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# THE DYNAMICS OF A MAIZE CANOPY DEVELOPMENT 2. LEAF AREA GROWTH*

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REID J. F., ZUR B. and HESKETH J.D. *The dynamics of a maize canopy development. 2. Leaf area growth.* BIOTRONICS **19**, 99–107, 1990. The results of two growth chamber experiments are used to demonstrate the influence of temperature and leaf position on the dynamics of leaf area emergence in maize plants. Maize plants were grown under temperature regimes of 30/24°C and 19/14°C with a day length of 16 h. Individual leaf area growth was measured at 2 to 5 day intervals from seedling emergence to anthesis on five plants at each temperature regime. Maximal individual leaf areas were expressed as a quadratic function of leaf position on the stalk and of temperature, with the higher temperatures producing smaller maximal leaf areas. Time-averaged leaf area growth rate was computed as the ratio of maximal leaf area and duration of leaf area growth. An equation was developed to relate time-averaged leaf area growth rate to leaf number and temperature. This equation in conjunction with equations representing the appearance of leaf tips and leaf collars was used compute individual leaf area growth in a maize canopy.

**Key words:** leaf area growth rate; maximal leaf area; maize canopy; time-averaged growth rate.

## INTRODUCTION

Solar energy absorption, assimilation of carbon dioxide and transpiration of water vapor all take place on the surfaces of plant leaves. Therefore, the dynamics of appearance of new leaves and of individual leaf area growth are of considerable importance. In grasses such as maize, leaf area growth involves mainly the enlargement of cells which were created inside the whorl. Appearance of a collar at the base of the leaf signals the termination of individual leaf area growth. The maximal area attained by a leaf is the product of its time-averaged rate of leaf area growth and its duration of leaf area growth. Duration of leaf area growth is determined

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by the difference between the time of appearance of a leaf tip and the time of appearance of a leaf collar. Zur *et al.* (*11*) showed that duration of leaf area growth in maize is inversely related to temperature and is a bell-shaped function of leaf position on the stalk. They proposed a generalized function relating duration of leaf area growth in maize to leaf number and temperature. Such an expression is the result of the difference between two functions relating the timing of leaf tip and leaf collar appearance to leaf number and temperature.

Information on individual leaf area growth in a maize canopy is surprisingly scarce. The sigmoidal-shaped increase in area with time for individual leaves has been described by logistic equations (*2*, *5*), the Gompertz equation (*1*, *2*), and Richards equation (*2*, *3*, *10*). Logistic and Gompertz equations employ three parameters while Richards equation uses four parameters to fit experimental results. Thus, it is not surprising to find that experimental results of individual leaf area growth could be adequately fit by these equations. However, these parameters do not appear to have any physiological significance. The value of using these equations is limited when the growth and development of individual leaves as part of the growth and development of the total leaf population of a plant is of interest. The parameters of these equations do not consistently represent the leaf-to-leaf changes in leaf area of the plant.

Another traditional method for representing leaf expansion has utilized the slope of the linear portion of the cumulative leaf area growth curve as the rate of expansion. The linear portion of the growth curve often represents the major period of leaf area growth, but it is a poor indicator of the time of leaf tip and leaf collar appearance. We propose to represent individual leaf area growth by the use of a time-averaged individual leaf area growth rate between the appearance of a leaf tip and leaf collar. An estimate of the time-averaged value is obtained by dividing the maximal leaf area attained by a leaf by its duration of leaf area growth. This approach lacks detail in the sigmoidal-shaped increase in leaf area over time, but provides a vital link between the phenological occurrence of leaf events and the area expansion of the individual leaves.

Dennett *et al.* (*3*) measured the appearance and growth of individual leaves of *Vicia faba* during two seasons under field conditions. They were not able to show a clear relationship between absolute leaf area growth rate and air temperature. However, they did observe a general dependence of leaf area growth rate on leaf position on the stalk. Hofstra *et al.* (*6*) observed a relationship between leaf area growth rate and leaf number for soybean plants but could not find a simple dependence of this rate on temperature. Dwyer and Stewart (*4*) reported a skewed, bell-shaped relationships between maximal leaf area and leaf position on the stalk in field grown maize plants. They also stated that the dependence of leaf area growth rate on temperature could not be generalized.

