SIMULATING COTTON PLANT HEIGHT AND LEAF AREA DEVELOPMENT

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Abstract

Cotton (*Gossypium hirsutum* L.) is grown commercially in temperatures that vary greatly during the season. Understanding response patterns of leaf and internode expansion and duration of growth to temperature is essential to building a process-level crop simulation model. Such a model would be useful to aid in-season strategic management decisions. Plants were grown in sunlit plant growth chambers in five temperatures, 20/12°C to 40/32°C (day/night), at ambient (350 µl l^{-1} CO_2) and twice ambient carbon dioxide levels in well watered and fertilized conditions. Plants were monitored daily for leaf unfolding dates, areas of leaves, and lengths of internodes at leaf unfolding, and growth of leaves and internodes. Durations of leaf and internode expansion were also determined. Leaf unfolding interval rates of both mainstem and fruiting branches increased as temperature increased; the rate of mainstem leaf unfolding interval increased more than the rate of branch leaf unfolding. Irrespective of sizes, leaves and internodes fit a single relationship of relative expansion rates and age for each temperature condition. Enriching CO_2 to twice the ambient level did not change these relationships. Increasing temperature increased maximum growth rate, decreased the decay in the rate of expansion due to age, and reduced growth duration of both leaves and internodes. Internodes typically took less time than leaves to elongate at all temperatures. Leaf area and internode length at leaf unfolding increased as temperature increased to 27°C to 30°C, then decreased at higher temperatures. Leaf area at unfolding increased with mainstem node number until the plants started producing squares, about node 5, and produced smaller leaves thereafter. Internode lengths at leaf unfolding also increased as position on the mainstem increased until the plants started producing fruit, about node 15, and produced progressively shorter internode lengths at higher node positions. The relationships between temperature and rate functions such as leaf unfolding interval rates, maximum rate of growth, rate of decay with age, and expansion duration rate combined with leaf and internode sizes at leaf unfolding provide the necessary functional parameters to build process-level simulation models.

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Introduction

Internode and leaf area extension are recognized as basic phenomena of shoot morphogenesis and growth. Internodes elevate other organs, particularly, leaves for effective photosynthetically active radiation capture and interception (Alm et al., 1991; Morrison et al., 1994). Anatomical and physiological aspects of growth have been described (Alm et al., 1991; Hesketh et al., 1991; Morrison et al., 1994), but few studies have investigated both morphogenesis and extension of individual plant organs .

Cotton is indeterminate in growth habit where the mainstem apex initiates leaves and axillary buds continuously. The axillary buds on the lower nodes develop into vegetative branches if conditions are favorable. The upper nodes, normally above node five, develop into fruiting structures. Vegetative branches behave much like the mainstem in that they produce both vegetative and fruiting branches. Fruiting branches, on the other hand, initiate one true leaf and then terminate as a flower. Branch elongation is accomplished by growth of axillary buds producing a sympodial zigzag structure (Mauney, 1984; Mutsaers, 1983a). Thus, the potential patterns of growth are determined by the apical and axillary meristems. Temperature, water, and nutrient supply influence the growth pattern by affecting both growth and developmental processes. The growth and development of each plant organ are influenced by competition from other organs as well as environmental conditions. Some growth and developmental processes slow or hasten when supply/demand ratios for photosynthate change (Mutsaers, 1983a, 1983b; Reddy et al., 1991; 1992; Hodges et al., 1993).

Development plays a pivotal role in crop production systems, controlling the production rate of new leaves, the total number of leaves produced, the duration of leaf area expansion of each leaf, and plant height extension (Warrington and Kanemasu, 1983; Baker et al., 1978). Although some information on leaf growth in cotton is available in the literature (Hesketh et al., 1972; Constable and Rawson, 1980; Mutsaers, 1983a, 1983b; Reddy et al., 1993a), very little information is available on internode growth, particularly in response to temperature. Reddy et al. (1993b) and Wells and Meredith (1984) showed that modern commercially grown cultivars have faster growth and developmental rates compared to cultivars grown two or three decades ago. Therefore it is essential to study the growth and development of modern cotton cultivars.

To mechanistically simulate plant height and leaf area development throughout the season, it is essential to simulate potential leaf and internode growth rates. The mechanism of internode expansion is similar in both dicots and monocots. Several authors illustrated that internode development is acropetal in dicots and basipetal in monocots primarily due to the location of intercalary

meristems (Evans, 1965; Sachs, 1965; Kaufman et al., 1965; Garrison, 1973; Easu, 1977; Morrison et al., 1994). Internodal expansion follows a sigmoidal growth curve, with the lower-growing internode completing its expansion phase as the upper-growing internode is beginning its expansion phase. In a detailed study of *Helianthus* internode elongation, Garrison (1973) described growth of each internode as resulting from simultaneous cell division and cell expansion. Expansion of each internode occurred in a wave of activity from the basal portion toward the apex over time.

