long days but in the female inflorescence more than in the male one. Together with the time of initiation, this effect determined the course of desynchronization with a maximum for photoperiods 12 → 20 h and a minimum for 20 → 12 h (Fig. 6). The distance between the male and the female curve is influenced by temperature. At lower temperatures, protandry can even be reversed to protogyny.

Tassel development. Long days increased the number of leaf and tassel-branch primordia but only during the relatively short period before tassel initiation. The production of leaf primordia already stopped before the transition to the double-ridge stage. The tassel branches are the first parts of the tassel to differentiate (Bonnett, 1966). The effects of photoperiod and temperature on the

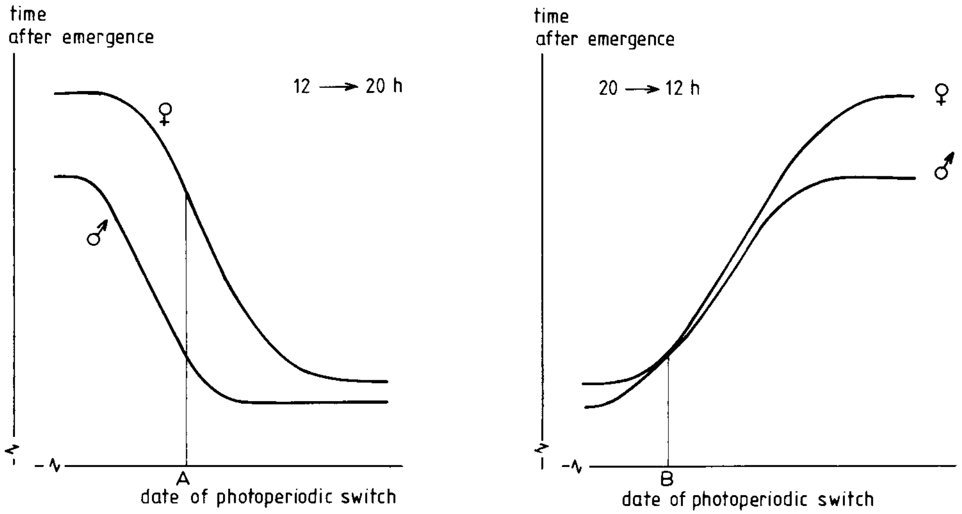

Fig. 6. Effects of photoperiodic switch on time to extrusion of anthers (♂) of silks (♀) (model). A gives the maximum desynchronization for 12 → 20 h. B gives the minimum desynchronization for 20 → 12 h.

number of tassel branches confirm those of Moss & Heslop-Harrison (1968) and Blondon & Gallais (1976). The development of the apex is very fast with short days: the larger the number of short days a plant undergoes during the sensitive stage, the fewer branches it will have. The minimum (number for treatment 12 → 12 h) was very soon reached. Development of the apex with long days took more time, so the maximum number of branches (number for 20 → 20 h) was reached much later.

Sex expression. Photoperiod caused mixing of ears and tassels in Trials 1 and 2. All flowers of a maize plant are originally bisexual and differentiation of the primordia proceeds acropetally (Bonnett, 1953). Sex reversal in the inflorescences would only be possible in the top of the ear or at the end of the tassel branches if it were caused by treatments after the 5.2-leaf stage. Moss & Heslop-Harrison (1968) found sex reversal in the tassel with very short days, and Galinat & Naylor (1951) even found proliferation of the tassel with short days. In Trial 2, female flowers reverted to male with high temperatures and a photoperiodic treatment of 12 → 20 h. In Trial 1, some sex reversal was found in the tassel at lower temperatures, especially for the photoperiods 12 → 12 h. These photoperiod and temperature effects on sex expression of a maize plant correspond to effects found in numerous other monoecious short-day plants (e.g. Heslop-Harrison, 1957).

Indirect responses. The effects on sex versatility, flowering dates and desynchronization, and number of leaf primordia and of tassel branches are the only specific reactions to the photoperiod stimulus, found in these trials (contrast Moss & Heslop-Harrison, 1968). Maximum reactions coincided with the period before and during the transition stage. These direct responses are 'qualitative' reactions to photoperiod, as they require a certain number of short days. Most other unspecific reactions are completely different, since they are consequences of effects on elongation of vegetative organs. They reached their maximum or minimum later, namely at about the first stage at which photoperiod no longer affected tassel-branch initiation. A later change in photoperiod changed no longer the rate of development of the main shoot, but reduced or augmented the number of long days during cell division or cell enlargement. So, most of the vegetative cells experienced the extreme number of long days available for growth at this point.

These indirect responses are due to 'quantitative' reactions to photoperiod: the effects depend on the number of long days after a certain stage, since the measure and duration of depression of the dominance of given reproductive organs is affected by this number.

Indirect responses with a different pattern. Two curves deviated from the general pattern. The relation for total leaf area was linear (Fig. 3), because the area of the individual leaves increased linearly with leaf stage. Under natural conditions, the transformation of the apex is responsible for a progressive decline in initial fractional growth rate of the successive leaf primordia (Williams, 1966). If the initiation or development is retarded, the decline may be retarded or reduced, respectively. Effects of day length on rate of development or initiation were recorded for the entire range of time, at which the switch was made in Trial 3. A further extension of the range would have provided sigmoid curves.

Number of kernels in the top ear showed two clear peaks for 12 → 20 h, one at the beginning of the stage at which the plant is sensitive to photoperiod and one almost coinciding with the peak in elongation. It might be expected that number of kernels would give curves like the desynchronization curves, as they reflect the time available for initiation of floret primordia and as it is unlikely that rates of initiation differ (Allison & Daynard, 1979). The number of kernels, however, was much lower than expected when the change occurred at stages with 4.5, 5.0, 5.5 and 6.0 leaves, which probably form the trasition stage. The initiation rate of female florets could decline when the intensity of the flowering stimulus is drastically reduced during that stage, in which the ear apices are susceptible because of their backwardness.

Concluding remarks. Photoperiod treatments of maize should last until the female flowering; on no account should they be stopped after tassel initiation as requirements for induction, initiation and development are not the same for the two inflorescences. The sensitive stage for some direct effects is shorter than for the indirect effects.

Since conditions like temperature, radiation during the basic light period and drought influence the apical dominance of the tassel and the measure of protandry, there is an interaction with photoperiod.

The genotypic variation in photoperiodic sensitivity is enormous. But even accepted 'day-neutral' hybrids showed a large effect of switch in photoperiod. The induction, initiation and development of female organs are possibly still too photosensitive for West Europe. The developmental rate of the main-shoot apex is the main determinant of the vegetative growth; the rate of ear development influences the maturing process. Selection for a greater sensitivity to photoperiod of the main-shoot apex relative to ear-shoot apices and a smaller sensitivity of the lateral branches would provide plants with larger leaf area and better synchronization; if so, genotypes are created, in which the early-maturing characteristics of the treatment with photoperiods 20 → 12 h are combined with some of the positive effects on vegetative development of 20 → 20 h. So the positive effects of early and late genotypes are united.

Growing maize under unfavourable conditions (poor light, dense planting) often leads to a poor grain-set, partly by desynchronization of inflorescences. The trials suggest that this decrease in fertility can be partly overcome by long day before tassel initiation. The methods used offer a new line for plant physiology, since sink-source relation can be affected in an unusual way and as processes in male and female flowering can be separated.

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