The final area attained by a leaf is difficult to predict. Temperature affects final leaf area in two ways; a positive effect through its influence on growth rate and a negative effect through its influence on duration of leaf area growth. In addtion, maximal individual leaf area depends on leaf position on the stalk (*4*). Also, leaf area growth rate and final leaf area are known to be sensitive to water and nitrogen stresses (*7*, *9*). The objective of the present paper was to analyze the growth and maximal area of individual leaves in a maize canopy under two temperature regimes and develop a method to represent individual leaf area expansion that links the increase in leaf area over time with the appearance of leaf tips and the maturity of leaves.

## MATERIALS AND METHODS

The experimental procedure was described in a previous paper (*11*). Temperature regimes used in the present study were 30°C day-24°C night (30/24°C) for experiment I and 19°C day-14°C night (19/14°C) for experiment II. Five plants in each temperature regime were sustained for the entire experimental period for collecting data on individual leaf area growth. Leaf area of individual leaves was obtained by measuring the length of leaf blades from their base to the leaf tip and the width of the leaf at its widest point and by multiplying the product of these values by a correction factor of 0.75 as suggested by McKee (*8*). The value of the correction factor was checked by calibrating against a commercial leaf area meter.

A linear leaf area growth rate was obtained by subjecting the values of measured leaf areas obtained during the linear growth stage to a linear regression analysis. Data points for the linear rate of growth were selected from plots of individual leaf area with time. Time-averaged leaf area growth rate was computed by dividing the measured maximal leaf area by the simulated duration of leaf area growth as proposed by Zur *et al.* (*11*).

## RESULTS AND DISCUSSION

Cumulative individual leaf area as a function of time for a number of leaf positions along the stalk are presented in Fig. 1 for the 30/24°C temperature regime and in Fig. 2 for the 19/14°C temperature regime. These figures illustrate the sigmoidal-shaped time course of individual leaf growth. Leaf position and temperature affect the shape of these curves and the maximal individual leaf area. In these experiments, maximal individual leaf area increased with leaf number up to leaf positions between 10 to 16 and then decreased with further increase in leaf number. Maximal individual leaf area was greatest under the cooler temperature regime.

Linear leaf area growth rates as a function of leaf position along the stalk under the two temperature regimes are presented in Fig. 3. Linear leaf area growth rates increased with leaf position along the stalk until leaf number 10 under the 30/24°C temperature regime and until leaf number 13 under the 19/14°C temperature regime. For the higher leaf positions, linear leaf area growth rates decreased with further increase in leaf number. It appears from the results presented in Fig. 3 that leaf position yields a larger influence on linear leaf area growth rate than temperature. Temperature effects on linear growth rates of individual leaves were clearly apparent for leaf numbers 1 to 11. No temperature effects could be observed for leaf num-

