Maize Leaf Development Biases Caused by Air–Apex Temperature Differences

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ABSTRACT

Accurate determination of leaf appearance rate is required in crop simulation models to estimate canopy development and ultimately crop yield. Most crop simulation models use air temperature for thermal time calculations to estimate leaf appearance rate, although the near soil temperature is more closely related to the growing apex temperature than air temperature before stem elongation. A field experiment was conducted in 1996 at East Lansing, MI, to determine the effect of soil, air, and apex temperatures on maize (*Zea mays* L.) leaf development. Maize leaf tip appearance dates and leaf numbers were observed on four sowing dates to provide variations in the thermal regime of developing plants. Solar irradiance and temperature of the air (1.5 m height), apex, and soil (1-, 3-, and 5-cm depths) were recorded on 0.5-h (half-hourly) intervals. The daily average soil temperature at the 3- to 5-cm depth was reasonably close (+0.6°C in average) to the daily average apex temperature for use as a surrogate for apex temperature to increase the accuracy of maize development simulation in the sowing to ninth leaf tip stage. Thereafter, the air temperature was sufficiently accurate to estimate plant development. Using apex temperatures from leaf 3 to 9, this study indicated that the phyllochron was near 55°C d (degree days) per leaf tip appearance. The consistent bias between air and apex temperature from sowing to V6 found in this study clearly indicates the necessity of using the right temperature in thermal time calculations for accurate maize development simulation.

Most maize phenological modeling is based on the concept of thermal time (TT) (Ritchie and NeSmith, 1991), because temperature is the primary factor driving maize development within fairly broad temperature ranges. Thermal time is usually calculated using air temperature while the specific location where temperature influences development is in the *apex*, the zone where plant cell-division and expansion is occurring (Ritchie, 1991). During the early growth stages of a maize plant, this zone is slightly below the soil surface; thus, the development rates (leaf initiation, leaf appearance, or reproductive-initiation rates) are more closely associated with temperature near the soil surface than with the air temperature (Beauchamp and Lathwell, 1967; Bonhomme et al., 1984; Cooper and Law, 1978; Duncan et al., 1973; Hesketh and Dale, 1987; Wilson et al., 1995). Experiments with different mulches on the soil surface (Fortin and Pierce, 1991; Dadoun, 1993; Stone et al., 1999) demonstrated that soil temperature was more accurate for thermal time calculations when the apex is below the surface and air temperature afterward to describe maize development. Previous studies have shown a difference between apex and air temperatures during short periods of the maize life cycle (Cellier et al., 1993; Ben-Haj-Salah and Tardieu, 1996). However, none of them quantified the effect of the bias on maize development. The differences between air and meristem temperature support the evidence of biases when air temperature is used in thermal time calculations instead of apex temperatures and highlight the importance of choosing the appropriate temperature to most accurately simulate phenology.

The phyllochron, time between the appearance of successive leaves on a shoot, is usually expressed in units of TT per leaf tip (McMaster and Wilhelm, 1995). The phyllochron provides a convenient method to describe plant vegetative development and aids in understanding and modeling crop development. Measurements of the phyllochron for maize were reported to vary between 30 and 50°Cd (degree days) per leaf tip using base temperatures ranging from 6 to 9°C. A summary of results from the literature (Table 1) provides phyllochron information derived from field and controlled environment experiments, from diverse sites, and for a broad range of maize cultivars. In all of these studies estimates were done using air temperature with no corrections for possible air–apex temperature biases.

Accurate phyllochron values are required in crop simulation models to estimate canopy development and ultimately crop yield. Consequently, the uncertainties of the plant–air temperature differences and their influence on maize leaf development should be considered. The objectives of this study were to determine (i) the relationship between apex temperature and maize leaf development rate, (ii) the capability of soil temperature of being a better estimator than air temperatures for apex temperature when the apex is below the soil surface, and (iii) quantify the bias associated with using air temperature to determine maize development rates.

