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# Temperature Dependence of Vegetative Growth and Dark Respiration: A Mathematical Model

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## ABSTRACT

**A mathematical model of the processes involved in carbon metabolism is described that predicts the influence of temperature on the growth of plants. The model assumes that the rate of production of dry matter depends both on the temperature and the level of nonstructural carbohydrate. The level of nonstructural carbohydrate is determined by the rates of photosynthesis, growth, and maintenance respiration. The model describes the rate of growth and dark respiration, and the levels of carbohydrate seen in vegetative growth of carnation and tomato. The model suggests that the growth of plants at low temperatures is limited by a shortage of respiratory energy, whereas at high temperatures growth is limited by the shortage of carbohydrate. Thermoperiodism, wherein a warm day and cool night results in faster growth than does constant temperature, is explained by the model as an increase in the level of nonstructural carbohydrate which promotes the rate of growth relative to the rate of maintenance respiration.**

Although temperature has a major influence on plant growth, attempts to predict the response are confounded by several phenomena. The heat sum or growing degree day concept (26) predicts the development of a crop growing in the field solely from the accumulation of heat units above a base temperature. A more complex temperature response of growth is seen under controlled, constant-temperature conditions. At 5 to 20°C, the rate of growth increases exponentially; at 20 to 30°C, it levels off; and above 30 to 35°C, the growth rate falls (9, 19, 27). This has been ascribed to inactivation of an enzyme crucial to growth metabolism both at high and low temperatures which modifies the usual exponential temperature dependence of an enzyme reaction rate (21). Neither model explains the nonadditive effect of fluctuating diurnal temperatures (27) or the influence of light and $CO_2$ (4, 9, 19) on the growth response.

At a constant temperature, the rate of plant growth is linearly related to the rate of photosynthesis (8, 13, 25). However, the temperature dependence of growth and photosynthesis is not the same. Photosynthesis increases with temperature in an asymptotic manner to a plateau above 15°C (5, 10), while the growth rate increases exponentially in this interval and falls rapidly at temperatures above 25°C (9, 19, 27). This divergence occurs because only some of the carbohydrate is used to promote growth and the rest is used to maintain the plant in the current state (15, 18, 20). That carbohydrate respired for maintenance can be distinguished experimentally from respiration due to growth by plotting the total dark respiration *versus* the growth rate (13, 23). Growth respiration and maintenance respiration increase exponentially up to 20°C (13, 18). Whereas growth starts to decrease above 25°C, maintenance keeps increasing. This concept accounts for the carbohydrate mass balance of plant metabolism; but, more information is required to explain why maintenance is promoted at higher temperatures and growth is not.

In this report, Okhams razor is applied to derive the simplest model that predicts the temperature response of the relative growth rate of a plant under minimal stress conditions. We assume that the growth rate is proportional to the level of temporary or nonstructural carbohydrate, an effect that has been observed in several plant species (16, 18, 25). This assumption results in the interaction of light, $CO_2$, and temperature on the growth response, and the complex response to temperature alone. The model is based on only three processes involved in metabolism of carbohydrate: these are photosynthesis, metabolism, respiration leading to growth, and respiration required for maintenance of cellular integrity. We use monotonic functions of temperature for each process and do not explicitly describe translocation or different temperature responses of different plant parts. The predictions of our model are compared with data on the vegetative growth of carnation and tomato in a greenhouse with similar day temperatures but with different temperatures during the night. The ability of the model to predict the relative growth rate, the carbon exchange rate, and the level of nonstructural carbohydrate is examined.

## MATERIALS AND METHODS

**The Model.** The model describes the flow of carbon between the $CO_2$ in the atmosphere, the temporary carbohydrate in the plant, and the carbon found in structural material (Figure 1). The level of TNC[2] (g TNC $g^{-1}$ dry weight), primarily consisting of starch and free sugars, plays a central role in the model. The rates of the three processes (photosynthesis, growth, and maintenance) determine a steady state level of TNC. A finite difference equation describes the rate of change of TNC in terms of the rates of photosynthesis ($P$), maintenance respiration ($R_m$), and the relative growth rate ($rgr$). Photosynthesis yields 0.682 g of sugars per g of $CO_2$ fixed (17), and the same ratio holds for respiration. Growth consumes 1.39 g of TNC and results in 0.68 g of $CO_2$ respired for every 1.0 g of structural material synthesized (18). Alternatively, 0.47 g of the TNC used is respired as $CO_2$ and 0.92 g appears in structural material. Respiration is expressed on a dry weight basis (g $CO_2$ $g^{-1}$ $h^{-1}$), but photosynthesis is usually expressed on a leaf area basis (g $CO_2$ $m^{-2}$ $h^{-1}$). To incorporate photosynthesis and respiration into the same equation, $P$ is divided by the leaf area ratio ($L_r$, g $m^{-2}$) and the leaf area index ($L_i$). The change in TNC per unit of time is

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[2] Abbreviation: TNC, total nonstructural carbohydrate.