Because crop simulation models are being used to aid on farm production decisions, there is considerable interest to more accurately predict the growth and developmental processes of crop plants. Simulating plant height and leaf area development is being used in several models to predict solar energy capture (Hodges and Ritchie, 1991; Baker et al., 1983). It is, therefore, important to accurately predict leaf and stem growth to successfully model other developmental and growth processes. As cotton is grown in a wide range of temperature conditions ranging seasonally from 5°C to 40°C with daily amplitudes from 10°C to 25°C (Reddy et al., 1995a), it is necessary to generate temperature response functions based on a wide range of temperature conditions.

The objective of the present investigation was to parameterize cotton leaf and internode growth under maximum growing conditions as functions of temperature. This information will be useful in building process-level simulation models. Such models are used to study various aspects of cotton growth and development, and to make strategic management decisions in a production environment. In this study we also examined the interactive effects of temperature and CO_2 enrichment on stem and leaf growth patterns. That information will be useful for developing process-level simulation models for either present-day environments or for future climatic conditions.

Materials and Methods

Soil-Plant-Atmosphere-Research (SPAR) units

The closed environment plant growth chambers, SPAR units, used for this study were described in detail by Phene et al. (1978), Acock et al. (1985) and Reddy et al. (1992). The SPAR units are located outside and control temperature and CO_2 concentration at predetermined set points for plant growth studies in natural solar radiation regimens. Each SPAR unit consisted of a steel soil bin (1 m tall by 2 m long by 0.5 m wide), a plexiglass chamber (2.5 m tall by 2.0 m long by 1.5 m wide) to accommodate aerial plant parts, a heating and cooling system, and an environmental monitoring and control system. The plexiglass allows 98% of solar radiation to pass without spectral variability in absorption.

Variable-density shade cloths around the edges of plants were adjusted regularly to match plant heights simulating the presence of other plants and eliminating the need for border plants. Air ducts located on the northern side of each SPAR unit connected the heating and cooling devices to each unit. Conditioned air passed through the plant canopy with sufficient flux to cause leaf flutter and returned to the ducts just above the soil level.

Chilled ethylene glycol was supplied to the cooling system via several parallel solenoid valves that opened and closed depending on the cooling requirement. Electrical resistance heaters provided short pulses of heat, as needed, to fine tune the air temperature control. A dedicated computer (Digital, Pro 380, Digital Equipment Corp., Maynard, MA) controlled air temperature, CO_2 concentration, and soil watering in each SPAR unit. The computer also conducted continuous monitoring of all important environmental and plant gas exchange variables.

Air temperature in each SPAR unit was monitored and adjusted every 10 s throughout the day and night and summarized over 900 s intervals. Air temperatures were maintained within ±0.5°C of treatment set points. The daytime temperature was initiated at sunrise and returned to the nighttime temperature 1 h after sunset. Average daily temperature was calculated by summing the average temperatures for each 900 s period during the day providing 96 per day.

The CO_2 concentrations in each SPAR unit were also monitored and adjusted every 10 s throughout the day. The CO_2 concentration was maintained within ± 10 µl l^{-1} of treatment set points during the daylight hours. Solar radiation was measured with a pyranometer and data summarized over 900 s intervals. Average daily total solar radiation during this experiment was 21.2 MJ m^{-2} d^{-1} with the highest and lowest radiation days having 29.9 and 5.8 MJ m^{-2} d^{-1}, respectively.

Plant culture

Cotton cultivars DPL 51, Acala Maxxa, and Paymaster HS 26 were selected because they represent a large portion of the commercial cotton produced in this country, and are adapted to diverse environments. In the Midsouth, DPL 50 is widely grown and, with DPL 51 which it is replacing, represented 18% of the total cotton acreage grown in the nation in 1994. Acala Maxxa constituted 59% of the cotton acreage in the irrigated desert of California, and Paymaster HS 26 was produced on 41% of the acreage grown in the high plains of Texas and Oklahoma (USDA-AMS, Cotton Division, 1994).

