EFFECT OF TEMPERATURE DURING GRAIN FILLING ON WHOLE PLANT AND GRAIN YIELD IN MAIZE (*Zea mays* L.)

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Received 13 May 1982, accepted 1 Oct. 1982.

BADU-APRAKU, B., HUNTER, R. B. AND TOLLENAAR, M. 1983. Effect of temperature during grain filling on whole plant and grain yield in maize (*Z. mays* L.). Can. J. Plant Sci. **63**: 357–363.

In a 2-yr study, plants of an adapted, short-season single cross maize (*Zea mays* L.) hybrid were grown outdoors until 18 days post-silking. At that stage, the plants were transferred to controlled-environment growth cabinets where temperature effects on leaf senescence, grain and whole plant dry matter (DM) production and DM distribution were studied. The day/night temperature regimes were 25/15°C, 25/25°C, 35/15°C and 35/25°C. Higher temperatures reduced whole plant DM accumulation during grain filling. The reduction in DM accumulation was primarily related to a reduction in the period of time from 18 days post-silking until 100% leaf senescence and, to a limited extent, to a lower rate of whole plant DM production. Grain yield per plant was also lower under higher temperatures. The decreases in grain yield were almost entirely determined by a shorter duration of grain filling, while no temperature effect was observed on kernel growth rates or on kernel number per ear. During rapid grain filling, the increase in kernel DM results from utilization of a combination of assimilates temporarily stored in the vegetative plant parts and assimilates produced through current photosynthesis. Under the highest temperature regime, assimilates remobilized from other plant parts accounted for a greater proportion of kernel weight gain. In addition, there was an indication that higher night temperatures resulted in an increased proportion of gain in kernel weight resulting from remobilization of stored DM.
Key words: Corn, temperature, grain-filling period, grain growth, yield components, leaf senescence

[Effet de la température durant la phase de remplissage du grain sur le rendement de la plante entière et du grain chez le maïs.]
Titre abrégé: Effet de la température sur le remplissage du grain du maïs.
Au cours d'une étude de 2 ans, les plantes d'un hybride simple de maïs à cycle court (*Zea mays* L.) ont été cultivés à l'extérieur jusqu'à 18 jours après la floraison femelle. A ce stade, elles ont été transférées dans des chambres de végétation dans lesquelles on a étudié les effets de la température sur la sénescence des feuilles, la production de matière sèche dans le grain et dans la plante entière, et la répartition de la matière sèche dans la plante. Les régimes thermiques jour-nuit étaient de 25/12°C, 25/25°C, 35/15°C et 35/25°C. Les températures élevées ont ralenti l'accumulation de la matière sèche dans la plante entière durant la phase de remplissage du grain. Cette réduction était principalement reliée au raccourcissement de l'intervalle de temps entre le 18[e] jour post-floraison et le stade de sénescence foliaire à 100%, et dans une moindre mesure à un taux inférieur de production de matière sèche de la plante. Par ailleurs, l'abaissement du rendement grainier par plante, résultat lui aussi des températures élevées, était presqu'entièrement dû au raccourcissement de la phase de remplissage du grain, la tem-

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pérature n'exerçant pas d'effet sur le taux de croissance du grain, ni sur le nombre de grains par épi. Durant la phase de remplissage rapide des grains, l'accroissement de la matière sèche des grains est le résultat de l'utilisation des assimilats temporairement stockés dans les parties végétatives ainsi que du produit de la photosynthèse courante. A haute température, les assimilats prélevés sur les autres parties de la plante forment une plus forte proportion de l'accroissement de poids du grain. En plus, il semble qu'en régime de température nocturne plus fraîche une plus faible proportion de l'accroissement de poids du grain provenait de la remobilisation des substances de réserve.
Mots clés: Maïs, température, période de remplissage du grain, croissance du grain, composantes du rendement, sénescence des feuilles