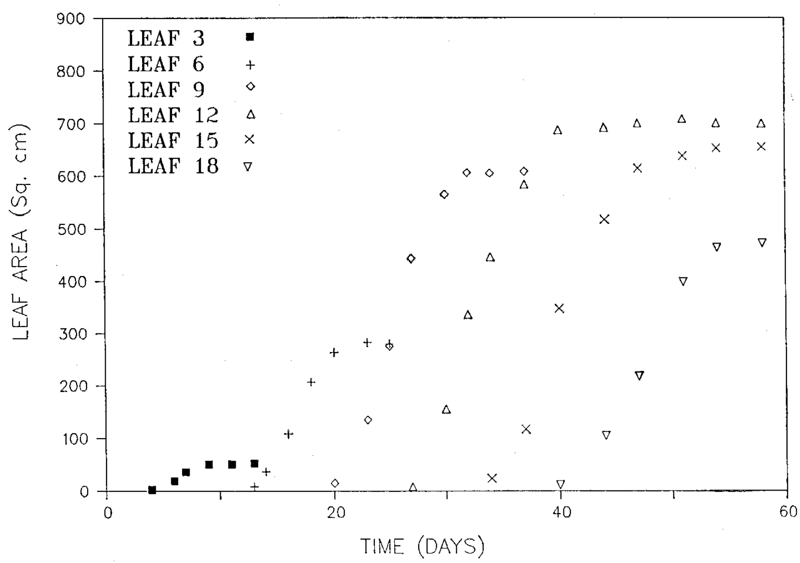


Fig. 1. Individual leaf areas for selected leaves under the 30/23°C temperature regime.

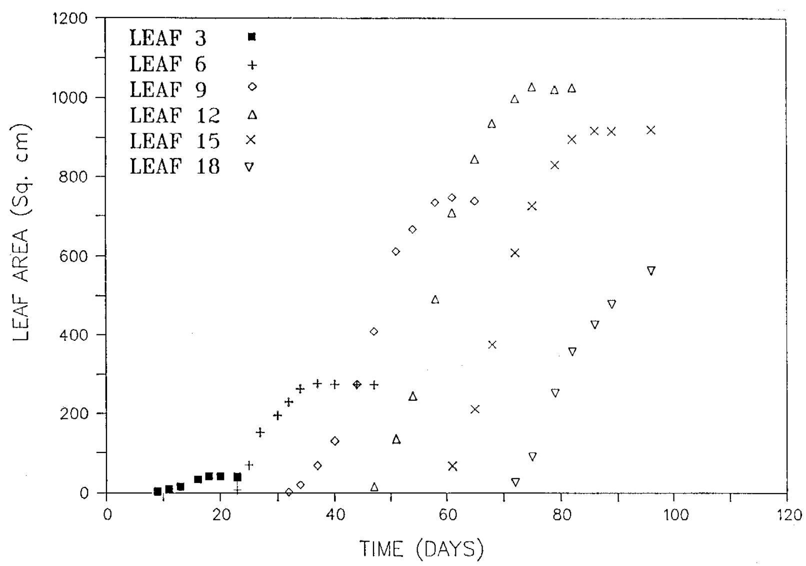


Fig. 2. Individual leaf areas for selected leaves under the 19/14°C temperature regime.

bers 12 to 17 while for the higher leaf numbers linear growth rates were higher for the warmer temperature regime. Our observations support reports by Hofstra *et al.* (*6*) and by Dwyer and Stewart (*4*) who concluded that a relationships between linear leaf area growth rate and temperature was not clearly apparent for soybean and maize leaves.

Measured maximal leaf areas as a function of leaf number for the two temperature regimes are presented in Fig. 4. Each data point value was an average of five plants. Maximal leaf area was a bell-shaped function of leaf position on the

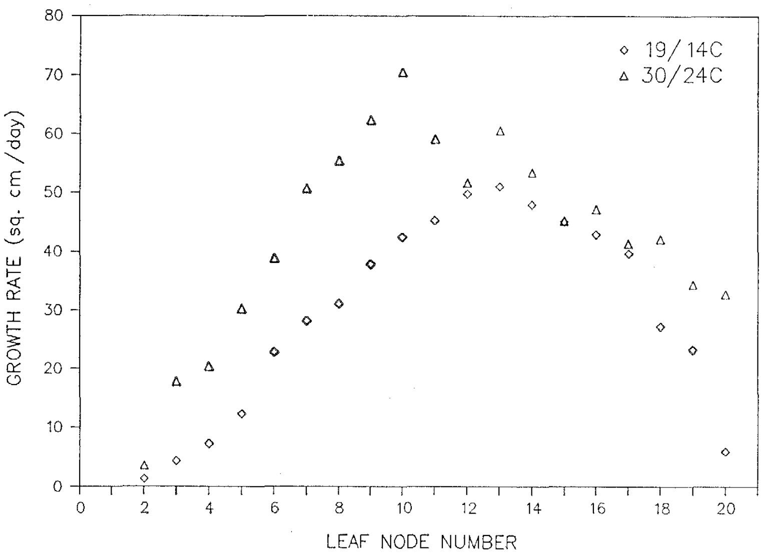


Fig. 3. The linear growth rates for individual leaf positions under the 30/23°C and 19/14°C temperature regimes.