Seeds were pregerminated in moistened paper towels at 30°C for 12 h. The imbibed seeds, with radicles emerging, were selected for uniformity and planted in the ten SPAR units on 26 April 1994. Seeds were planted in three rows of five plants per row, one row per cultivar. These rows

were 667 mm apart. The soil bins were filled with pure, fine sand. Five SPAR units were maintained at 350 µl l^{-1} of CO_2 while the other five were maintained at twice ambient CO_2 concentration (700 µl l^{-1}). Air temperatures were controlled at 30/22°C (day/night) in all units. Fifty percent emergence was observed 4 d after planting. On 25 May 1994, 25 DAE, the day/night temperature cycles of 20/12°C, 25/17°C, 30/22°C, 35/27°C, and 40/32°C were imposed at each CO_2 treatment. The average temperatures were 17.4°C for 20/12°C, 22.4°C for 25/17°C, 27.1°C for 30/22°C, 31.9°C for 35/27°C and 35.9°C for 40/32°C during the 42 days of treatment. The reasons to grow the plants at 30/22°C for the first 25 DAE were to have uniform plants in a linear growth phase at the beginning of the temperature treatment and to have vigorously growing healthy plants.

A computer-controlled timing device applied half-strength Hoagland's nutrient solution (Hewitt, 1952) to each row of plants via a drip irrigation system. The total water added each day was twice the previous day's evaporation from a standard evaporation pan located about 50 m from the site. Excess water was allowed to drain from a small opening at the bottom of the soil bin.

Growth and Developmental Measurements

Daily measurements were obtained on lengths of mainstem leaves 10, 11, and 12 and their subtending internodes on all plants. Plant height extension and total leaf area growth rates were linear when these leaves unfolded. Leaf and internode length measurements were started when the leaf at that particular position was unfolded. Leaf length was measured from the point of petiole attachment to the tip of the center lobe. Individual leaf areas were calculated from the relationship $A = 7.4585 - 0.1688 * L + 0.097 * L^2$; $R^2 = 0.99$, where A is area in cm^2, L is length in mm. The relationship was developed by measuring lengths and areas of leaves of different ages at the end of the experiment with a leaf area meter (Hayashi Denko Co., Tokyo, Japan). Leaf expansion and internode elongation durations were estimated from the time of leaf unfolding until final size was attained. Leaf unfolding was defined when three main veins were visible from the upper side of the leaf; therefore the leaf unfolding event, and leaf area and internode length at the time of leaf unfolding may be observed as discrete events and measurements. The maximum size of each organ was defined as the size when no additional growth was found for three consecutive days. Leaf unfolding dates on successive leaves 10 to 15 on the mainstem and on fruiting branch leaves on branch 10, 11, and 12 were observed.

Analysis of data

Statistical analysis was conducted by descriptive statistical procedures of general linear models (SAS Institute, 1990). The standard errors of each mean were calculated and presented in the figures. Standard errors of the mean were determined from measurements of 15 plants per SPAR unit as there were no significant differences (p=0.05) on any of the parameters measured among cultivars. As there was no significant difference between the observed parameters for CO_2 concentrations, we used the both CO_2 treatments for generating the rate parameters.

Results and Discussion

Leaf Unfolding Interval Rates

Developing mainstem and fruiting branch nodes are important aspects of cotton development because these determine the number of leaves produced, and thus canopy development and photosynthetically active radiation interception. Figure 1 depicts the rate of leaf unfolding intervals on the mainstem and on fruiting branches as functions of temperature. Daily developmental rates were accumulated until the cumulative value equals one or greater, which predicts a new leaf either on the mainstem or on the fruiting branches. Developmental rates were not linear over the biologically meaningful-temperature range and quadratic fit to the data proved superior to other forms. Leaf unfolding interval rates of both mainstem and fruiting branch leaves increased with increasing temperature. At 30°C, 2.2 days were required to produce a new leaf on the mainstem, while 5.0 days were needed to produce a leaf at 20°C. Fruiting branches, on the other hand, required 9.5 days at 20°C and 6.0 days at 30°C. The ratio of mainstem and fruiting branch leaf unfolding interval was not constant as assumed by others (Hearn, 1969; Mutsaers, 1983a) and decreased at higher temperatures. Thus, the growing temperature alters the architectural form of the plant. Leaf unfolding intervals, generally referred in the literature as phyllochron intervals, were not different from square appearance intervals in cotton. Similar results were reported by Hesketh et al. (1972) and Reddy et al. (1993b). Squares will normally appear when the leaf at a given node is unfolded with main veins visible from the top. Defined in this way, the same response rate functions can be applied for square intervals to mark the appearance reproductive organs.