Temperature is one of the major factors affecting grain yield of maize (*Zea mays*). Kiesselbach (1950) concluded from long-term weather data that increased mean seasonal temperatures during June, July and August resulted in a decrease in grain yield. However, despite the importance of temperature for grain growth, temperature effects on grain growth in maize have not been extensively studied. Available reports indicate that temperature influences both the rate and duration of grain growth. Wilson et al. (1973) reported differences in the length of the period from silking to maturity for two maize genotypes grown under three temperature regimes. Duncan et al. (1965) found a significant correlation ($r = 0.42$) between temperature and kernel growth rate. Temperature also affects the persistence and productivity of leaves. Wilson et al. (1973) indicated that maize grown at an average outdoor temperature of 21°C had greater leaf area duration (LAD) after silking than plants grown at an average temperature of either 25°C or 18°C. They concluded that the greater LAD contributed to higher dry matter (DM) production and greater grain yield. In a study of 10 short-season maize hybrids, Tollenaar and Daynard (1978a) observed a faster rate of leaf senescence and lower final DM yields when the environment during the grain-filling period was warmer. Peters et al. (1971) found that high night temperatures resulted in earlier leaf senescence, and a reduction in grain yield because of a shortening of the grain-filling period.

The objective of this study was to examine the effect of temperature during grain filling on DM production and distribution, leaf senescence pattern and the rate and duration of grain filling.

MATERIALS AND METHODS

In 1978 and 1979, plants of an adapted, short-season, single-cross maize hybrid, Guelph GX 122 were grown outdoors at the Elora Research Station until 18 days post-silking. At that time, the plants were transferred to controlled environment growth cabinets where they were subjected to one of four temperature regimes for the remainder of their life cycle. The day/night temperature regimes were 25/15°C, 25/25°C, 35/15°C, and 35/25°C.

Throughout the growth period, the plants were grown in cylindrical 19-L pails utilizing Turface (Wyandotte Chemicals of Canada Limited, Scarborough, Ont.), a montmorillonite clay, as the support medium. The plants were supplied twice daily with water and nutrients by the addition of a solution consisting of 300 g 28.14.14 water-soluble fertilizer, 200 g $MgSO_4 \cdot 7H_2O$, 150 g Ca $(NO_3)_2 \cdot 4H_2O$, 0.2 g $ZnSO_4 \cdot 7H_2O$ and 0.02 g $CuCl_2$ dissolved in 200 L of water and adjusted with HCl to a pH of 5.8. The nutrient culture system was utilized to facilitate the transfer of the plants from the field to the growth cabinets. In addition, the system enabled good recovery of root tissue. In the field, the pails were placed in a second set of identical pails inserted in the soil so that the Turface surface and the surrounding soil surface were at the same level (Fairey and Daynard 1978).

The field arrangement consisted of four rows, 2 m apart, each with 36 double pails. The plants were placed 0.5 m apart within the row. Pails were planted with two seeds each in the latter part of May and after emergence were thinned to one plant per pail. Two rows of border plants were planted between the rows of pails so that the resultant plant density averaged 45 000 plants per hectare. In addition, there were four rows of border plants around the entire experiment.

When present, tillers were removed from plants and pollination of the second ear was prevented by shoot bagging. In 1979, there was an infestation of silks by adult northern corn rootworm, *Diabrotica longicornis* (Hbn). In order to control this pest the corn was sprayed with carbaryl (I-naphthyl-N-methyl-carbamate) at the rate of 1 g a.i. per 2 L of water per 28 m^3 of plant canopy. Despite the spraying, there was a reduction in kernel establishment, resulting in fewer grains per ear in about 20% of the experimental plants.

Silking dates of individual plants were recorded. Plants were considered to be silked on the date of the first silk extrusion from the husks. At 18 ($\pm$2) days post-silking, 132 plants were selected for the temperature study. Plants were selected for uniformity of plant type, silking date (all plants selected had silked within a 4-day period) and kernel establishment. Plant leaf area was measured on each of the selected plants. Leaf area was determined by measuring the length and maximum width of all green leaves. The total green leaf area per plant was calculated as leaf length $\times$ maximum width $\times$ 0.75 (Montgomery 1911) summed for all leaves measured on each plant. Twenty of the selected plants were then utilized to determine the initial dry matter yields of the leaves, stalk (including leaf sheaths), roots, ear shoot (cob + husk + shank) and grain. The components were oven-dried to constant weight at 80°C. A 100-kernel dry weight was determined utilizing kernels number 6 to 15, numbered from the base of the ear.