MATERIALS AND METHODS

A field experiment was conducted in 1996 at the Michigan State University Research Farm, East Lansing, MI (42°78′ N, 84°60′ W), on a Capac loam soil (fine-loamy, mixed, mesic Aeric Ochraqualf). Maize (hybrid 'Pioneer 3572') was planted at a density of 6.5 plants m^{-2} and at 5 cm depth on four dates: 29 May, 30 June, 2 August, and 29 August to expose the crop to different thermal environments. Sowing dates were randomly assigned to the experimental units. Each adjacent experimental unit was 45 m^2, with five rows 15 m in length and 0.75 m apart, except for the fourth sowing, which had only one row 15 m in length. The experimental field was homogeneous and surrounded by growing crops.

All plots were moldboard plowed in the fall and received secondary tillage before planting in the spring. Plots were raked before planting to level the surface. Starter fertilizer

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Abbreviations: TT, thermal time; °Cd, degree days; PAR, photosynthetically active radiation; PPFD, photosynthetic photon flux density.

Table 1. Experimental conditions, base temperature (T_b, °C), and phyllochron (°Cd) measured in differing environments.

Author	T_b	Type of experiment	Phyllochron
Ritchie and NeSmith (1991)	8	Field, temperate, and growth cabinet	38–45
Zur et al. (1989); Tollenaar et al. (1979)	6–9	Growth cabinet	33–42
Picard et al. (1985)	6	Field, temperate	35–43
Verheul et al. (1996)	6	Field, cold temperate	43
J.D. Hesketh, unpublished data, cited in Hesketh and Warrington (1989)	8	Field, temperate	37–42
Kiniry and Bonhomme (1991)	8	Field, warmer temperate	34–41
Cooper (1979)	9	Field, tropical	41
Carberry (1991)	8	Field, tropical	48,3
Manrique and Hodges (1991)	8	Field, tropical	49–50
Birch et al. (1998a)	8	Field, subtropical	40–50

was applied at sowing at a rate of 45–19.7–37.4 kg ha^{-1} (N–P–K). Weeds were hand removed during the growing season. An irrigation of 25 mm was applied on 24 July.

Soil temperatures at 1 cm (S1), 3 cm (S3), and 5 cm (S5) depths (1400-103 Soil temperature sensor, LI-COR, Lincoln, NE), air temperature at screen level (1.5-m height) (1400-101 Air temperature sensor, LI-COR, Lincoln, NE), and near apex temperature were measured for each sowing date every 5 s, and 0.5-h (half-hourly) average values were recorded and stored in a data logger (LI-COR 1000, LI-COR, Lincoln, NE, and/or Campbell CR 10, Campbell Scientific, Logan, UT). Two replications for each temperature measurement were obtained from each plot during most of the last three sowing dates. Solar irradiance was recorded during the entire experiment with a pyranometer (LI-200SA Pyranometer sensor, LI-COR, Lincoln, NE) and transformed to photosynthetically active radiation (PAR) by multiplying by 0.45. Near apex temperature was measured using thin copper-constantan thermocouple needles 0.020 cm (0.008 inch) diameter (Omega HYP-0-33-1-T-G-120-SMP-M, Mini Hypodermic thermocouple probe, Omega Engineering, Stamford, CT). Each needle was thermally insulated with silicone and covered with shrinkable tubing, leaving only 5 mm uncovered at its end where the thermocouple junction was placed. The needle was changed to a new plant daily to avoid error in temperature values due to the possible effect of damaged tissue where the sensor was inserted. The location of the meristematic zone was checked by dissection of a nearby plant at the same vegetative development stage. Maximum and minimum soil, air, and apex temperatures were recorded at the same frequency. Data were aggregated across the day, and the daily maximum, minimum, and average temperature values were calculated from the 0.5-h maximum, minimum, and average recording.

Phenological stages were determined using the Ritchie and Hanway (1982) procedure. Vegetative plant development was studied using appearance of leaf tips in 10 consecutive plants near the center plots. Plants studied were marked at the beginning of the growing season. The number of leaf tips on each plant was observed at least three times per week.

Thermal time (TT) was calculated as follows:

$$\mathrm{TT} = \sum_{i=1}^{n} (\overline{T} - T_b)$$

where $\overline{T}$ is daily mean air, soil, or apex temperatures for each of the four sowing from emergence until the last tip appeared, and T_b is the base temperature (8°C according to Ritchie and NeSmith, 1991). When $\overline{T} < T_b$, no value was added to the total. Temperatures measured at different locations (S1, S3, S5, air, and apex) were used to calculate TT to compare with observed leaf tip appearance. The phyllochron was calculated for each TT–leaf tip relationships using air, soil, and apex temperatures.