The daily developmental rates (Y) for mainstem and fruiting branch leaf unfolding intervals as functions of temperature are as follows:
Mainstem leaf unfolding interval rate:

$$\mathbf{Y = -0.6698 + 0.0570 * X - 0.0006765 * X^2;\ R^2 = 0.94,} \qquad \textbf{Eq. 1}$$

Fruiting branch leaf unfolding interval rate:

$$\mathbf{Y = -0.3645 + 0.03389 * X - 0.0005199 * X^2;\ R^2 = 0.84,} \qquad \textbf{Eq. 2}$$

where X is average temperature for that period.

Leaf Expansion and Internode Elongation Duration

The reciprocals of duration of leaf expansion and internode elongation from leaf unfolding are presented in Fig 2. The reciprocal of time between two events is a measure of the

rate at which these processes are completed. Internodes typically took less time to reach final size compared to leaves at all temperatures and the ratios between leaf and internode expansion durations decrease as temperature increased. Hesketh et al. (1972) found a linear relationship between leaf expansion duration and temperature for the cultivars used two or three decades ago. Leaf petiole elongation occurred simultaneously with lamina expansion. Leaf expansion duration at a particular temperature was similar despite leaf position on the mainstem (Reddy et al., 1993b).

The equations describing daily developmental rates (Y) as functions of temperature are as follows:
Mainstem leaf expansion duration rate:

$$Y = -0.09365 + 0.01070 * X - 0.0001697 * X^2;\ R^2 = 0.95, \quad \text{Eq. 3}$$

Mainstem internode elongation duration rate:

$$Y = -0.04312 + 0.007383 * X - 0.0001046 * X^2;\ R^2 = 0.96, \quad \text{Eq. 4}$$

where X is average temperature for that period.

Leaf Area Expansion and Internode elongation Rates

From daily measurements of leaf area and the subtending internode length, rate functions were calculated by plotting relative leaf expansion rate (RLER) and relative internode elongation rate (RIER) as functions of days after leaf unfolding for each leaf and internode in each treatment. The linearly-extrapolated intercepts, maximum RLER (cm^2 cm^{-2}) or maximum RIER (cm cm^{-1}) at day 1, and the slopes, the rates of growth reduction for leaf or internode with age, (cm^2 cm^{-2} d^{-1} for leaves or cm cm^{-1} d^{-1} for internodes) were calculated and presented in Fig 3 and 4 as functions of temperature.

The equations describing these rate parameters for leaves as functions of temperature are as follows:
Intercept (Maximum RLER, cm^2 cm^{-2}) (Y):

$$Y = -0.03390 + 0.02041 * X;\ R^2 = 0.95, \quad \text{Eq. 5}$$

Slope (Rate of reduction with age, cm^2 cm^{-2} d^{-1}) (Y):

$$Y = 0.01341 - 0.001879 * X;\ R^2 = 0.98, \quad \text{Eq. 6}$$

where X is average temperature for that period.

The equations describing these rate parameters for internodes as functions of temperature is as follows:
Intercept (Maximum RLER, cm cm^{-1}) (Y):

$$Y = -0.001427 + 0.0166 * X;\ R^2 = 0.97, \quad \text{Eq. 7}$$

Slope (Rate of reduction with age, cm cm^{-1} d^{-1}) (Y):

$$Y = 0.02479 - 0.001994 * X;\ R^2 = 0.97, \quad \text{Eq. 8}$$

where X is average temperature for that period.

The intercepts and slopes for leaves and internodes changed progressively with temperature, and the two are apparently inversely related. The maximum RLER was 23% higher than the maximum RIER across temperatures while the slope or the rate of reduction with age was 5% lower for the leaves than the internodes. The effect of temperature on the final area of a leaf or final length of an internode is the net result of both temperature effects on duration (Fig 2) and rates of growth (Fig 3 and 4).

Leaf Area and Internode Length at Leaf Unfolding

Leaf area and internode length at leaf unfolding increased progressively with mainstem node number over the growing season, and the increase is associated with major reproductive events on the plant (Fig 5 and 6). The equations describing initial leaf area in cm^2 (Y) as a function of mainstem node number are as follows:
Leaves 1 to 6:

$$Y = 6.061 + 1.8069 * X;\ R^2 = 0.91, \quad \text{Eq. 9}$$

Leaves 7 and above:

$$Y = 18.3812 - 0.523 * X;\ R^2 = 0.95, \quad \text{Eq. 10}$$

where X is mainstem node number for plants grown at 27.1°C.

