Published July, 1972

Simulation of Growth and Yield in Cotton: I. Gross Photosynthesis, Respiration, and Growth[1]

D. N. Baker, J. D. Hesketh, and W. G. Duncan[2]

ABSTRACT

A valid simulation of crop growth and yield requires quantitative data on the effect of the environment on photosynthesis, respiration and organ development. Seedling growth and boll growth of cotton, (*Gossypium hirsutum* L.) were studied in the phytotron at Duke University. We found extremely high respiration rates in the seedlings and an efficiency in the conversion of photosynthate to dry matter of 33% for the first 0.3 g accumulated and 53.5% for the next 0.5 g. Boll growth is exponential at first and then becomes linear. Growth efficiency in young bolls ranges from 67% at 18 C to 77% at 28 C. Later boll growth efficiency was essentially constant at about 61% at mean temperatures commonly found in the cotton belt, e.g., 26 — 27 C. Photosynthesis and respiration were measured in field stands during the boll-filling stage with 2m × 2m plexiglass chambers. Light respiration varied with temperature (25 to 42 C) from 8 to 15% of gross photosynthesis at a light intensity of 700 Wm^{-2}. The ratio of total respiration to photosynthesis (R/P) varied diurnally, ranging from 0.29 under intense light [0900 local standard time (LST)] to infinity at sundown.

Additional index words: **Temperature, Light, Net assimilation rate, Morphogenesis.**

CROP production is essentially the manufacture and disposal, over time, of photosynthate. As noted elsewhere (2, 5) the instantaneous balance of these processes on a land area basis can be obtained from the expression,

$$dW/dt = P - RW \qquad [1]$$

where W is dry weight per unit ground area (mg dm^{-2}), t is time (min), R is the rate of respiration per unit dry weight (mg g^{-1} min^{-1}), W is plant dry weight per unit ground area (g dm^{-2}), and P is the rate of photosynthesis (mg dm^{-2} min^{-1}). If we know the effects of the various elements of the environment on the rates of photosynthesis and respiration, weather data can be used in a dynamic model to predict crop production. The objectives of the work reported here were (i) to characterize the effect of temperature on respiration and photosynthesis in cotton (*Gossypium hirsutum* L.), (ii) to determine the fraction of the plant's gross photosynthate production that is expended in respiration, and (iii) to determine the efficiency with which photosynthate is converted into various plant tissues. Since these aspects of growth are so important in developing plant models, we will attempt to present a fairly critical analysis of our experimental results in this context.

MATERIALS AND METHODS

Apparent Photosynthesis

On May 21, 1970, in a field planting, 'Deltapine Smoothleaf' cotton was drilled in 100-cm north-south rows. N, P, K, and Mg fertilizer was drilled in at rates of 90, 24, 51, and 30 kg/hectare. By September 1 the crop was 129 cm tall and was intercepting more than 98% of the incident solar plus sky radiation at noon.

A semiclosed system (1) was used to measure apparent photosynthesis. The plexiglass chamber transmitted over 98% of the incident solar plus sky radiation to the enclosed stand. Leaf temperatures were measured with thermocouples in four upper exposed leaves. A vacuum pump located in the chamber pulled air through a psychrometer where wet bulb and dry bulb temperature measurements were made. This air then was pumped into an instrument trailer for carbon dioxide analysis via a Beckman 15-A®[3] infrared gas analyzer. Carbon dioxide flow rates into the chamber were measured by a Hastings Raydist[3] mass flow meter. Solar radiation (I_0) was measured outside the chamber with an Eppley[3] pyranometer.

The first chamber "setup" began on September 3. The soil, a clay with high water holding capacity, was close to field capacity, i.e., the soil suction was less than 0.4 bar. Apparent photosynthesis measurements were made at 25, 30, 36, and 42 C air temperature on September 4, 7, 8, and 9, respectively. The carbon dioxide level was maintained at 300 ppm v/v. On each of those days there were occasional cloudy periods. The soil was sealed off around the stems at ground level in this experiment with polyethylene film, so the measurements represent only the gas exchange in the above ground plant parts (in both setups approximately 10% of the plant dry weight was in root). The above ground plant dry weight totaled 3452 g. Fruit dry weight totaled 1192 g.