Plants not utilized for determination of DM yields were transferred from the field to controlled-environment growth cabinets and the temperature treatments commenced. Fourteen plants were grown in each cabinet. The spacing was 0.18 m^2 per plant resulting in a stand density of 47 000 plants per hectare. Replication was accomplished by having two cabinets per temperature treatment. In order to accommodate the plants in the cabinets, the tassel and top leaf of each plant had to be cut off. Similarly, the top of each of the 20 plants utilized for the determination of the initial dry matter yields were cut off before the dry weights were determined.

The plants were illuminated by fluorescent lights supplemented with 40-W incandescent bulbs providing a light intensity of 55 $nE \cdot cm^{-2} \cdot sec^{-1}$ (400–700 nm) at 1 m from the light source. Air temperatures were monitored with shielded thermocouples. The photoperiod was 15/9 h day/night. An attempt was made to maintain the relative humidity between 50 and 70% but this was not always possible.

Beginning at 18 days post-silking, the extent of leaf senescence was determined by visually rating the proportion of leaves and part-leaves remaining green. Initially, the ratings were done at weekly intervals, but as leaf senescence accelerated towards the end of the grain-filling period the interval was reduced to 2 or 3 days. The leaf area duration (LAD) after silking was obtained by integration of the green leaf area per plant over the period from 18 days post-silking to complete leaf senescence i.e.

$$\mathrm{LAD} = \int_{t_0}^{t_s} \mathrm{LAI}\, dt,$$

where t_0 represents the date of 18 days post-silking and t_s the date of complete leaf senescence.

Seven randomly selected plants per cabinet were utilized for the determination of the kernel DM accumulation. Sampling began at 23 days post-silking and was continued at 5-day intervals thereafter until complete leaf senescence and black layer formation in the 1978 and 1979 experiments, respectively. In order to sample kernels, a small cut was made through the husks just above the base of the ear. The husks were carefully pulled upward until two rows of kernels were exposed on the basal portion of the ear. Beginning just above the basifixed kernels, 10 kernels were removed from each of two exposed adjacent rows (kernel numbers 6–15 from the base). The first two rows to be sampled were chosen at random. Subsequent samples were taken from pairs of rows moving clockwise around the ear, leaving two rows between each sampling (Tollenaar and Daynard 1978b). To prevent fungal growth, a thin layer of petroleum jelly was applied to the ear where the kernels were removed. After each sampling, the husks were pulled together and held in the original position by a rubber band. The kernels removed from each plant were weighed before and after drying to constant weight at 80°C.

The seven plants utilized for the determination of the kernel DM accumulation were examined at 2-day intervals for date of kernel black layer formation (Daynard 1972). At maturity, the seven plants per cabinet which were not used to determine the kernel DM accumulation were harvested and dry weights of leaves, stalk (including leaf sheaths), roots, ear shoot (cob + husk + shank) and grain were determined. One-hundred-kernel dry weights were also determined and the mean number of kernels per ear was estimated by dividing total dry grain yield per plant by 100-kernel weight.

Linear regression analysis was used to estimate the slope of the line of best fit during the linear phase of grain growth and to determine the upper limit of the linear phase. The first three data points of the linear phase of grain growth were selected to determine the linear regression coefficient of kernel weight on time. The initial linear phase was then progressively extended by calculating the predicted value for each successive data point, setting 95% confidence interval on the predicted value. This procedure was continued until a particular data point fell outside the confidence interval for its predicted value. That data point was then discarded and the slope of the line of best fit previously calculated was considered as the growth rate (Sofield et al. 1977).

RESULTS AND DISCUSSION

The data from both the 1978 and 1979 experiments show that the characteristics of leaf senescence, DM distribution among the principal plant parts, and grain growth were very similar in both years. Apart from kernel number per ear, there was no temperature × year interaction for any of the characters studied. Thus, 2-yr average data are reported and believed to portray the results accurately.