Initial leaf areas increased linearly to leaf six on the mainstem and then declined. In a separate study using pima (*Gossypium barbadense* L.) cotton, cv. S-6, grown at 30/22°C for 93 days, mature leaf sizes followed a similar pattern on the mainstem as found for leaf sizes at leaf unfolding in this experiment (Fig. 7). Mature leaf sizes increased as mainstem node number increased until node six was produced, then succeeding mature mainstem leaves were progressively smaller with higher node numbers. In that study, the first square was produced on the fruiting branch on node six. A possible explanation is that initial leaf sizes and leaf area expansion were competing with branches and reproductive structures for photosynthates. In this experiment, squares were formed when the leaf at node five was unfolded; and fruiting branches and other reproductive structures started being initiated more rapidly with time and competed for the same resources. Bolls were first produced when the leaf at node 15 was unfolded. Similar patterns in mature leaf areas were observed in the field (Constable and Rawson, 1980; Constable, 1986), and in the growth chamber studies (Mustsaers, 1984a). Mutsaers (1983a) found a positive relationship between leaf sizes and cell number.

Initial Internode length, on the other hand, increased linearly as node number increased until the plants started to produce bolls and then each succeeding internode length was shorter. Mature internode lengths also followed a

similar pattern on the mainstem as found for internode lengths at leaf unfolding. Mature internode lengths increased as mainstem node number increased until nodes 15 to 17; then subsequently produced internodes were progressively shorter. Again, the first flower was produced at the time the leaf on node 17 was unfolding (Fig. 7). Mature internode lengths were correlated with internode lengths at leaf unfolding ($R^2 = 0.78$). It seems likely those potential internode lengths and leaf areas are determined at or before leaf unfolding. Similar results were observed for mature internode lengths in growth chamber grown plants (Mutsaers, 1984).

The equations describing initial internode lengths in cm (Y) as a function of mainstem node number are as follows: Internodes 1 to 14:

$Y = 0.05738 + 0.05605 * X; R^2 = 0.93,$ **Eq. 11**

internodes 15 and above:

$Y = 1.3589 - 0.0407 * X; R^2 = 0.91,$ **Eq.12**

where X is mainstem node number for plants grown at 27.1°C.

Leaf area and internode lengths at leaf unfolding for leaves 10, 11 and 12 increased as temperature increased to about 27° to 30°C and declined at higher temperatures.

The equations describing initial leaf area in cm^2 (Y) and internode lengths in cm (Y) as functions of temperature are as follows:

Leaves, $Y = - 18.599 + 2.186 * X - 0.0381 * X^2; R^2 = 0.62,$ **Eq. 13**

Internodes, $Y = - 0.06853 + 0.1077 * X - 0.002031 * X^2; R^2 = 0.11,$ **Eq. 14**

where X is the average temperature for that period.

Branch initial leaf area decreased linearly with nodes on the branches. The equation describing initial leaf area in cm^2 (Y) as a function of branch node number is as follows:

$Y = 13.457 - 1.179 * X; R^2 = 0.98,$ **Eq. 15**

where X is the branch node number.

This is consistent with the change in mature leaf size by position on the branch (Mutsaers, 1983a). This suggests that leaf size be largely determined by number of cells formed before the leaf begins to expand.

Summary and Applications

Leaf area, vertical leaf area distribution, and plant height are the major factors determining photosynthetically active radiation (PAR) interception by row crops. Total leaf area is determined by the number and size of individual leaves in the canopy with the space between leaves also strongly influencing PAR interception. The time required to initiate a new leaf, and the growth rate and duration of the expansion process determine both the rates of individual leaf growth and the vertical extension of the canopy (Fig. 1, 2, and 3). We found that the sizes of leaves at unfolding also helped predict final leaf size, and this was influenced by both node positions on the mainstem (Fig. 5), and temperature. Area of leaves produced on the fruiting branches was influenced by position on the fruiting branches and by temperature. The information provided can be used to estimate the time required to produce new leaves, and thus the potential leaf area of a complete canopy.

Plant height is also a summation of all its internode parts. Information provided on the time required to initiate a node (Fig. 1), the influence of temperature on the duration of elongation (Fig. 2), rate of elongation (Fig. 4), the variation of internode lengths on the mainstem (Fig. 6) and the influence of temperature on initial internode length can be used to estimate the length of individual internodes and more importantly plant height. Leaf area and internode length at leaf unfolding is influenced by reproductive status of the plant. The maximum leaf area at leaf unfolding occurred at first square and the maximum internode length at leaf unfolding occurred at first flower (Fig. 5 and 6).

The step by step model development and applications are as follows:

1. Cotton potential leaf unfolding interval rates can be described with Eq. (1) and Eq. (2). Vegetative branch leaf unfolding intervals follow the mainstem axis. Of course nutritional, and water deficit effects must be added to account for morphogenetic delays of these processes to simulate field grown cotton.

