

# EFFECTS OF PHOTOPERIOD AND TEMPERATURE ON VEGETATIVE AND REPRODUCTIVE GROWTH OF A MAIZE (*ZEA MAYS*) HYBRID

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*Received 21 Mar. 1977, accepted 30 June 1977.*

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

A single-cross maize (*Zea mays* L.) hybrid was grown to maturity in the four combinations of two temperatures, 20 and 30 C, and two photoperiods, 10 and 20 h, in controlled-environment growth cabinets. Measurements of dry weights of plant components were made at tassel initiation, mid-anthesis, mid-anthesis plus 16 days, and maturity. The longer photoperiod and cooler temperature treatment produced the highest final plant dry weight. Average daily dry matter (DM) production was greater for plants grown at the longer photoperiod. This could largely be attributed to a higher leaf area per plant. The duration of DM production was longer at the cooler temperature. Grain yields were higher under the lower temperature because of an increase in the length of the grain-filling period and because a greater proportion of the post-anthesis DM was allocated to the grain. The results of this study showed a significant photoperiod  $\times$  temperature interaction for length of the grain-filling period, kernel number and grain yield. Post-anthesis DM accumulation did not appear to be a limiting factor for grain yield. The effects of temperature and photoperiod on length of the grain-filling period and grain yield may have been partly mediated through the size of the grain sink.

On a cultivé en cabinet à ambiance contrôlée jusqu'à maturité un hybride simple de maïs (*Zea mays* L.) à quatre combinaisons de deux températures, 20 et 30 C et de deux photopériodes, 10 et 20 h. Les mesures du poids sec des diverses composantes de la plante ont été prises aux stades de l'ébauche de la panicule, de la mi-anthèse, de la mi-anthèse plus 16 jours et de la maturité. C'est la combinaison photopériode longue et température fraîche qui a donné le poids sec final le plus fort; de même, la production moyenne de matière sèche (MS) par jour a été plus intense en jours longs, ce qui peut s'expliquer en grande partie à une plus grande surface foliaire par plante. La production de MS a duré plus longtemps dans le régime de température fraîche, lequel a également produit un rendement de grain plus élevé, du fait à la fois de la prolongation de la période de remplissage du grain et de la proportion plus importante de la MS élaborée après l'anthèse qui a servi à la formation du grain. L'expérience fait ressortir une interaction significative photopériode  $\times$  température pour la durée de la période de formation du grain, le nombre de graines et le rendement de grain. L'accumulation de la MS après l'anthèse ne semble pas avoir eu d'effet limitant sur le rendement de grain. Il est possible que les effets de la température et de la photopériode sur la durée de la période de remplissage du grain et sur le rendement soient dus, en partie, aux potentiel d'accumulation d'hydrates de carbone du grain.

In a previous paper (Breuer et al. 1976), rate of development of the single-cross maize hybrid Harrow 691 was found to be affected by photoperiod (10 and 20 h) and

*Can. J. Plant Sci.* **57**: 1127-1133 (Oct. 1977)

temperature (20 and 30 C). Long photoperiod and low temperature independently increased the number of days between planting and tassel initiation. Rate of development after tassel initiation was

primarily affected by temperature, but a photoperiod  $\times$  temperature interaction did occur during the grain-filling period. However, the fact that photoperiod affected the duration of the grain-filling period does not necessarily imply that photoperiod during this phase influenced directly the rate of development. Altered vegetative and/or reproductive development, resulting from a photoperiod or photoperiod  $\times$  temperature response during pre-anthesis development could have caused the observed photoperiod effect on the duration of the grain-filling period.

Garner and Allard (1923) were the first to report that photoperiod and temperature altered not only the rate of development in maize but also the general pattern of vegetative growth. Several workers (e.g. Chase and Nanada 1967; Stevenson and Goodman 1972; Coligado and Brown 1975) have reported increases in leaf number per plant with increasing temperature and with lengthening photoperiod, and Hesketh et al. (1969) showed that this could result in an increased leaf area per plant. That temperature can affect leaf area per plant has also been shown by Wilson et al. (1973). They reported that plants grown at an average temperature of 21 C had a higher LAI and a greater leaf area duration after silking than plants grown at average temperatures of 25 and 18 C. The higher LAI and greater leaf area duration after silking resulted in higher dry weight increase after silking. Fuchs (1968) reported that the duration of the period from emergence to tassel initiation affected not only number of leaves (i.e. all leaves are initiated before tassel initiation), but also plant weight and height at maturity, and height of ear insertion.