Because the thermocouple needles were not available until the second sowing, apex temperature was not measured for the first sowing. There were some instances of failure (11 d) in the recording of the apex temperature at the beginning of the third sowing. The missing data of the third sowing were estimated using regression analysis ($r^2 = 0.77$, $P < 0.0018$) developed with the available apex and soil temperature data for that sowing.

RESULTS AND DISCUSSION

Seasonal variation in daily average maximum and minimum air temperatures and daily total solar irradiance is depicted in Fig. 1. These data demonstrate a broad range of thermal environments for the four sowing dates with air temperatures ranging from about 0 to 36°C.

The apical meristem remained belowground until a few days before V6 stage (Ritchie and Hanway, 1982), when the number of leaf tips was nine for the first three

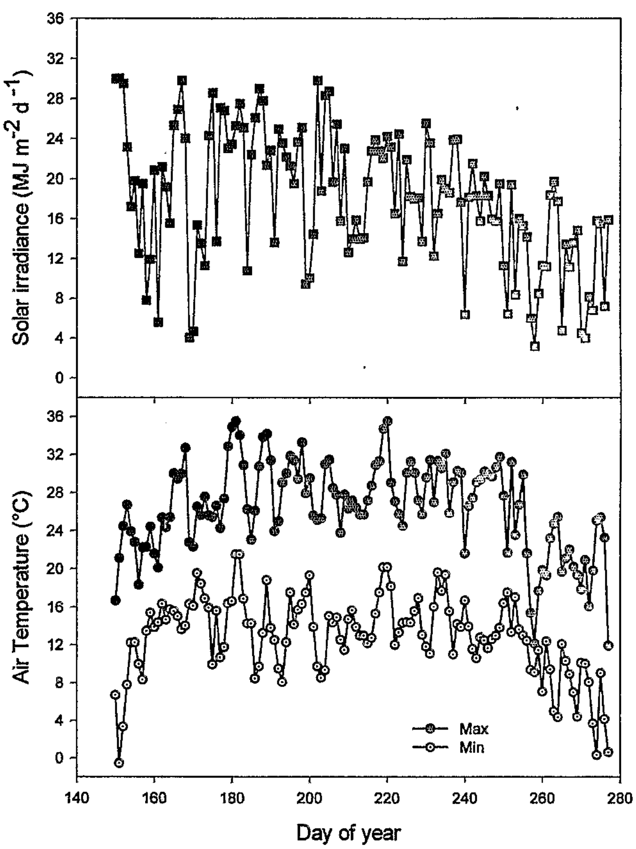

Fig. 1. Daily mean, maximum, and minimum air temperatures and solar irradiance during the period of the study at East Lansing, MI, 1996.

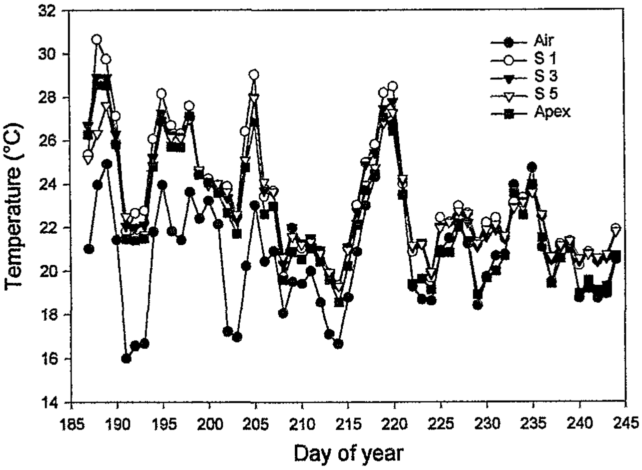

Fig. 2. Seasonal variation in daily average air, soil, and apex temperatures from emergence until the final leaf tip appeared for the second sowing. Appearance of the ninth leaf tip on Day of the year 213. Soil temperatures are at 1-cm (S1), 3-cm (S3), and 5-cm (S5) depths, respectively.

sowings. No data for this stage were available for the fourth sowing, because plants were killed by a frost at the V4 stage with six leaf tips. Apex and soil temperatures were warmer than air temperatures by about 5°C on clear days and 2°C on overcast days for the last three sowings when the apex was below the soil surface (Fig. 2). Considerably less difference between air and apex temperatures occurred when stem elongation moved the apex above the soil surface. When above the surface, the apex temperature was quite close to air temperature, a finding in agreement with previous research (Cellier et al., 1993). Soil and apex temperatures were quite close together when the apex was below the soil surface (Fig. 2, Table 2).