The second chamber setup began on September 14. Again the soil was sealed off; however, this time the soil was dry. Furrow irrigation was begun on September 14 and continued on the 15th and 16th. Photosynthetic rates were low on September 15 and 16, but by September 17 had returned to normal. Thereafter we found that even with the plants wilted by exposure to high temperature and VPD, photosynthesis was no less than that of turgid plants at slightly lower temperatures. Chamber temperature was maintained at 25 C on September 17 and at 35 C on September 20. The aboveground plant parts weighed 3,910 g, of which 1,532 g was fruit.

Respiration

After the apparent photosynthesis measurements in each setup were completed, day and night respiration rates were measured using a standard closed system technique.

To measure night respiration the chamber was made light tight with black plastic film at sundown on the day prior to the measurements. At about 1000 LST measurements were begun. After establishing an air temperature in the chamber a duct was opened briefly, dropping the carbon dioxide concentration in the system to the level of the outside air. The duct was then closed and respiration was determined from the slope of the carbon dioxide vs time curve. Temperature recording was begun after closing the duct. This procedure was repeated at air temperatures ranging from 14 to 42 C, with about 20 minutes allowed before each measurement for the plants to equilibrate to the new temperature. Similar measurements were made at night.

For the day respiration measurements the chamber was kept closed. The chamber was uncovered and carbon dioxide was metered in during the morning and respiration measurements were begun at 1200 LST. After 20 minutes of photosynthesis at the desired temperature, and at 300 ppm carbon dioxide, the

[1] Contribution from the Southern Branch, Soil and Water Conservation Research Division, Agricultural Research Service, USDA, in cooperation with the Entomology Research Division and the Mississippi Agricultural and Forestry Experiment Station. Received Sept. 18, 1971.

[2] Research Soil Scientists, USDA, Boll Weevil Research Laboratory, and Department of Agronomy, State College, Mississippi 39762 and Professor, Department of Agronomy, The University of Florida, Gainesville, Florida, respectively.

[3] The use of trade or proprietary names does not necessarily imply the endorsement of these products by the U. S. Department of Agriculture.

chamber was darkened and the carbon dioxide level was traced for 6 minutes. Day and night respiration measurements were made both on intact plants and, in the second setup, on the defruited plants.

Growth

Cotton growth and respiration were measured under a variety of temperature conditions in the Duke Phytotron (SEPEL) c.f. (4). Stoneville 213 cotton plants were grown in 25-cm pots at 32/29, 32/23, 29/26, 26/23, 23/20, 20/17, and 17/11 C day/night temperatures. The mean temperature values for the 32/23, 29/26, and 26/26 C regimes are close to the midsummer mean of 26-27 C at State College, Miss. The day temperature lasted from 0800 to 1600, and the natural photoperiod (May 6 to October 6) was extended to 16 hours by incandescent lights. Plants were grown in a 1:1 mixture of vermiculite and gravel, were irrigated in the morning with a half-strength Hoagland nutrient solution, and were watered in the afternoon. Each day all of the plants were inspected and new bolls were tagged. At approximately 10-day intervals some bolls representing all boll ages to that date were harvested. In some cases the harvest was made at night and in others it was made during the day after a period of bright light. Respiration measurements were made on the harvested bolls using a leaf chamber technique (9). Then, the bolls were dried for a weight determination.

A second experiment was performed in the phytotron with cotton seellings. Seedlings were grown in waxed paper cups in the above growth medium in the following day/night temperature regimes: 32/29, 32/23, 29/26, and 26/26 C. When the plants had accumulated about 0.5 g dry matter, they were given nutrient solution and watered frequently to maintain a low water stress. On cloudy days, the plants were moved into growth rooms under fluorescent plus some incandescent light at an intensity of 4,000 ft-c. Day and night respiration rates were measured on each of six plants at four or more times during growth; dry weights for nine plants, including the above six, were taken on five or more occasions over a 10- to 12-day period. The first sample was taken several days after the seedlings emerged. Respiration was measured on the intact plants, and included carbon dioxide evolving from the undisturbed root system.