Reports on the effects of photoperiod and temperature on reproductive development of maize are limited. Galinat and Naylor (1951) showed that photoperiods longer than 15 h tended to cause prolific growth of the staminate inflorescence. Work on sex reversal in the tassel of cv. Golden Bantam (Heslop-Harrison 1961) indicated that

long-day treatments produced fewer female flowers in the tassel than short days. Moss and Heslop-Harrison (1968) reported that long-day treatments produced more ears and may have raised the number of spikelet primordia found in the female inflorescence. Ragland et al. (1966) studied the growth and development of the female inflorescence of field-grown maize plants that had been treated with long photoperiods produced by supplementary radiation during the middle of the night. They observed a slight increase in number of kernel rows per ear and a 10% increase in the number of kernels per row at 14 days after silking. At maturity, however, the plants grown under the supplementary radiation actually had fewer mature kernels per ear because not all the kernels present were filled.

#### MATERIALS AND METHODS

Harrow 691, a single-cross maize hybrid, was grown to maturity to study the effects of two photoperiods (10 and 20 h) and two temperatures (20 and 30 C) on vegetative and reproductive growth. Detailed information on cultural procedures, physical parameters and experimental design have been reported elsewhere (Breuer et al. 1976).

In brief, plants were grown under 10- and 20-h photoperiod regimes at constant temperatures of 20 and 30 C in controlled-environment growth cabinets. The 20-h photoperiod was obtained by extending a basic 10-h high intensity regime to 20 h with two 40 W incandescent lamps which produced a photon flux of 0.4 nE  $\text{cm}^{-2} \text{sec}^{-1}$  (400-700 nm) at 90 cm from the bulbs. The photon flux during the high intensity regime was 55 nE  $\text{cm}^{-2} \text{sec}^{-1}$  (400-700 nm) at 90 cm from the lamps. The plants were grown in cylindrical glazed pots filled with silica sand and supplied twice daily with 400 ml of modified Hoagland's solution.

Measurements of dry weights of plant components were made at tassel initiation, mid-anthesis, mid-anthesis plus 16 days, and maturity. Two replications of four plants each were sampled at each of these stages of development. Total plant yield was calculated by summing the dry weights of the plant components: stem, roots, leaves, tassel, shank and husks, and ear.

Final leaf number, leaf area, average daily dry matter (DM) accumulation and average plastochrone interval also were determined. For calculation of plastochrone interval (the time interval between the initiation of successive leaf primordia), it was assumed that this genotype had five leaves initiated in the embryo (Kieselbach 1949). Thus, final leaf number minus five was taken as the number of leaves initiated between planting and tassel initiation. Total leaf area per plant was measured with an optical planimeter (Hayashi Denko type AAM-5) on eight plants at 16 days after anthesis.

Measurements were taken on the following reproductive yield components: number of kernel rows per ear, number of kernels per row and kernel weight. Number of florets per row was determined at anthesis. The number of viable kernels was determined at 16 days after anthesis and maturity. Although the distinction between viable and non-viable kernels is somewhat ambiguous, we feel the values give a general impression of kernel development on an ear. Kernel weight was determined at maturity. Number of kernels per ear was estimated by multiplying number of kernel rows by number of kernels per row. At silking, all ears were hand-pollinated with fresh pollen.

## RESULTS AND DISCUSSION

Both photoperiod and temperature affected plant DM yield, with the longer photoperiod and cooler temperature producing the highest final dry weight (Table 1). Final yield is the resultant of rate and duration of DM accumulation, which both were affected by temperature and photoperiod (Table 2; Breuer et al. 1976).