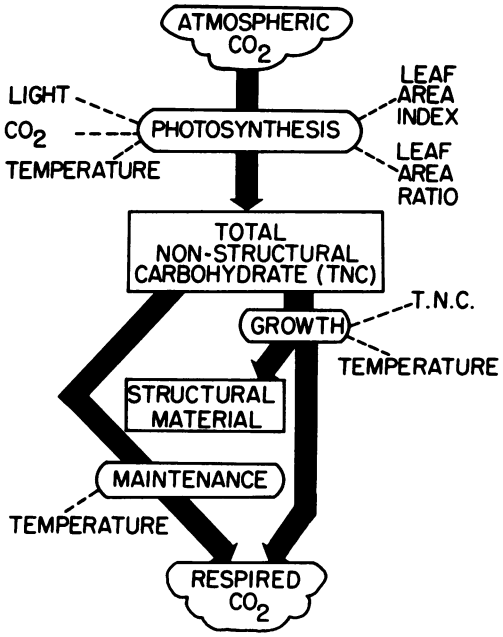


FIG. 1. Flow of carbon between $CO_2$ in the atmosphere, temporary carbohydrate in the plant, and that found in structural material. Variables that affect the transformation processes are connected to the processes by dotted lines.

$$\frac{d(\text{TNC})}{dt} = 0.68\left[\frac{P}{L_i L_r} - R_m - R_g rgr\right] - 0.92 rgr \quad (1)$$

The expression in brackets corresponds in the light to the $CO_2$ exchange rate per unit dry weight ($CER$, g $CO_2$ $g^{-1}$ $h^{-1}$), and in the dark to the dark respiration rate ($R_d$, g $CO_2$ $g^{-1}$ $h^{-1}$).

While $P$ depends on three environmental factors (light flux density, $I$ [w $m^{-2}$ PAR]; $CO_2$ concentration, $CO_2$ [$\mu$l $l^{-1}$]; and temperature, $T$ [°C]), $rgr$ and $R_m$ only depend directly on temperature. A multiplicative formula has been shown to give a good description of $P$ as a function of environment (6):

$$P = f(I)\, g(CO_2)\, h(T) \quad (2)$$

The functions $f$, $g$, and $h$ are different for different plants and are described below for tomato and carnation.

Growth and maintenance processes are separated by examining the relation between growth and dark respiration (13, 23):

$$R_d' = R_m W + R_g\, dW/dt \quad (3)$$

where $W$ is the weight of the plant. Dividing by $W$ gives the rate of respiration per g:

$$R_d = R_m + R_g rgr \quad (4)$$

where $R_g$ is the ratio between $rgr$ and the rate of growth respiration which equals 0.68 according to the stoichiometry of the reactions in growth metabolism (17). The rate of growth respiration and $rgr$ have an exponential temperature dependence with a $Q_{10}$ of 2 from 10°C to 30°C (13, 15). At constant temperature, $rgr$ is proportional to TNC, but the coefficient of temperature dependence is independent of TNC (18):

$$rgr = K_g \text{TNC} \exp(0.0693[T - 25°\text{C}]) \quad (5)$$

where the coefficient $K_g$ (g $g^{-1}$ $TNC^{-1}$ $h^{-1}$) relates the rate of growth to TNC and temperature.

Maintenance respiration ($R_m$) does not appear to depend on TNC and appears to double every 10°C (15, 18). Thus:

$$R_m = K_m \exp(0.0693[T - 25°\text{C}]) \quad (6)$$

where the coefficient $K_m$ (g $CO_2$ $g^{-1}$ $h^{-1}$) sets the rate of maintenance respiration. The ratio of growing to mature tissue may differ between species so the coefficients $K_g$ and $K_m$ are determined empirically.

We assume that respiration and growth occur in constant ratio for all parts of the plant. This is compatible with the observation that the ratio of dry weight among plant parts is constant during vegetative growth. The model does not explicitly account for translocation or redistribution mechanisms; but, all plant parts are assumed to have access to TNC resulting in all parts of the plant having the same relative growth response.