The temperature treatments were commenced at 18 days post-silking on the assumption that at this time kernel numbers and potential sink size of each kernel would be established (Kiesselbach 1949; Duvick 1951; Tollenaar and Daynard 1978c). The objective was to restrict this study to the effect of temperature on grain-filling without confounding the results by having differences in kernel numbers and potential kernel size. The lack of a treatment effect on kernel number per ear at maturity (Table 1) assures that any temperature effect on kernel growth and development was independent on effects on grain number.

The temperature regime from 18 days post-silking to grain physiological maturity had a marked effect on final whole plant DM yield with more DM being produced as the day or night temperature was reduced (Table 1). The weight differences reflect differences in both the rate and duration of DM accumulation (Table 2). The lowest daily rate of whole plant DM production from 18 days post-silking to grain physiological maturity (Table 2) is primarily associated with the highest temperature treatment. The low mean rate of DM production at the 35/25°C temperature regime probably resulted, at least in part, from both increased rates of respiration and reduced rates of photosynthesis (Thiagarajah

Table 1. Effect of temperature on whole plant yield, grain yield and grain yield components of maize during the interval from 18 days post-silking to grain maturity†

Temperature regime (°C)	Whole plant wt (g)	Grain wt per plant (g)	Kernel number per ear	Kernel size (mg)
25/15	317 *a*†	124 *a*	550 *a*	213 *a*
25/25	293 *b*	103 *b*	580 *a*	175 *b*
35/15	277 *c*	72 *c*	593 *a*	130 *c*
35/25	254 *d*	69 *c*	606 *a*	119 *c*

†Values for all data are means of 2 yr.

a–d In each column, values followed by the same letters are not significantly different at the 0.05 level of probability.

Table 2. Effect of temperature on the rate of plant and kernel growth, leaf area duration, and the duration of grain filling of maize during the interval from 18 days post-silking to grain maturity†

Temperature regime (°C)	Whole plant rate of DM production from 18 days post-silking to grain physiological maturity† (g/day)	Interval from 18 days post-silking to 100% leaf senescence (days)	Leaf area duration (days from 18 days post-silking)	Kernel growth rate (mg/day)‡	Interval from 18 days post-silking to grain physiological maturity (days)	Duration of linear phase of grain growth (days)	Interval from complete leaf senescence to grain blacklayer (days)
25/15	2.3 *a*	34 *a*	90 *a*	7.4 *a*	39 *a*	25	5 *a*
25/25	2.2 *a*	28 *b*	77 *b*	7.4 *a*	31 *b*	18	3 *a*
35/15	2.1 *a*	21 *c*	54 *c*	7.1 *a*	24 *c*	15	3 *a*
35/25	1.3 *b*	17 *d*	43 *d*	6.9 *a*	21 *d*	10	4 *a*

†Values for all characters are means of 2 yr.
‡Values were obtained from equations of linear regression of kernel dry weight on time.
a–d In each column, values followed by the same letter are not significantly different at the 0.05 level of probability.

et al. 1979). Higher temperatures also caused a decrease in the duration of DM production and a reduction in leaf area duration (LAD) (Table 2). In fact, the effect of temperature on both of these traits was even greater than the effect on mean rate of DM production. At the lowest temperature, LAD was more than two times greater than at the 35/25°C temperature regime.

The reduction in whole plant yield under the higher temperature regimes was accompanied by a considerable reduction in grain yield per plant (Table 1). Since there was no treatment effect on the number of kernels per ear, and only a single ear per plant was allowed to develop grain, the differences in grain yield are attributable to differences in mean kernel weight (Table 1). Temperature effects on kernel weight and grain yield were associated with differences in duration of grain filling (Table 2).

Temperature had no significant effect on the rate of filling during the linear phase of kernel filling (Table 2). Published literature does not appear to exist on the effect of temperature on the rate of kernel filling during the linear phase of maize grain growth. However, Thorne (1974) and Ford and Thorne (1975) in experiments with wheat found that a temperature increase from 15 to 20°C, from 21 to 37 days post-anthesis, did not lead to significant increases in kernel-filling rate.