RESULTS AND DISCUSSION

Respiration in the Plant Canopy

Canopy respiration data are presented in Fig. 1. Since there was no difference between the respiration rates in the two intact stands on a dry weight basis, the data were pooled for fitting the curves in the figure.

Below 20 C there was very little difference in day and night respiration rates of the intact plants. Above 20 C the day respiration rate exceeded the night respiration rate by 20 to 25%. Day respiration exceeded night respiration by as much as 29% in the defruited plants at 34 C. The defruited plants had about 20% greater respiration rates than the intact plants over most of the temperature range.

The apparent photosynthesis data (P_N) data were fitted to a multiple regression model with linear and quadratic terms for light intensity, air temperature, vapor pressure deficit, and all first order interactions. A multiple R^2 value of 0.96 was obtained. This model was used to calculate the points from which the lines in Fig. 2 were drawn. These data are essentially identical to those published by Ludwig, Saeki, and Evans (7) except that we extended our observations to much higher light levels.

Close inspection of the intact day respiration data revealed that all points well above the line had been obtained after exposure to very bright light, and the points below the line were obtained after exposure to rather low light intensities. Therefore we fitted these data to the model $R = a + b_1I_0 + b_2T + b_3I_0^2 + b_4T^2 + b_5I_0T$, where I_0 and T were the average light intensity and temperature respectively, during the measurement period. Assuming that at $I_0 = 0$, P_N is entirely respiration, we included the four P_N values for $I_0 = 0$ (Fig. 2) among the data. As expected, the terms containing I_0 in this analysis were all highly significant.

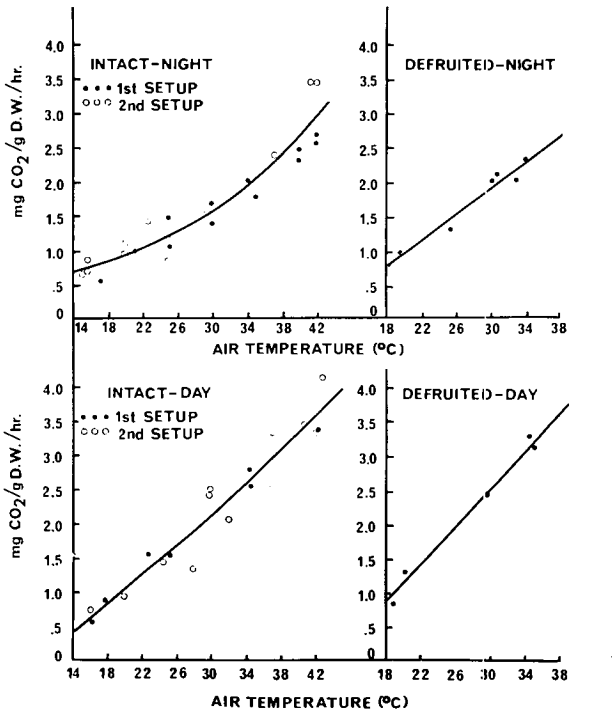

Fig. 1. Respiration rates vs. air temperature in intact and in defruited cotton. Total dry weights of above ground plant parts for the 1st setup, 2nd setup and defruited were 3,452 g, 3,910 g, and 2,878 g, respectively.

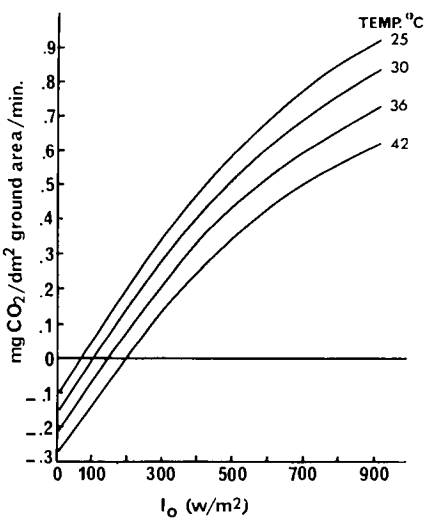

Fig. 2. Apparent photosynthesis vs. light intensity at a vapor pressure deficit of 10 mb.