The calculations are made as follows. The diurnal cycle is divided into a day period with one constant temperature and a night period with another constant temperature. The light varies in a sinusoidal fashion from zero to the maximum light flux density at a time equal to half the daylength. The simulation begins with no TNC at the beginning of the 1st d. At 0.1-h intervals, $P$, $rgr$, and $R_m$ are calculated from equations 2, 5, and 6. The change in TNC is calculated from equation 1, and the level is diluted by the fractional increase in dry weight due to growth. The new value of TNC is used in the calculation for the next interval. The steady state is defined as a change in $rgr$ of less than 5% over a 3-d interval. The diurnal variation in $CER$ and TNC and the average daily $rgr$ and TNC level are reported. At the steady-state, these quantities repeat the same variation from day to day but they are not constant over 24 h. Typically, the steady-state condition is achieved after about 10 d of simulated growth.

The coefficients of the model that describe photosynthesis were determined from gas exchange studies under controlled conditions and measurement of $L_i$ and $L_r$. These were used to estimate the total carbon input for each day from the light, $CO_2$, and temperature response of photosynthesis. This input was the same for plants grown under the same-day conditions. The experiments did not define or test the coefficients describing photosynthesis. Only the coefficients $K_g$ and $K_m$ were adjusted to account for the observed difference in $R_d$, TNC, and $rgr$ for plants grown at different night temperatures.

**Growth Conditions and Measurements of Tomato.** Tomato plants (*Lycopersicon esculentum* var Patio hybrid) were grown in two sections of a greenhouse in Connecticut during the winter and spring (7). Growth was measured throughout the interval as the plants increased from 1 to 25 g dry weight. Photosynthesis and TNC levels were determined at early flowering, in late March. Plants grown in the control section had a minimum temperature of 15°C throughout. Plants grown in the other section had a minimum temperature of 15°C during the first part of the night and 7°C during the last 8 h of the night. This was the split-night section. During the day, the minimum temperature was 15°C in both sections and the average temperature was 20°C. At the end of March, the daily maximum light flux density was 240 w $m^{-2}$ PAR, the $CO_2$ concentration was 350 $\mu$l $l^{-1}$, $L_r$ was 100 g $m^{-2}$, and $L_i$ was 2. These conditions were used to simulate growth.

Constants describing the response of photosynthesis to light, $CO_2$, and temperature were derived from data collected on attached leaves of three different plants which were grown in the greenhouse until the day of measurement. The terminal leaflet of the most recently expanded leaf was placed in a flow-through cuvette in which $I$, $CO_2$, and $T$ were controlled (Gent and Reed, unpublished results). A complete factorial experiment in which $I$ at 0, 7, 43, 150, and 560 w $m^{-2}$ PAR; $T$ at 5, 15, 25, 35, and 45°C; and $CO_2$ at 5, 300, and 900 $\mu$l $l^{-1}$ was applied.

TNC levels were determined four times per d (1700, 2300, 500, and 1100 h) on one day at the end of March. At these times, three plants from each treatment were harvested, immediately frozen, and freeze dried. Leaf, stem, and root tissues were weighed and ground. Twenty-mg subsamples of tissue were rehydrated, digested with $\alpha$-amylase for 40 h at 37°C, and free sugars were

determined by a colorimetric procedure to determine the reduction of $K_3FeCN_6$ (22).

**Growth Conditions and Measurement of Carnation.** During the winter in Israel, potted carnation plants (*Dianthus caryophyllus*) were grown in a greenhouse during the day and in three different controlled temperature chambers at night (11). Measurements of growth and gas exchange were made over a 6-week interval. The plants were grown in a 8-h daylength with a daily maximum light flux density of 90 w $m^{-2}$ PAR and a temperature of 21°C. At night, the plants were placed in constant-temperature chambers at temperatures of 6, 17, or 30°C for 16 h. A $CO_2$ concentration of 350 $\mu l\ l^{-1}$, $L_r$ of 133 g $m^{-2}$, and $L_i$ of 2 were used to simulate growth.

The constants describing the response of $P$ to $I$, $CO_2$, and $T$ were derived from data collected on another set of plants in a flow-through chamber in which an entire plant was enclosed and the three quantities were varied independently (6). A complete factorial design was applied with $I$ at 0, 45, 125, 250, and 450 w $m^{-2}$ PAR; $T$ at 10, 15, 20, 25, 30, and 35°C; and $CO_2$ at 200, 350, 700, 1500, and 3100 $\mu l\ l^{-1}$. The plant was placed in a given light and $CO_2$ environment at 20°C on the day preceding the measurement and then subjected to the six leaf temperatures twice in 1 d. Measurements of dark respiration were made at 20°C in the 1st 0.5 h after darkness following a day with a particular light and $CO_2$ level. Estimates of $R_d$ at different temperatures were made assuming an exponential temperature dependence with a $Q_{10}$ of 2. The observed *CER* in the light was corrected for $R_d$ measured in the following period of darkness in order to extract $P$ (6).