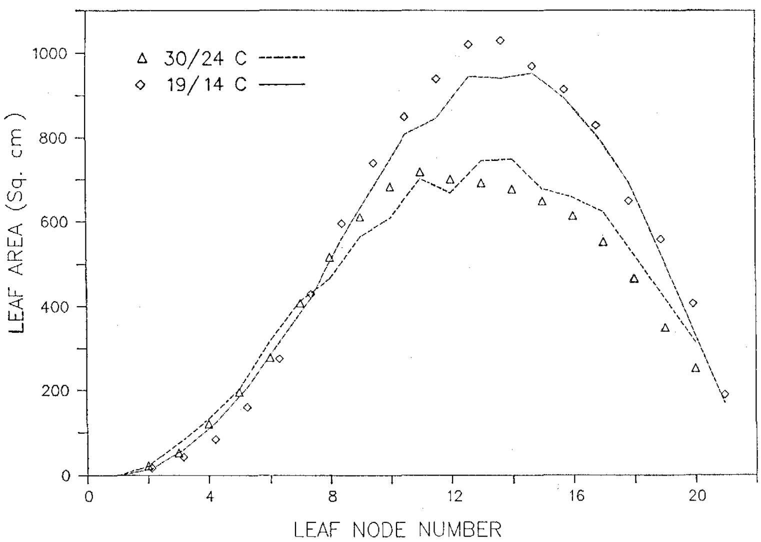


Fig. 4. Maximal leaf areas of individual leaves under the 30/23°C and 19/14°C temperature regimes.

stalk in agreement with data reported by Dwyer and Stewart (*4*). The effect of temperature on maximal leaf area depended on leaf number. Maximal leaf areas did not exhibit a temperature effect for leaves numbers 1 to 7 and 18 to 20. However, the maximal leaf areas for leaves 8 to 18 were consistently larger for the cooler, 19/14°C, temperature regime.

The time-averaged leaf area growth rate, $G_{av}$, was calculated by taking the ratio of the maximal individual leaf area and the equation for the duration of individual leaf area growth proposed by Zur *et al.* (*11*, Eq. (*9*)). Computed time-averaged

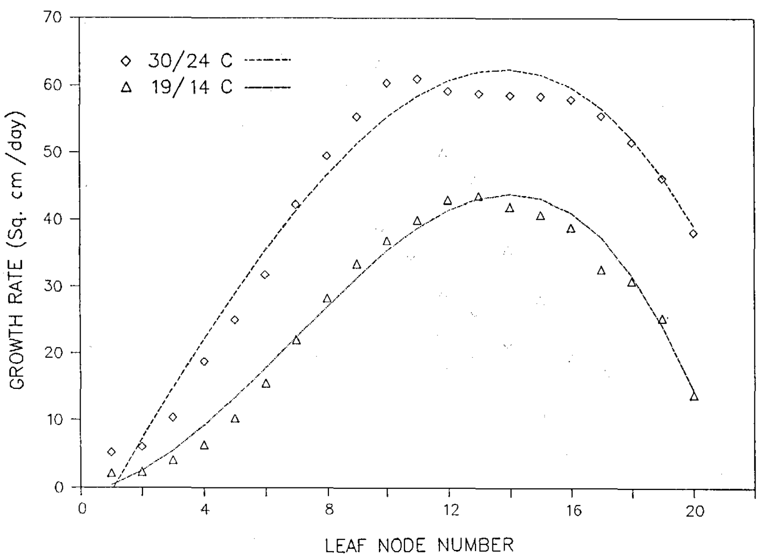


Fig. 5. Time-averaged growth rates for individual leaf positions under two temperature regimes.