In maize, it is well documented that the vegetative plant parts, particularly the stem, are capable of acting as a temporary sink for assimilates (Hume and Campbell 1972). Maximum amounts of stored assimilates are normally present in the stalk at 2–4 wk after anthesis. A portion of the stored assimilates may be remobilized into the grain during the period of rapid grain filling (Daynard et al. 1969; Genter et al. 1970; Fairey and Daynard 1978). The demand for the assimilates stored in the vegetative plant parts appears to be affected by both the demand from the filling kernels and the level of current photosynthate production. The greater the difference between demand by the kernels and current photosynthate production, the greater the tendency for vegetatively stored assimilate to be remobilized to the kernels. In the present study, the change in weight of the plant components during grain-filling is outlined in Table 3. The net loss in weight of the non-grain components from 18 days post-silking to maturity was taken as an estimate of the amount of material translocated from these plant parts to the grain during grain-filling. The increase in whole plant dry matter yield during the filling period was taken as an estimate of the net contribution of current photosynthetic assimilation to grain yield (Table 3). Utilizing these estimates, the proportion of dry matter coming from these two sources was calculated and found to vary considerably among treatments. Under the highest temperature regime (35/25°C) the remobilization of assimilates into the grain from other plant parts accounted for 51% of the total increase in grain yield, the remainder coming from currently produced photosynthate. Under lower temperature regimes, a greater portion of the grain DM increase appeared to come from current photosynthesis (74–86%). This probably reflects both increased LAD as well as higher levels of plant DM production. There was an indication that lower night temperatures resulted in a decreased proportion of gain in grain weight resulting from remobilization. It should be noted that the estimated proportion of the gain in grain weight per plant from remobilization is probably biased upwards due to respiratory losses in the non-grain plant components. The upward bias might be expected to be greater at the higher temperatures. The absolute DM increase in grain yield attributable to translocation was not greatly affected by temperature treatments with the exception of the 35/15°C regime which showed a lower contribution (Table 3). The reason for this difference is not clear.

Table 3. Effect of temperature on dry matter distribution among principal plant components of maize during the interval from 18 days post-silking to grain maturity†

Temperature regime (°C)	Total loss of DM from vegetative parts‡ (g)	Loss in root wt (g)	Loss in stalk plus sheath wt (g)	Loss in leaf wt (g)	Loss in secondary ear wt (g)	Loss in husk plus shank wt of primary ear (g)	Gain in cob wt (g)	Gain in grain wt per plant (g)	Estimated proportion of gain in grain wt per plant from current photosynthetic assimilation (%)	Estimated proportion of gain in grain wt per plant from remobilization‡ (%)
25/15	23.5 *a*	6.3 *a*	10.8 *b*	−2.7 *a*	1.7 *c*	7.4 *a*	3.1 *a*	111.6 *a*	82	18
25/25	27.2 *a*	3.1 *a*	14.8 *a*	1.0 *c*	3.9 *b*	4.4 *a*	3.7 *a*	91.1 *b*	74	26
35/15	11.1 *b*	0.6 *a*	3.5 *d*	−1.0 *b*	4.2 *b*	3.8 *a*	2.7 *a*	59.9 *c*	86	14
35/25	30.9 *a*	4.9 *a*	7.6 *c*	5.0 *d*	7.9 *a*	5.5 *a*	2.3 *a*	56.2 *d*	49	51

†Values for all characters are means of 2 yr.

‡Calculated by subtracting the grain in cob weight from the total loss of DM from vegetative parts and dividing by gain in grain weight per plant and multiplying the resultant by 100.

a–d In each column, values followed by the same letter are not significantly different at the 0.05 level of probability.

In conclusion, this study indicates that a high temperature regime during the grain-filling period reduces both total dry matter and grain yield of the maize hybrid Guelph GX 122. Reductions in total dry matter production were associated with lower LAD and rate of DM accumulation; reductions in grain yield were associated with a shorter duration of the grain-filling period. Temperature did not affect rate of grain filling. This suggests that the temperature dependent processes involved in transportation of assimilates to the grain and in accumulation of dry matter in the grain were not rate limiting under the environmental conditions established in this study.

ACKNOWLEDGMENTS

This research was made possible through the assistance of the Ontario Ministry of Agriculture and Food.

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