## RESULTS AND DISCUSSION

**Tomato Plants Subjected to Control or Split-Night Temperatures.** The equation to predict the photosynthetic rate assumed that at high levels of either $I$, $CO_2$, or $T$, a saturation occurred so that $P$ was no longer dependent on that variable. The specific mathematical form of the dependence was:

$$P = 12.0\left[\frac{I}{50 + I}\right]\left[\frac{CO_2}{300 + CO_2}\right]\left[\frac{T}{12 + T}\right] \quad (7)$$

Inasmuch as conditions during the day were the same and no significant differences in CER, stomatal conductance, or $L_r$ were observed (7), the daily production of TNC was the same for plants in the control and split-night conditions. Values of $K_g = 5.0 \cdot 10^{-2}$ g $g^{-1}$ $TNC^{-1}$ $h^{-1}$ and $K_m = 3.0 \cdot 10^{-3}$ g $CO_2$ $g^{-1}$ $h^{-1}$ were used to predict the diurnal variation of TNC and the rates of respiration and growth of the two treatments.

Model predictions of both *CER* and TNC for tomato plants subjected to the control and split-night conditions are shown in Figure 2. Plants subjected to split-night had higher TNC because they respired less during the cool period of the night. The minimum and maximum values of TNC occurred at the same time of day in plants of the two treatments, but there was less diurnal variation of TNC in the plants subjected to split-night. When the temperatures of the two treatments were the same, the model predicted a difference in *CER* and in $R_d$ because the higher TNC in plants subjected to split-night enhanced *rgr*. Averaged over the day, the growth under both conditions was predicted to be the same; *rgr* was 0.83 $day^{-1}$. We now compare these predictions with our observations.

Analysis of TNC in plants harvested at four different times during the day showed that the minimum and maximum values of TNC occurred at the same time of day in the leaves as in the stem. The TNC in the roots was much lower, typically 3% to 6%, and showed diurnal changes that were not in synchrony with the variation in the stem and the leaves. A weighted average of the TNC for all plant parts was compared to the predictions of the model (Table I). The TNC measured for control plants had

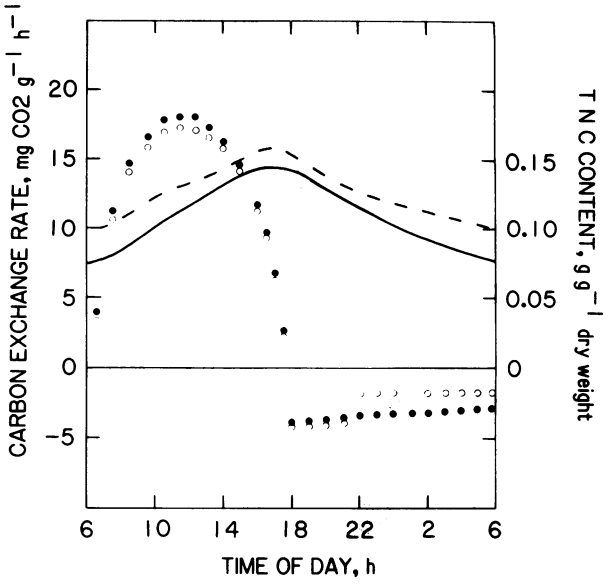


FIG. 2. Diurnal variation in $CO_2$ exchange and TNC levels predicted for tomato grown under control and split-night temperatures. $CO_2$ exchange rates for split-night (○) and control (●) plants. TNC level for split-night (— — —) and control (——) plants.

Table I. *A Comparison of TNC Levels in Tomato Plants Grown under Control and Split-Night Temperatures*

| Time of Day | TNC Levels | | | |
|---|---|---|---|---|
| | Control | | Split-Night | |
| | Observed | Predicted | Observed | Predicted |
| | % dry wt | | | |
| 5 PM | 13.8 | 14.5 | 13.9 | 15.5 |
| 11 PM | 13.3 | 10.9 | 14.1 | 12.2 |
| 5 AM | 8.6 | 8.0 | 14.3 | 10.4 |
| 11 AM | 12.0 | 10.9 | 13.6 | 12.8 |
| $LSD_{0.05}$ | 2.7% | | 4.1% | |

maximum and minimum values at 5 PM and 5 AM, respectively, which the model predicted. The observed TNC for plants subjected to split-night was always higher than that for the control plants but any diurnal variation was not detected due to the greater experimental uncertainty of these data. The model was correct in predicting a greater diurnal variation of TNC for the control plants and higher TNC at all times for the split-night treatment.