Calculation of P

Entering the above model with appropriate light intensity and temperature data, a respiration rate (R, in mg CO_2 g^{-1} min^{-1}) was calculated for each of the

P_N values and multiplied by the appropriate weight. Gross photosynthesis (P) was then computed from the expression

$$P = P_N + RW \quad [2]$$

where P and P_N are mg CO_2 dm^{-2} min^{-1}. These data points are graphed in Fig. 3b. The importance of accounting for the intensity of the light just prior to the day respiration measurement is shown by a comparison of the data in Fig. 3a and 3b. It was not accounted for in Fig. 3a, and at the low light levels RW was overestimated, producing a significant error in the estimate of P. This enhancement of repiration in the light may be associated with the classical photorespiration of Forrester et al. (3). It may also be a manifestation of energy expenditure in the translocation process in petioles, stems, etc.

Vapor pressure deficits (VPD) ranged from 5 to 23 millibars (mb) in this study, and they tended to vary with temperature, although the highest VPDs were obtained in the 36 C treatment rather than at 42 C. We fitted these data (Fig. 3) to a multiple regression model to separate the effects of temperature and VPD. The analysis showed statistically significant effects due to both temperature and VPD but neither changed the estimate of P by as much as 5% over the range of experimental conditions. In other words, there was no great temperature enhancement of photosynthesis offset by a moisture stress at high VPDs. At the high temperatures the plants were visibly wilted.

The Carbon Balance

In an earlier communication (5) we separated respiration into two parts, maintenance and growth viz.,

$$RW = R_0W + G_R\ (dW/dt) \quad [3]$$

where R_0 represents the respiratory cost of maintaining a gram of live tissue and G_R is the respiratory loss in forming new tissue. We also noted that one mole of CO_2 is equivalent to one mole of CH_2O dry matter and that for cotton bolls, 1 gram of dry matter made up of protein, fat, fiber, N-free extract and mineral matter had the carbon equivalent of one gram CH_2O. We may therefore, interchange P_N in eq. 2 with dW/dt in eq. 1, and rearranging eq. 1.

$$dW/dt = P - RW \quad [4]$$

and, $$dW/dt = P - R_0W - G_R(dW/dt) \quad [5]$$

or, $$dW/dt = (P - R_0W)/(1 + G_R) \quad [6]$$

This is reasonable for organs which are largely nonphotosynthetic. It is obvious now, however, that a carbon balance used in the simulation of crop growth (at least in some species) must contain a term for day respiration (PR_L), and we are using the following form:

$$dW/dt = [P(1 - R_L) - R_0W]/(1 + G_R) \quad [7]$$

where R_L is mg mg^{-1} photosynthate.

PR_L was calculated by using the regression equation for the day respiration data and subtracting an R value at ($I_0 = 0$) from the R value obtained at (I_0 = some light intensity). P, then, was obtained from the data in Figure 3b assuming the appropriate values of I_0 and T, and dividing this into PR_L, we estimated R_L. The ratio of day respiration to photosynthesis (PR_L/P) was computed for various temperatures and light intensities. It did not vary with light intensity. However, it did increase with temperature over the range 25 C to 41 C from 0.09 to 0.14 at 300 W m^{-2} and from 0.08 to 0.15 at 700 W m^{-2}.