Differences in rate of DM accumulation between the photoperiod treatments could be largely attributed to differences in leaf area. Photoperiod and temperature treatments had a profound effect on leaf area per plant (Table 2). Leaf area is a function of leaf number and leaf size. Leaf number is determined by (a) the duration of the phase over which leaves are initiated (inductive phase) and (b) the rate of leaf production. Because Harrow 691 responds as a quantitative short-day plant (Hunter et al. 1974), the time required for tassel initiation is lengthened under a long photoperiod re-

gime. This results in more leaves, as evident from Table 2. Temperature also affected leaf number, more leaves being produced at the higher temperature. At the higher temperature, there is a smaller plastochrone interval between the initiation of successive leaves. The data further show that at a given temperature, photoperiod had little effect on the plastochrone interval. It is the interaction between plastochrone interval and the length of the inductive period that leads to the differences in leaf number (Table 2). Not all the differences in final leaf area can be attributed to a greater number of leaves. Fewer leaves were produced by the 20 C/20 h than by the 30 C/20 h treatment, yet the leaf area for the 20 C/20 h treatment was greater. This implies a temperature effect on leaf expansion. Thiagarajah (1973) also found a reduction in leaf dimension when the day/night temperature was raised from 25 C/20 C to 30 C/25 C. The optimal average temperature for leaf size and leaf area per plant appears to be in the range of 20–25 C, since leaf dimension (Thiagarajah 1973; Landi and Conti 1976) and leaf area per plant (Daynard 1972; Wilson et al. 1973) also decrease by lowering the average temperature below 20 C.

Final grain yield depends on the capacity of the grain to accommodate assimilate (sink) and on the availability of assimilate for grain growth during the grain-filling period (source). Photoperiod affected grain yield by increasing post-anthesis assimilate production at the longer photoperiod (Table 1), and temperature affected grain yield by the greater proportion of the post-anthesis assimilate allocated to the grain at the lower temperature (Table 3).

Most of the post-anthesis assimilate is a potential source for grain growth, since the proportion of post-anthesis assimilate used for structural growth of vegetative organs is small: DM accumulation in roots, stem and vegetative parts of the ear occurs after anthesis, but a large proportion of accumulated DM in the latter two is non-structural

Table 1. Photoperiod and temperature effects on total and component dry weight of Harrow 69 | at tassel initiation, anthesis, 16 days after anthesis, and maturity

Stage at harvest	Treatment	Plant part										Total		
		Stem	Roots	Leaves	Tassel	Grain	Cob	Shank + husks	Lower shoots					
Tassel initiation	30 C/10 h	0.06	0.24	1.07										1.37
	30 C/20 h	0.25	0.48	2.79										3.52
	20 C/10 h	0.03	0.28	0.46										0.77
	20 C/20 h	0.12	0.85	1.67										2.64
LSD .05														0.13
Anthesis	30 C/10 h	17.53	11.93	21.05	5.08	2.70†						3.25	0.49	62.03
	30 C/20 h	28.68	16.63	30.28	4.57	2.52†						3.60	0.22	86.50
	20 C/10 h	14.24	19.68	22.95	5.71	0.96†						1.55	1.43	66.52
	20 C/20 h	35.63	34.30	53.54	8.43	0.84†						1.45	1.03	135.22
LSD .05														9.89
Anthesis + 16 days	30 C/10 h	21.81	13.63	21.70	3.66	39.67†						10.63	0.97	112.08
	30 C/20 h	44.83	33.51	38.11	4.60	42.79†						13.68	1.66	179.18
	20 C/10 h	21.70	21.90	24.60	4.58	11.43†						9.97	3.16	97.34
	20 C/20 h	59.25	47.73	57.17	5.25	17.27†						17.52	7.18	211.42
LSD .05														16.65
Maturity	30 C/10 h	39.50	17.70	24.10	4.45	57.20	22.35					8.03	0.82	174.14
	30 C/20 h	76.67	38.16	39.75	4.54	55.40	24.73					9.74	1.30	250.29
	20 C/10 h	21.70	22.60	25.60	3.57	113.90	19.98					11.17	2.16	219.68
	20 C/20 h	83.80	66.20	58.30	4.91	193.90	34.34					21.77	14.97	478.19
LSD .05														27.07

†Grain + cob.