A higher respiration rate was observed for plants under split-night than for those under control conditions when the temperature was the same (7) but the data did not justify a quantitative determination of this difference in $R_d$. At the same temperature, the model predicted $R_d$ for plants under split-night to be 9% greater than under the control condition. Others have noted that conditions that increase photosynthesis, and thereby TNC, also increase dark respiration in tomato (12).

The relative growth rate under control conditions (0.110 g $g^{-1}$ $d^{-1}$) was significantly faster than for plants under split-night (0.093 g $g^{-1}$ $d^{-1}$). The model predicted no difference in *rgr* under these two conditions.

**Carnation Plants Subjected to Three Different Night Temperatures.** Values for the coefficients describing $P$, *rgr*, and $R_m$ were different for carnation than for tomato. For carnation, a suitable mathematical description of whole plant photosynthesis corrected for respiration is (6):

$$P = 0.0312\ I^{0.789}\ CO_2^{0.241}\ T^{0.167} \quad (8)$$

This equation accounted for 90% of the observed variation in apparent photosynthesis over a 4-fold range of light, a 15-fold range of $CO_2$, and leaf temperatures between 10°C and 35°C. Little difference in *CER* during the day was observed for plants grown under the three different night temperature conditions (5), so total carbon input should have been the same for each condition. Values of $K_g = 4.4\ 10^{-2}$ g g$^{-1}$ TNC$^{-1}$ h$^{-1}$ and $K_m = 3.25\ 10^{-3}$ g $CO_2$ g$^{-1}$ h$^{-1}$ were used to simulate the effect of night temperature on *rgr* and $R_m$.

The model predicted TNC to be very different for plants subjected to the three night temperatures. Whereas plants kept at 6°C had a maximum and minimum TNC of 14.3% and 9.5%, those plants grown under 30°C nights had TNC of 6.7% and −1.1%, respectively (Fig. 3). Plants grown under 17°C at night had intermediate levels of carbohydrate. These differences were due to the inhibition of respiration at cool nighttime temperatures. According to the model, the treatments drastically altered TNC which, in turn, caused a difference in growth and respiration due to growth. The model predicted the fastest growth for plants kept at 6°C at night (0.048 g g$^{-1}$ d$^{-1}$). A similar *rgr* was predicted for plants at 17°C, but plants kept at 30°C were predicted to grow much slower (0.029 g g$^{-1}$ d$^{-1}$).

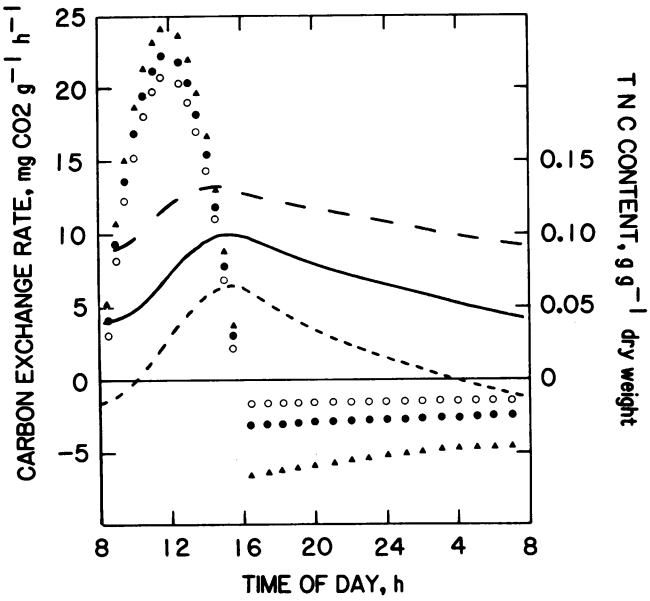


FIG. 3. Diurnal variation in $CO_2$ exchange and TNC levels predicted for carnation grown under three different night temperatures. $CO_2$ exchange rates for 6°C (○), 17°C (●), and 30°C (▲) night temperatures. The TNC level for 6°C (— — —), 17°C (——), and 30°C (- - -) night temperatures.