Half-hourly values of all measured temperatures are shown for the second sowing date in Fig. 3 for a clear and a cloudy day. Differences between apex and air temperature are evident after sunrise, increasing during

Table 2. Mean air, soil, and apex temperatures values and mean photosynthetically active radiation (PAR) values for four sowing dates from emergence to appearance of the ninth leaf tip and from the ninth leaf tip to the appearance of the last leaf tip.

	Sowing no.			
	1	2	3	4†
Mean temperatures (°C) and mean PAR (MJ PAR m^{-2} d^{-1})				
		Emergence–leaf tip 9		
Air	21.5	20.5	20.9	14.9
S 1	24.2	24.5	24.5	16.6
S 3	23.9	24.2	23.9	16.8
S 5	23.6	24.0	23.6	17.3
Apex	–	23.7	23.7	15.8
PAR	9.3	9.4	8.5	5.1
		Leaf tip 9–Last tip		
Air	–	21.1	15.6	–
S 1	–	22.4	17.6	–
S 3	–	22.2	17.4	–
S 5	–	22.2	17.8	–
Apex	–	21.2	16.2	–
PAR		8.9	5.5	

† Until leaf tip six, crop died due to frost.

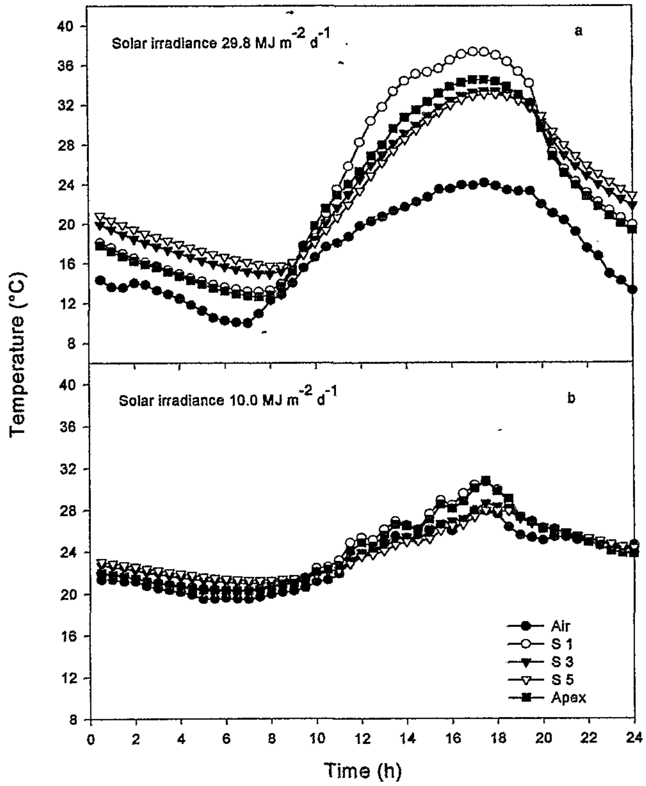

Fig. 3. Diurnal variations of apex, soil, and air temperatures for (a) a clear day (20 July 1996) and (b) a cloudy day (18 July 1996) for the second sowing experiment. Soil temperatures are at 1-cm (S1), 3-cm (S3), and 5-cm (S5) depths, respectively. Maize in V4, six leaf tips; apex at approximately 1 cm below soil surface.

the day with a maximum around noon (almost +10°C difference) and decreasing in the late afternoon (Fig. 3a). A similar pattern was observed in the soil temperature at 1 cm depth, while a delay in the time of occurrence of maximum and minimum temperatures was found for the other two soil depths. Smaller differences between all temperature measurements are evident on overcast days (Fig. 3b), because soil heating decreased due to less solar irradiance reaching the soil surface. On cloudy days the apex and soil temperatures were slightly higher than air temperatures.