Table 2. Photoperiod and temperature effects on plastochrone interval†, leaf number, leaf area and average daily rate of dry matter accumulation from anthesis to 16 days post-anthesis

Treatment	Plastochrone interval (days)	Leaf no.	Leaf area (cm <sup>2</sup> )	Dry matter accumulation from anthesis to 16 days post-anthesis	
				(g day <sup>-1</sup> )	(g day <sup>-1</sup> m <sup>-2</sup> leaf area)
30 C/10 h	1.3	16.9	2,740	3.13	11.4
30 C/20 h	1.3	20.1	4,650	5.79	12.5
20 C/10 h	2.0	15.4	3,190	1.93	6.1
20 C/20 h	1.8	18.6	6,470	4.76	7.4
LSD .05		0.7	1,390	0.10	

†Time interval between initiation of successive leaf primordia.

carbohydrate, which can be relocated to the grain (Daynard et al. 1969). Despite a lower rate of DM accumulation per unit leaf area at 20 C, total DM accumulation after anthesis was higher in the 20 C treatments than in the 30 C treatments, because of a longer duration of the grain-filling period. Temperature effects were dominant to photoperiod effects, for number of days between anthesis and black layer, but a significant photoperiod × temperature interaction did occur (Breuer et al. 1976).

Grain sink strength is determined by number of kernels per plant and the capacity of each kernel to accommodate assimilate. Floret number on the topmost ear at anthesis appeared to be more affected by temperature than by photoperiod (Table 3). At 20 C, the number of kernel rows was higher at the 20-h photoperiod. Ragland et al. (1966)

also reported an increase in kernel rows with a longer photoperiod. As plants developed beyond anthesis, there was a decline in kernel number on the topmost ear (Table 3). Only the number of viable kernels are presented in Table 3. At 16 days after anthesis, there was a marked difference in kernel number between the 20 C and 30 C treatments. The sharp decline in viable kernel number at 30 C relative to 20 C can partly be attributed to faster kernel development at 30 C. Kernels at the tip of the ear frequently cease development at the onset of rapid kernel DM accumulation (Tollenaar and Daynard 1977a), and the data in Table 1 indicate that at 16 days after anthesis, plants in the 30 C treatments are beyond the onset of rapid kernel DM accumulation. Kernel number at maturity suggests that numbers of growing kernels

Table 3. Grain yield components at two photoperiods and two temperatures

Treatment	1000-kernel wt at maturity (g)	No. of kernel rows at maturity	No. of florets or viable kernels at:			Post-anthesis dry matter that goes to grain production (%)
			Anthesis	Anthesis plus 16 days	Maturity	
30 C/10 h	192	12.9	576	316	379	51
30 C/20 h	171	12.9	633	453	399	34
20 C/10 h	281	13.8	724	691	427	74
20 C/20 h	338	14.6	808	731	607	56
LSD .05	22	0.6	125	57	91	

during the period of rapid grain growth did not differ between the 30 C treatments and the 20 C/10 h treatment. Hence, a photoperiod  $\times$  temperature interaction also occurred for kernel number.

The proportion of post-anthesis assimilate that will end up in the grain will depend on grain sink size, post-anthesis assimilation and length of the grain-filling period. The length of the grain-filling period will to some extent depend on the sink and source size: grain filling will cease either when potential kernel storage capacity has been filled, or when all assimilate for kernel growth has been depleted (Tollenaar and Daynard 1977b). Stem weight increased after 16 days post-anthesis in the 30 C/10 h, 30 C/20 h and 20 C/20 h treatments. Hence, it is unlikely that post-anthesis assimilate production was a limiting factor for grain yield in these treatments. The differences in grain yield may therefore, to some extent, be attributable to differences in grain sink size. In particular, the difference between the 30 C/20 h and 20 C/10 h treatments is striking, since post-anthesis DM production in the former was higher, whereas grain yield and kernel weight were lower. Kernel sink size (i.e., endosperm cell number) and numbers of kernels per plant are established at approximately the onset of rapid kernel DM accumulation (Duvick 1951; Tollenaar and Daynard 1977a). It seems possible that temperature and photoperiod effects on length of the grain-filling period and on grain yield are partly mediated through grain sink size.

In summary, the longer photoperiod used in this study favored grain yield because of higher leaf area per plant resulting in increased DM production. The lower temperature increased grain yield because it increased the length of the grain-filling period, resulting in increased post-anthesis DM production and a longer duration of grain filling. The results of this study show a significant photoperiod  $\times$  temperature interaction for length of the grain-filling period, kernel number and grain yield.

## ACKNOWLEDGMENTS

The authors gratefully acknowledge the financial support of the Ontario Ministry of Agriculture and Food and the National Research Council of Canada (Grant No. A 6243). This research constitutes a portion of a M.Sc. thesis conducted by C. M. Breuer.

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