Table II. *Rate of Dark Respiration in Carnation Grown under Different Night Temperatures*

All rates were measured at 17°C.

| Night Temperature | Time of Day | Dark Respiration | |
|---|---|---|---|
| | | Observed | Predicted |
| °C | | mg $CO_2$ g$^{-1}$ h$^{-1}$ | |
| 6.0 | 4 PM | 4.3 | 3.5 |
| | 8 AM | 3.5 | 3.1 |
| 17.0 | 4 PM | 3.1 | 3.2 |
| | 8 AM | 2.1 | 2.4 |
| 30.0 | 4 PM | 3.2 | 2.7 |
| | 8 AM | 1.9 | 1.9 |

Precise observations of dark respiration were made at the beginning and end of the night for plants grown under the three different night temperatures. Even when $R_d$ was compared at the same temperature, very different rates of respiration were both observed and predicted (Table II). Two trends were seen. First, plants grown at cooler night temperatures had higher $R_d$ both at the beginning and at the end of the night. Second, the change in $R_d$ from the beginning to the end of the night, expressed as a percentage of the average rate, was much larger for plants grown at 30°C than 6°C nights. At 6°C, the observed change in $R_d$ was 19% over the 16-h period, while at 30°C the observed change was 42%. The model predicted changes of 14% and 35% for night temperatures of 6°C and 30°C, respectively. The model predicted both the absolute rate of respiration and the percentage change over the 16-h night period reasonably well.

The model predicted significantly faster growth for plants under cool nights than for those kept at 30°C. The same order of growth rates was observed (Table III), but the model underestimated *rgr* at high night temperatures.

**Observed and Predicted Seasonal Variation in Growth of Carnation.** After the model was calibrated to predict both growth and respiration of carnation under controlled conditions, we attempted to predict *rgr* for carnation through the seasons of the year. Bunt (2) in England determined the *rgr* of newly rooted cuttings during 3-week intervals throughout the year and correlated these measurements with integrated radiation and average temperature. We transformed the integrated radiation and temperature for each growth interval into values for constant day and night temperatures and maximum light flux density. This transformation made use of the seasonal values for daylength at the latitude of 51°N and it assumed a minimum greenhouse temperature of 12°C at night, a $CO_2$ level of 350 μl l$^{-1}$, and a parabolic variation in light flux density during the day.

Our predictions were quite sensitive to the leaf area ratio, $L_r$. If $L_r$ was set to a constant value of 200 g m$^{-2}$ for all growth intervals, no growth was predicted during the winter months but *rgr* increased to 0.100 g g$^{-1}$ d$^{-1}$ in the middle of summer. However, the minimum and maximum *rgr* observed was 0.009 and 0.047 g g$^{-1}$ d$^{-1}$.

Bunt (2) states that there was a 3-fold variation in the initial dry weight of the cuttings; they were lightest in March and heaviest in June. In contrast, the length of the cuttings and the number of visible leaves did not vary with the season so there must have been a change in $L_r$. $L_r$ is known to vary according to the light flux density; higher light decreases $L_r$ (3, 19). The most reasonable predictions were obtained if $L_r$ was proportional to the mean of initial weight and light flux density for each growth interval, both expressed as a percentage of the mean for all growth intervals. This accounted for the effect of light on $L_r$ both before and during the interval of the growth measurement. The mean $L_r$ used in the prediction was 250 g m$^{-2}$ and it varied from a minimum of 125 g m$^{-2}$ in December to 405 g m$^{-2}$ in July. The observed *rgr* and the predictions resulting from the above procedure are shown in Figure 4. The model accounted for 63% of the observed variation in *rgr*. Bunt found that second-order regression *versus* both mean temperature and integrated radiation accounted for 89% of the

Table III. *Relative Growth Rate of Carnation Grown under Different Night Temperatures*

| Night Temperature | Relative Growth Rate | |
|---|---|---|
| | Observed | Predicted |
| °C | g g$^{-1}$ d$^{-1}$ | |
| 6.0 | 0.049 | 0.050 |
| 17.0 | 0.047 | 0.046 |
| 30.0 | 0.039 | 0.028 |

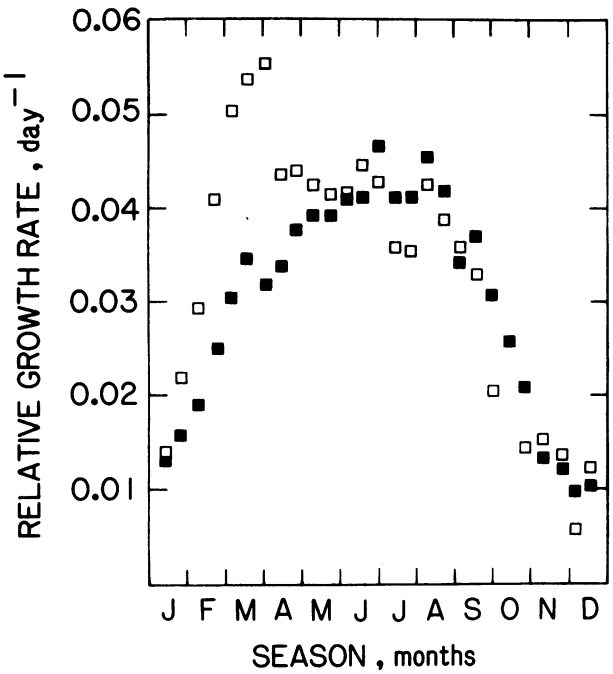


FIG. 4. Observed (■) and predicted (□) seasonal variation in the relative growth rate of carnation.

observed variation (2). While Bunt's regression did fit his own data better than our model, it did not correctly predict the growth of carnation under three different night temperatures described above (11).