Mean temperatures in the soil and apex were greater, and thus accumulation of TT was faster for soil and apex than for the air for all sowings (Table 2). Differences in the TT to reach different development stages were due to variations in the patterns of soil, apex, and air temperatures observed for the four sowing dates. These differences were evident during the first stages of crop development (Day of the year 187–212) when soil and air temperatures had larger differences than after the ninth leaf tip stage (Fig. 2). Apex TT was 85 and 72°Cd higher than air TT at the appearance of the ninth leaf tip, whereas the difference was 91°Cd at the appearance of the last observed tip.

To characterize maize leaf development, the relation between total number of leaf tips and TT calculated with the different temperatures was evaluated. The analysis of TT accumulation was separated into two stages. The first stage was between the third and the ninth leaf tip. The stage before the third leaf tip was not considered because the first and second tips appear faster than subsequent ones. The second stage analyzed was for leaf appearance above tip nine. At about leaf tip nine, the apex moved above the soil surface after rapid stem elongation started. Leaf development was highly correlated with TT calculated with the measured air, soil, and apex temperatures in all sowing dates, although the number of leaves measured was different among sowings because of our experimental difficulties for the first sowing and the early termination of the last sowing by frost. For the first sowing the number of leaf tips analyzed was nine because there was no soil temperature data available after tip nine. The total number of leaf tips measured for the second, third, and fourth sowing was 16, 15, and 6, respectively.

Although cumulative leaf tip appearance was highly related to TT calculated with either the air, apex, or soil temperatures in all cases since they all are cumulated in time, differences arise when the slope of the relationship, or the phyllochron value is considered. For the third to ninth leaf tip and the ninth to the last tip of the second and third sowing dates, the phyllochrons calculated using air TT (Table 3) were larger than the range of values reported by Ritchie and NeSmith (1991). In the first and fourth sowing, values of the phyllochron based on air temperature were within the range or slightly higher than those reported for tropical and subtropical environments (Carberry, 1991; Manrique and Hodges, 1991; Birch et al., 1998a). Larger values of the phyllochron in the first and fourth sowings could be caused by the bias between the apex and air temperature before tassel initiation, with lower irradiance increasing phyllochrons (Birch et al., 1998b). The PAR decreased from 9.3 MJ PAR m^{-2} d^{-1} in the first sowing to 5.1 MJ PAR m^{-2} d^{-1} in the fourth sowing date, while the air temperature also decreased from 21.5 to 14.9°C, respectively (Table 2). Using air temperature, differences in phyllochrons between sowing dates agree with those reported by Birch et al. (1998b). Phyllochrons calculated using apex temperature were close to the ones calculated using S5 temperatures for the second and third sowing and to S1 for the fourth sowing when the number of leaf tips where between three and nine. A difference of approximately 11°Cd per phyllochron was found when air TT was used instead of apex TT for the third to the ninth leaf tip and for the second and third sowing dates (Table 3). This bias will lead to an overcalculation of the total leaf number and consequently crop development by models that use a constant phyllochron based on air temperature (Kiniry and Bonhomme, 1991; Birch et al., 1998a; Stone et al., 1999). For the second and third sowings, the difference between the measured and calculated number of leaf tips using air temperature instead of apex temperature was equivalent to about 100°Cd or two leaf tips. After the appearance of the ninth leaf tip and when the apex was above the soil surface, phyllochrons calculated with air or apex temperature have similar values (Table 3), indicating the differences are determined while the apex is below the soil surface, where its is affected by soil temperatures rather than air temperatures.