2. Once the leaves and internodes are initiated, their potential growth can be simulated with three rate functions: growth duration, maximum RLER or RIER, and rate of decay with age (Eqs. 3 to 8).

3. Variable internode lengths or leaf areas on the mainstem and on branches can be simulated by using initial values from Eqs. 9 to 15 assuming ontogenetic patterns seen in the mature internode and leaf profiles are set at or before leaf unfolding.

4. Potential growth of plant height or whole plant leaf area simulation can be generated by integrating the growth rates of successive internodes on the mainstem or all the leaves both on the mainstem and branches capable of growth. Information on the response of canopy development to temperature is scarce. Parameterizing the response functions to temperature under potential growing conditions makes the data unique and important.

Nutritional and water deficit effects should be used to decrement these potential growth rates to simulate cotton growth in a production environment.

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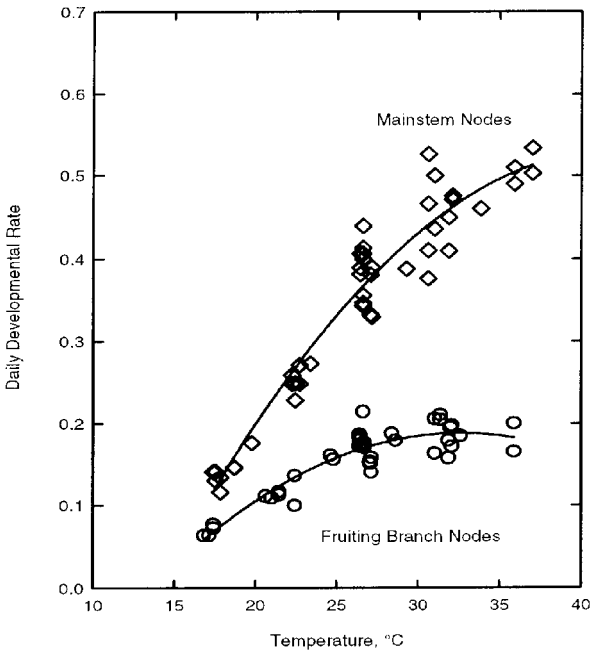

Figure 1. The influence of temperature on daily developmental rate (the reciprocal of time between two successive leaf unfolding events) of mainstem and fruiting branch nodes. The data were collected from several cultivars grown at ambient (350µl l^{-1}) and twice ambient CO_2 levels. No significant differences were observed between CO_2 levels and also between cultivars (Reddy et al., 1993).

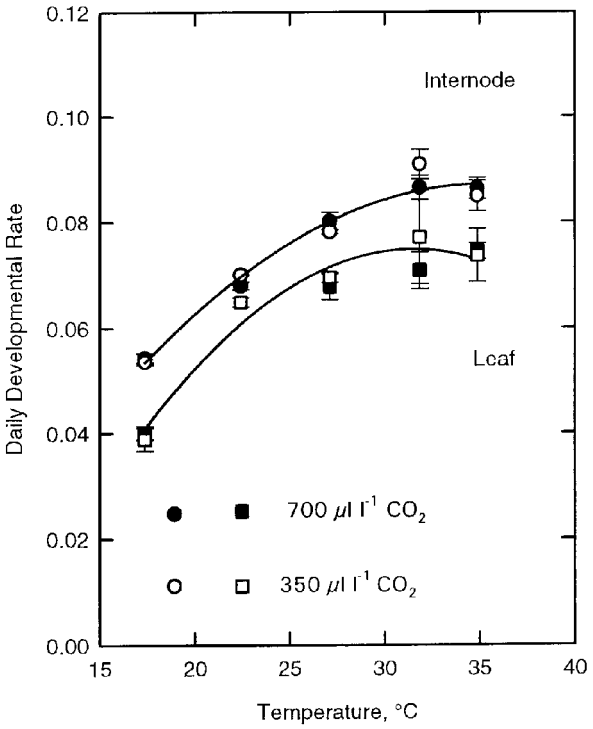

Figure 2. Influence of temperature on extension duration of leaves and internodes estimated by the recipropcal of time from leaf unfolding to final leaf or internode size.