**A Critique of the Assumptions of the Model.** Our model suggests temperature influences growth through carbohydrate metabolism. Although it provides insight into the mechanism of growth, it is also an oversimplification. For instance, the model always predicts faster growth if the night is cooler than the day, although below a certain limit cool temperatures at night inhibit growth. Whether carbohydrate metabolism is the only factor determining the temperature dependence of plant growth will not be argued here. The advantage of our model is that it predicts *CER*, TNC, and *rgr* simultaneously and it explains the relation between these processes. The model assumes that the TNC level determines the amount of carbohydrate used in growth relative to maintenance processes.

A significant difference to previous investigations is that we apply the model to plants grown under fluctuating diurnal temperatures. Because both growth and maintenance are temperature dependent, previous studies usually chose conditions with different growth rates at the same temperature to affect a resolution of these two processes. Because of the nature of our experiments, we cannot put strict limits on the accuracy of the coefficients of the model. The assumptions that maintenance and growth respiration have the same temperature dependence (8, 15), that growth is linearly related to TNC (16, 18, 25), or that maintenance respiration is entirely independent of growth (1, 15, 24) have been examined in more detail elsewhere. We found these simplifying assumptions sufficient to predict the relationship between TNC, $R_d$, and *rgr* under diurnally fluctuating temperature conditions.

**The Relation between the Metabolism of TNC and Thermoperiodism.** Growth is a composite process that requires TNC as a substrate and energy from respiration as the driving force for transforming TNC into structural material. Maintenance competes with growth for TNC. Whereas at high levels of TNC a large fraction of the available energy from respiration is used for growth (8, 14, 17), at low levels it is mostly used for maintenance. The increase in structural dry matter is limited at low temperature by an insufficient supply of energy from respiration. At high temperatures, growth is limited by the supply of TNC instead (18). The optimal temperature for growth maintains a high rate of both a supply of TNC and respiration to convert the TNC into structural material. It follows that the optimal temperature for growth depends on the rate of photosynthesis, which is affected by light, temperature, and $CO_2$.

The model predicts faster growth for plants grown at higher day than night temperatures. This effect has been noted for several plant species (9, 11, 27). If photosynthesis were the same for plants grown under cool-night temperatures as for plants grown under warm nights, then the same amount of TNC would be produced per d. The steady-state requires this amount of TNC to be consumed each day in growth and maintenance processes. Inasmuch as the average level of TNC in cool night plants will be higher, the amount of TNC used for growth relative to maintenance will always be higher (20), even though warm-night and cool-night plants process the same amount of TNC each day. Thus, the model provides a physiological explanation for the advantage of lower night than day temperatures.

A recent study of *CER* and growth of clover found less dry matter accumulation under fluctuating diurnal temperatures than at a constant temperature during 3 d after switching the plants from a constant high-temperature environment (14). However, these results are not inconsistent with our model because the plants did not reach a steady-state diurnal cycle of carbohydrate metabolism. Plants switched into a high day and low night temperature regime would spend the experimental period increasing TNC at the expense of growth in comparison to those plants under constant temperatures which would not be accumulating TNC.