When all tip appearance data were aggregated (Fig. 4) using apex TT for the last three sowing dates and soil TT calculated with S5 as a surrogate the apex temperature for the first sowing, the average phyllochron was 52.4°Cd (inverse of the slope), with the exception of the first two tips, which were not used in the regression. The accumulated tip number using apex TT agreed remarkably well for the diversity of thermal environments represented by the sowing dates. There were consistent deviations from the near linear relationship for all sowing dates, especially between leaf tip 11 and 14 where the rate of tip appearance was found to be somewhat faster. These small deviations in appearance rate may be attributed to the dynamics of leaf production,

Table 3. Phyllochron values (°Cd per leaf tip) for leaf tip number predictions calculated using thermal time (TT) obtained from air, apex, and soil temperatures at 1-cm (S1), 3-cm (S3), and 5-cm (S5) depths for four different sowing.†

TT	Sowing no. First	Second	Third	Fourth‡
	From the third to the ninth leaf tip			
Air	51.2 ± 1.1	44.2 ± 0.9	47.8 ± 1.0	49.8 ± 1.5
S1	61.7 ± 1.8	58.0 ± 0.8	61.4 ± 1.3	61.7 ± 2.2
S3	60.9 ± 1.6	56.9 ± 0.9	59.1 ± 1.2	63.9 ± 2.3
S5	59.7 ± 1.5	56.9 ± 0.9	57.8 ± 1.2	68.0 ± 2.5
Apex	–	55.1 ± 0.8	57.9 ± 1.2	55.5 ± 1.8
	From the ninth to the last leaf tip			
Air		46.7 ± 2.1	37.4 ± 2.0	
S1		51.1 ± 2.2	46.1 ± 2.3	
S3		50.4 ± 2.2	46.1 ± 2.2	
S5		50.4 ± 2.2	48.0 ± 2.2	
Apex		46.6 ± 2.1	39.6 ± 2.2	

† Coefficient of determination $r^2 = 0.99$ in all cases for the first, second, and third (from the third to the ninth leaf tip) and fourth sowing dates; $r^2 = 0.98$ in all cases for the second sowing date (from the ninth to the last leaf tip) and for S1, S3, S5 from the ninth to the last leaf tip in the third sowing date. $r^2 = 0.97$ for air and apex in the third sowing date. $P < 0.0001$ in all cases.
‡ Leaf tip three to six.

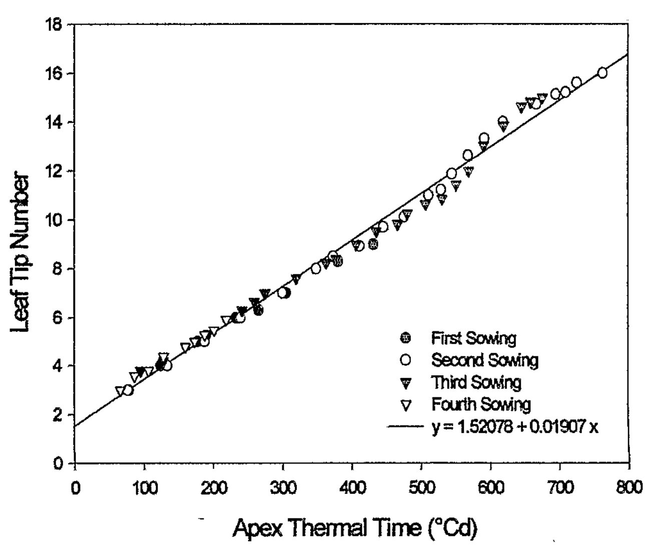

Fig. 4. Total number of leaf tips as a function of TT calculated using soil temperature at 5-cm depth (first sowing) and apex temperature for the other three sowing dates. Slope = 0.01907 leaves per °Cd, Phyllochron = 52.4°Cd per leaf tip.

e.g., the relationships between duration and rate of internode elongation and the variations in sheath and blade length. The slope was somewhat less for leaf tips 3 to 11. The rate of tip appearance was slightly lower after leaf 15, possibly because of the decreasing length of the last few leaves to appear before tassel appearance (Thiagarajah and Hunt, 1982), but we cannot draw definite conclusions because our data were so scarce in that range. These small deviation in leaf tip appearance rates are of little consequence in modeling if the average rate for the whole period of leaf development is approximately correct.

When phyllochron data from the entire leaf range for the second sowing date (Table 3) were averaged using air TT, the average phyllochron was 45.5°Cd, whereas the apex average was 50.9°Cd. These differences in phyllochrons calculated using air or apex temperatures clearly indicate a bias in using air temperature for the entire vegetative season and in using soil temperature at 3 to 5 cm depth after V6 under our experimental conditions. The results demonstrate that near-surface soil temperature should be used for calculating TT until stage V6, and air temperature should be used for the remainder of the vegetative growth stages. Because the temperature bias is consistently higher before V6, we believe this bias to be the primary reason for the differences in phyllochrons reported in the literature for field studies (Table 1), being mostly below the 52.4°Cd average we found.