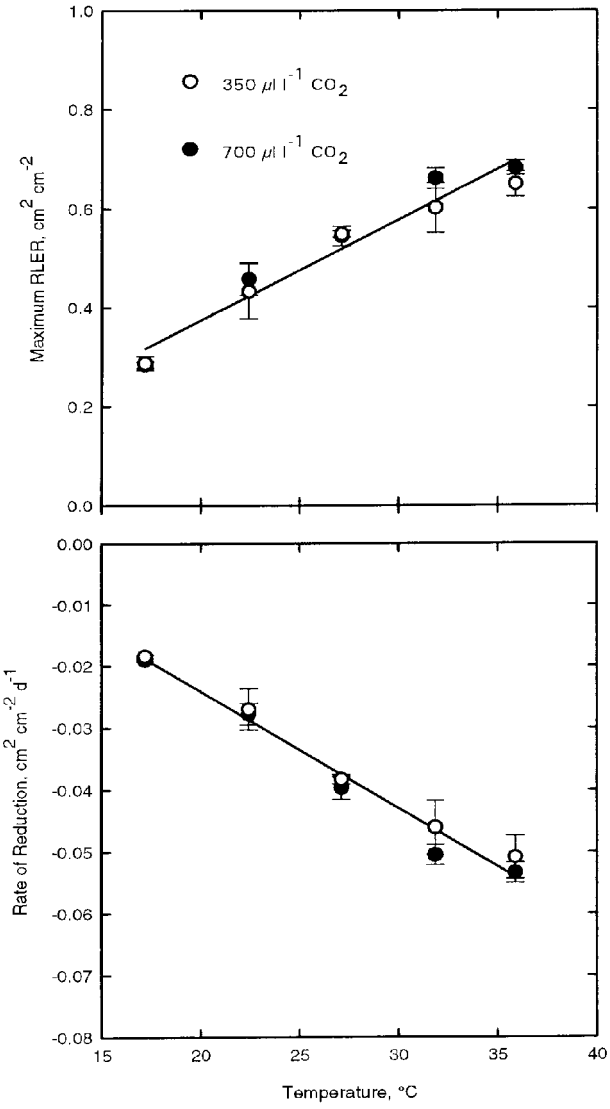

Figure 3. Influence of temperature on maximum relative expansion rate (RLER) and rate of reduction with age (reduction rate or slope, $cm^2\ cm^{-2}\ d^{-1}$). The maximum RLER and slope were calculated by linear regressions fitted between leaf age and relative leaf expansion rate for each leaf.

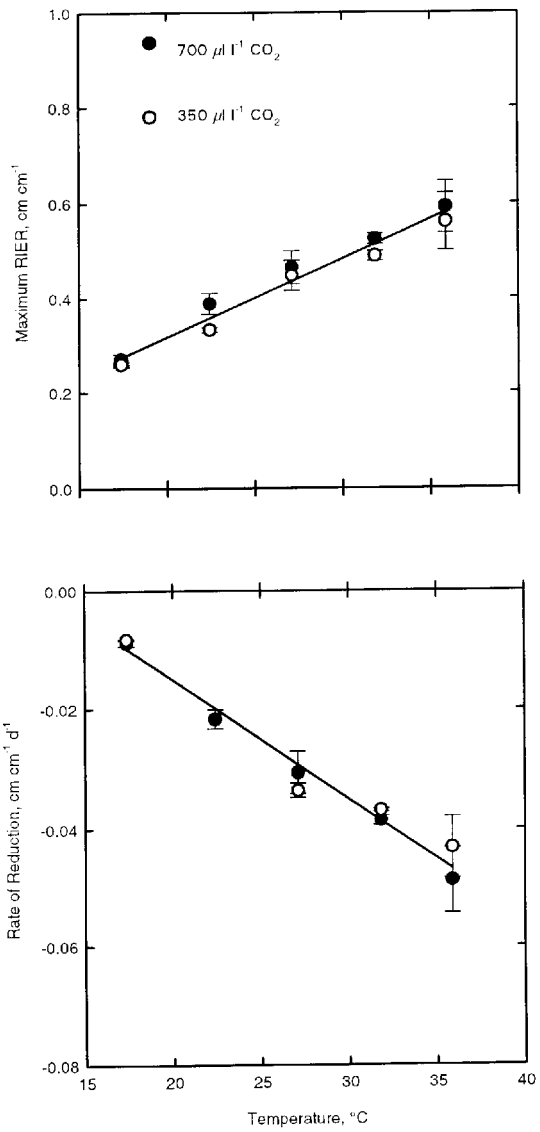

Figure 4. Influence of temperature on maximum relative internode elongation rate (RIER) and rate of reduction with age (reduction rate or slope, $cm\ cm^{-1}\ d^{-1}$). The maximum RIER and slope were calculated by linear regressions fitted between internode age