## LITERATURE CITED

1. BARNES A, CC HOLE 1978 A theoretical basis of growth and maintenance respiration. Ann Bot 42: 1217–1221
2. BUNT AC 1972 Effect of season on the carnation (*Dianthus caryophyllus*). I. Growth rate. J Hortic Sci 47: 467–477
3. CHALLA H 1976 Analysis of the diurnal course of growth, $CO_2$ exchange and carbohydrate reserve content of cucumber. Agric Res Rep (Wageningen) 861
4. EENICK AH, L SMEETS 1978 Genotype × environment interactions with lettuce (*Lactuca L.*) in relation to the development of genotypes for growing under poor energy conditions. Neth J Agric Sci 26: 81–88
5. ENOCH HZ, RG HURD 1977 Effect of light intensity, $CO_2$ concentration and leaf temperature on gas exchange of spray carnation plants. Exp Bot 28: 84–95
6. ENOCH HZ, JM SACHS 1978 An empirical model of $CO_2$ exchange of a $C_3$ plant in relation to light, $CO_2$ concentration, and temperature. Photosynthetica 12: 150–157
7. GENT MPN, JH THORNE, DE AYLOR 1979 Split night temperatures in a greenhouse: the effects on the physiology and growth of plants. Conn Agric Exp Stn Bull (New Haven) 781
8. HANSEN GK, CR JENSEN 1977 Growth and maintenance respiration in whole plants, tops, and roots of *Lolium multiflorum*. Physiol Plant 39: 155–164
9. HARSEMMA H 1977 Root temperature and growth of young tomato plants. Meded Landbouwhogesch Wageningen 77: 19
10. HOFSTRA G, JD HESKETH 1969 Effects of temperature on gas exchange of leaves in the light and dark. Planta 85: 228–238
11. HURD RG, HZ ENOCH 1976 Effect of night temperature on photosynthesis, transpiration, and growth of spray carnations. J Exp Bot 27: 695–703
12. LUDWIG LJ, DA CHARLES EDWARDS, AC WITHERS 1975 Tomato leaf photosynthesis in various light and $CO_2$ environments. *In* R Marcelle, ed, Environmental and Biological Control of Photosynthesis. Dr. W Junk, The Hague, pp 29–39
13. MCCREE KJ 1974 Equations for the rate of dark respiration of white clover and grain sorgum, as functions of dry weight, photosynthetic rate, and temperature. Crop Sci 14: 509–514
14. MCCREE KJ, ME AMTHOR 1982 Effects of diurnal variation in temperature on the carbon balance of white clover plants. Crop Sci 22: 822–827
15. MCCREE KJ, JH SILSBURY 1978 Growth and maintenance requirements of subterranean clover. Crop Sci 18: 13–18
16. MOLDAU H, A KAROLIN 1977 Effect of the reserve pool on the relationship between respiration and photosynthesis. Photosynthetica 11: 38–47
17. PENNING DE VRIES FWT, AHM BRUNSTING, HH VAN LAAR 1974 Products, requirements, and efficiency of biosynthesis: a quantitative approach. J Theor Biol 45: 339–377
18. PENNING DE VRIES FWT, JM WITLAGE, D KREMER 1979 Rates of respiration and increase in structural dry matter in young wheat, ryegrass and maize plants. Ann Bot 44: 595–610

19. RAJAN AK, GE BLACKMAN 1975 The interacting effects of light and day and night temperature on the growth of four species in the vegetative phase. Ann Bot 39: 733–743
20. RYLE GHA, JM COBBY, CE POWELL 1977 Synthetic and maintenance respiratory losses of $^{14}CO_2$ in uniculm barley and maize. Ann Bot 40: 571–586
21. SHARPE JPH, DW DEMICHELLE 1977 Reaction kinetics of poikilotherm development. J Theor Biol 64: 649–670
22. STREETER JG, DL JEFFERS 1979 Distribution of total nonstructural carbohydrates in soybean plants having increased reproductive load. Crop Sci 19: 729–734
23. THORNLEY JHM 1976 Mathematical Models in Plant Physiology. Academic Press, New York
24. THORNLEY JHM 1977 Growth, maintenance, and respiration: a reinterpretation. Ann Bot 41: 1191–1203
25. THORNLEY JHM, RG HURD 1974 An analysis of the growth of young tomato plants in water culture at different light integrals and $CO_2$ concentrations. Ann Bot 38: 389–400
26. WANG JY 1960 A critique of the heat unit approach to plant response studies. Ecology 41: 785–790
27. WENT FW 1957 The Experimental Control of Plant Growth. Chronica Botanica, Waltham, MA

## APPENDIX

$CER$: carbon dioxide exchange rate, g $CO_2$ $g^{-1}$ $h^{-1}$;
$CO_2$: carbon dioxide concentration, $\mu l$ $l^{-1}$;
$I$: light flux density, w $m^{-2}$ PAR;
$K_g$: growth coefficient, g $g^{-1}$ $TNC^{-1}$ $h^{-1}$;
$K_m$: maintenance coefficient, g $CO_2$ $g^{-1}$ $h^{-1}$;
$L_i$: leaf area index,
$L_r$: leaf area ratio, g $m^{-2}$;
$P$: photosynthesis − photorespiration, g $CO_2$ $m^{-2}$ $h^{-1}$;
$rgr$: relative growth rate, g $g^{-1}$ $d^{-1}$;
$R_d$: dark respiration rate, g $CO_2$ $g^{-1}$ $h^{-1}$;
$R_g$: growth to respiration ratio, g $CO_2$ $g^{-1}$;
$R_m$: maintenance respiration rate, g $CO_2$ $g^{-1}$ $h^{-1}$;
$T$: temperature.