individual leaf area growth rates as a function of leaf number under the two temperature regimes are presented in Fig. 5. An equation was developed for the time-averaged leaf area growth rate as a function of leaf number ($N$) and temperature ($T$). Leaf position effects were modeled with a cubic relationship and temperature effects were assumed to be linear,

$$\begin{aligned} G_{av} = & -0.7571(T-15.65)+0.7176(T-15.78)N-0.0623(T-26.22)N^2 \\ & +0.00171(T-33.83)N^3 \end{aligned} \quad (1)$$

The solid lines in Fig. 5 represent the solution of Eq. (1) for the two temperature regimes.

Using equations for leaf tip appearance and leaf area growth duration proposed by Zur *et al.* (*11*) and Eq. (1), cumulative leaf area growth curves for leaves numbers 4, 8, 12, and 16 were generated and compared with experimental results in Fig. 6 for the 30/24°C temperature regime and in Fig. 7 for the 19/14°C temperature regime. The curves were generated using a LOTUS 1-2-3 spreadsheet. For each day, an average experimental temperature was used to generate a rate of leaf tip appearance and a rate of leaf maturity using equations from Zur *et al.* (*11*). The daily rates were accumulated to provide an estimate of the total number of leaf tips and mature leaves on the plant at that point in time. Areas for the individual leaves were generated using Eq. (1) to calculate the time-averaged growth rate. Before a leaf tip appeared, the growth rate was zero. From the appearance of the leaf tip to the maturity of the leaf, the leaf area increased daily at the time-averaged growth rate. After the maturity of the leaf, leaf area was held at the maximal value. Generally, this method was successful in computing the leaf area growth rates for all the leaves under both temperature regimes. Leaves appeared and matured at the proper time and the rate of growth was similar to the slope of the linear portion

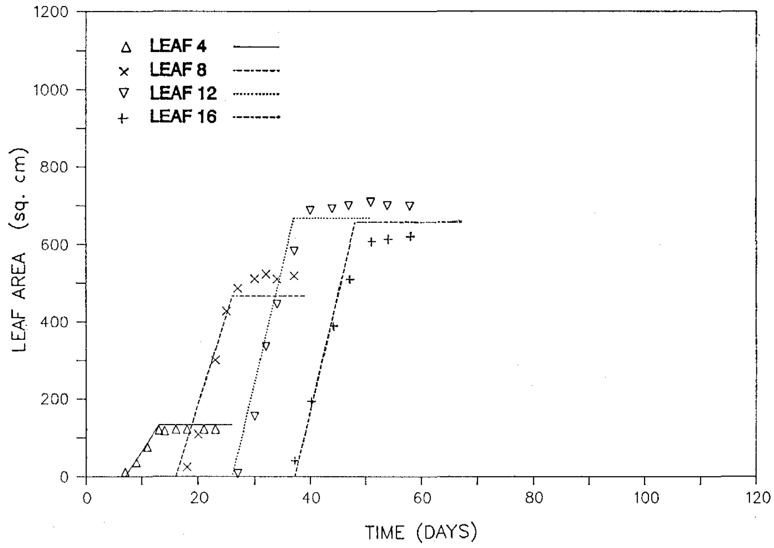


Fig. 6. Individual leaf areas for leaves 4, 8, 12 and 16 under the 30/23°C temperature regime.