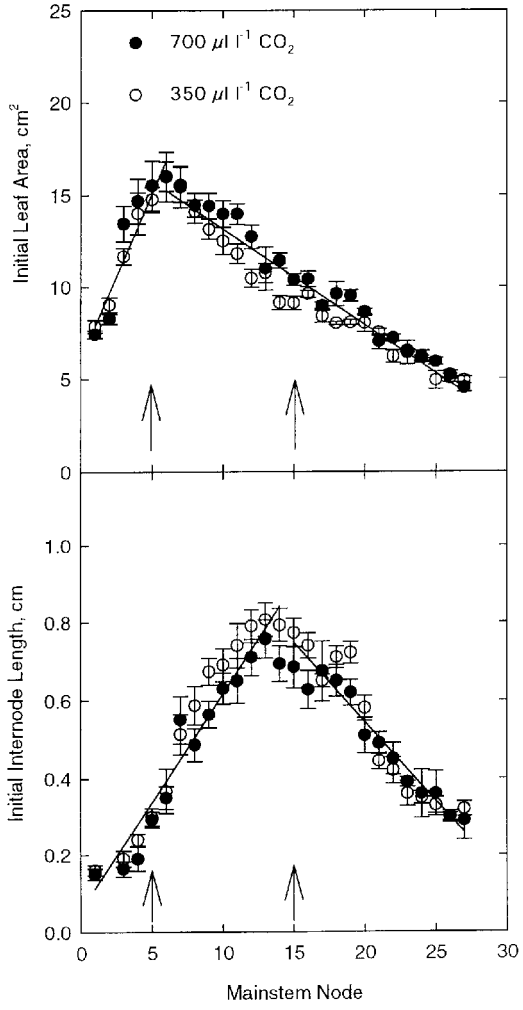

Figure 5. Profile of leaf areas and internode lengths on the mainstem at both CO_2 concentrations for plants grown in 27°C. Arrows at node 5 indicates the appearance of first square when the leaf was unfolding at node 5, and arrow at node 15 shows the apperance of first flower at node 5 when the leaf at node 15 was unfolding.

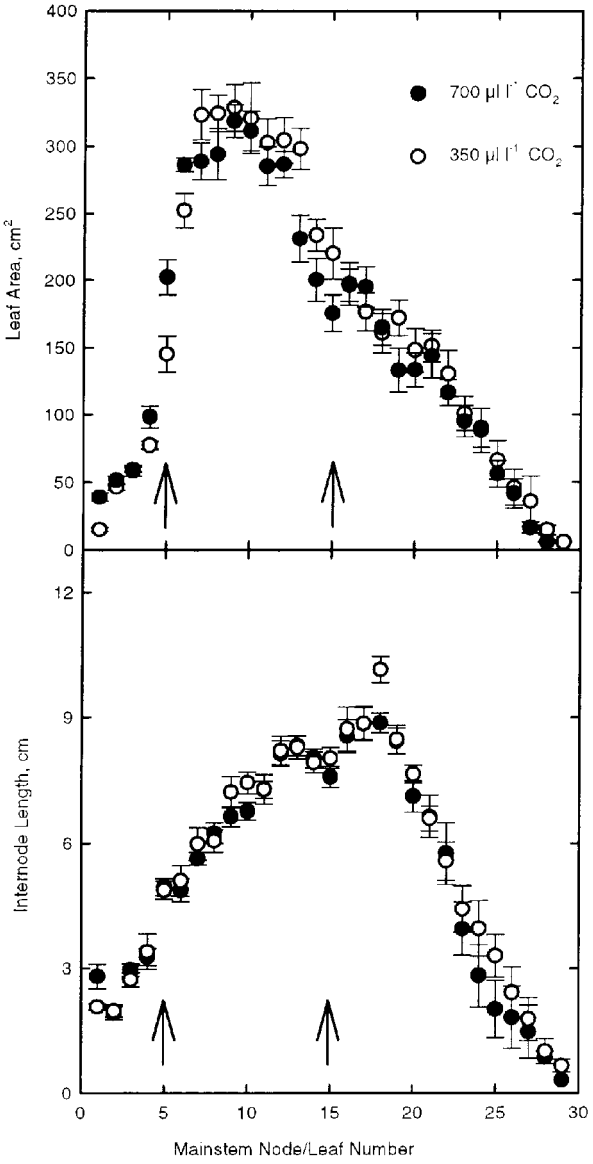

Figure 6. Profile of mature leaf areas and internode lengths on the mainstem at both CO_2 concentrations for plants grown in 27°C. Arrows at node 5 indicates the appearance of first square when the leaf was unfolding at node 5, and arrow at node 15 shows the appearance of first flower at node 5 when the leaf at node 15 was unfolding.