Assuming that 52.4°Cd is near a constant for maize when the apex temperature is used for calculating TT, there appears to be a relatively large bias in growth cabinet phyllochron evaluations. Using a base temperature of 8°C and linearizing the growth cabinet data from Tollenaar et al. (1979), as done in Ritchie and NeSmith (1991), phyllochron values were about 39°Cd in the range of 10 to 33°C. If the observed results were related to a bias in temperature between the cabinet air temperature and the apex temperature, the bias would be about 4, 5, 7, and 10°C for growth cabinet air temperatures of 15, 20, 25, and 30°C, respectively. Growth cabinet experiments reported by Tollenaar (1999), in which light intensity was varied but with air temperature constant (avg. 24.5°C), there would be a temperature bias of approximately 7.5, 6.5, and 11.5°C, respectively, for treatments 10 h, 20 h low photosynthetic photon flux density (PPFD), and 20 h high PPFD. The 10 and 20 refer to photoperiod hours and the PPFD refer to high and low light intensity during the illumination cycle. If this analysis is approximately correct, the biases were proportional to the total radiation received as found in our study for plants in the prestem elongation phase.

CONCLUSIONS

This study clearly demonstrated under the conditions of our field experiment that there was a consistent bias between apex temperature and air temperature during early growth stages of crop development when the maize apex is below the soil surface. The bias was greater under conditions of high solar irradiance and less on cloudy days. Since the apex temperature was almost always warmer than the air while in the soil, the extent of error caused by the bias depends on the energy balance near the soil surface. It appears from our research and the summary provided by Birch et al. (1998b) that the bias is greatest when the air and soil temperatures are relatively low, as they are in temperate regions at the time of spring sowing. The error in estimating plant development caused by the bias between air and apex temperature at low temperatures can be quite large if the air temperature is near the base temperature. For example, if the average air temperature is 11°C and the bias on a clear day is 4°C warmer as we found on several days, the daily TT (base 8°C) is 3°Cd using air temperature and 7°Cd for the apex temperature. This large difference in development rate is reflected in the Birch et al. (1998b, their Fig. 2) data in which the phyllochrons in field locations with air temperatures near 12°C were about 27°Cd based on TT calculated with air temperature, or about half of the 52°Cd found in our study and in their report for air temperatures greater than 24°C.

The general agreement of phyllochron values of about 52°Cd between our limited scope field trial and the Birch et al. (1998b) analysis for warmer conditions where the soil heat flux is likely to be near zero for a 24-h period suggests that phyllochron values of about 52°Cd are the most appropriate for use in maize models if a single value is to be used throughout the leaf expansion cycle. This constant phyllochron argument applies only when the apex temperature is measured or reasonably estimated from soil temperature near the surface for vegetative stages up to about V6. Air temperature appears to be adequate for use in development simulation after V6. Since soil temperature is not usually measured in routine maize production trials, an accurate model of the near-surface soil temperature (2–5 cm) or the apex temperature (Guilioni et al., 2000) is needed for more accurate simulation of vegetative development from sowing to the V6 stage. Without the correction of the bias, the use of TT for accurate maize development simulation will require the use of calibrated phyllochron values that depend on the temperature and radiation of the region for the period between sowing and stem elongation.

Studies that have established the base temperature used in the TT concept have consisted of potentially biased field and growth cabinet studies. Therefore, it is possible that the base temperature of 8°Cd that has been derived from several studies may not be the most appropriate one. Since the base temperature has to be extrapolated from development rates measured at temperatures higher than the base and the low air temperatures appear to be the ones causing the largest bias in the field, it would be desirable to do future maize leaf development experiments in which the apex temperature is measured within a large enough range of temperatures to more accurately obtain an appropriate base temperature. We believe 8°C is approximately correct because we obtained almost identical phyllochrons for the four sowing dates in our experiment (Fig. 4) with a fairly large range of air temperatures.

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