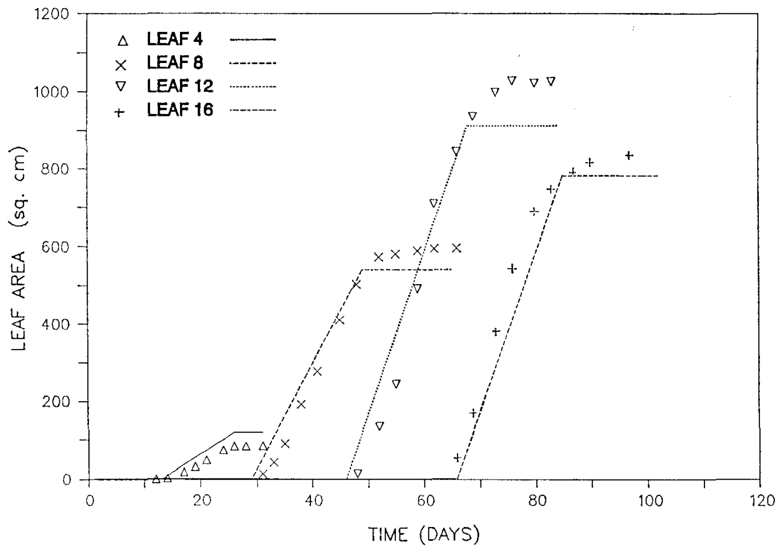


Fig. 7. Individual leaf areas for leaves 4, 8, 12 and 16 under the 19/14°C temperature regime.

of the sigmoidal-shaped growth curves. The maximal leaf areas for these equations are plotted as solid lines in Fig. 4. These results compared favorably with the experimental data points. Computed maximal leaf area that deviated from the experimental values resulted from using discrete daily intervals in the spreadsheet calculation of leaf tip appearance and leaf maturity. Thus, the calculated duration of growth was limited to a discrete number of days.

Cumulative plant leaf area as a function of time was computed by summing up the individual leaf areas generated in the spreadsheet at various times. Computed

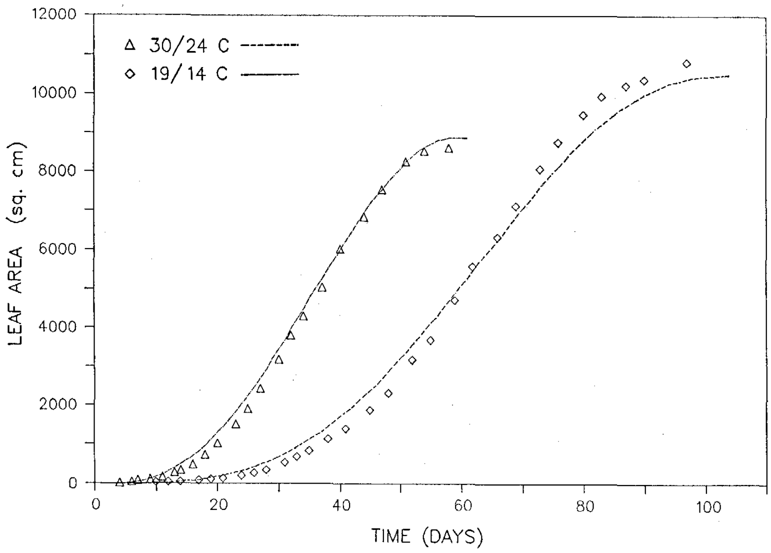


Fig. 8. Total plant leaf area for the 30/23°C and the 19/14°C temperature regime.

results for the two temperature regimes are compared with measured values in Fig. 8. Under the low temperature regime the process of leaf area accumulation spans over a longer time but reaches a considerably higher value compared to the process under the warmer temperature regime. The time course of computed and measured cumulative plant leaf areas under the two temperature regimes was similar.

## SUMMARY AND CONCLUSIONS

The dynamics of individual leaf area formation was defined as the product of the rate of individual leaf area growth and the duration of its growth period. The rate of leaf area growth is a positive function of both leaf number and temperature, with leaf position yielding a greater influence. Duration of individual leaf area growth depends on leaf number and on temperature with temperature having a negative effect. The dependence of leaf area growth rate and duration of leaf area growth on leaf number was found to be bell-shaped. In the present paper we have defined time-averaged leaf area growth rate as the ratio between maximal leaf area and duration of leaf area growth. Based on results from our limited controlled growth chamber experiments, an equation representing the time-averaged leaf area growth rate as a function of leaf number and temperature were developed. This equation, in conjunction with equations representing the appearance of leaf tips and leaf collars were used to compute individual leaf area development and growth in a maize canopy.

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