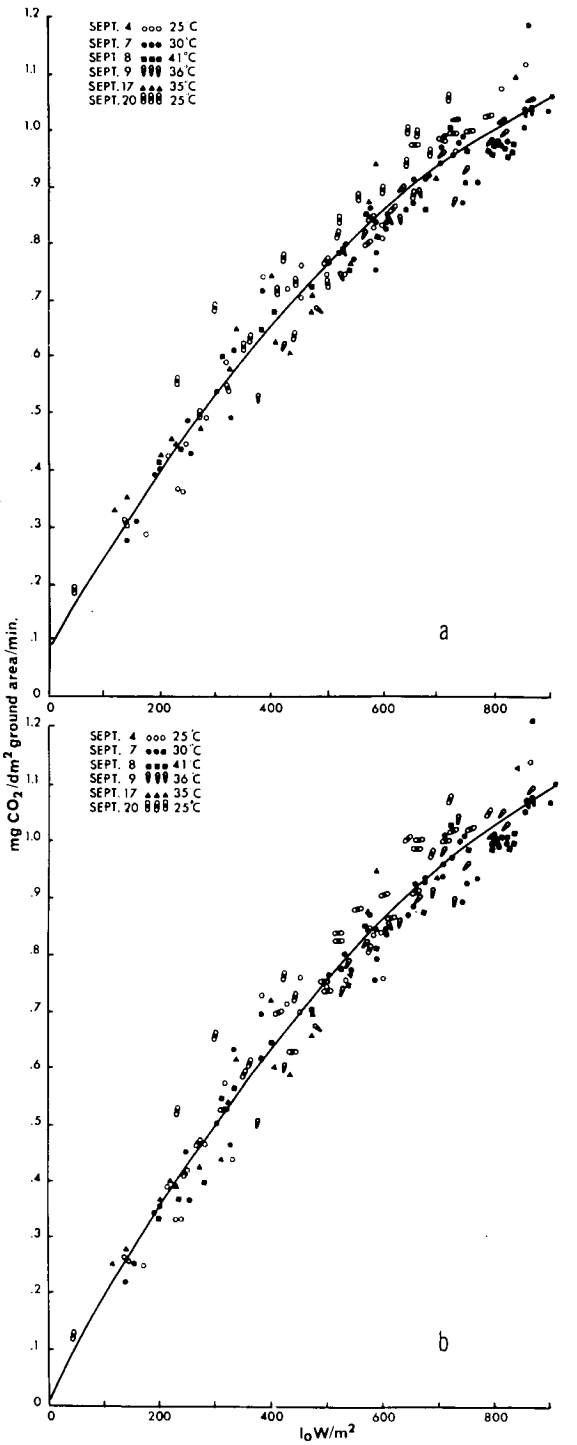

Fig. 3. Gross photosynthesis estimated using Equation 2 vs. light intensity in cotton crops of different weights, and at various air temperatures and vapor pressure deficits. Data pooled in a. Light respiration accounted for in b.

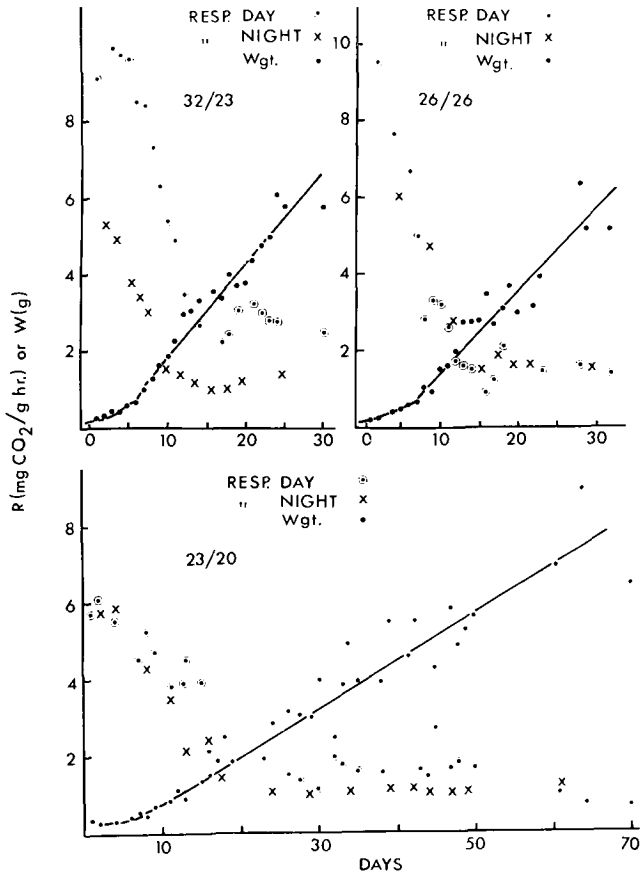

Fig. 4. The time course of respiration rate and growth of cotton bolls in various temperature environments.

Growth

Fruit growth and respiration data for plants grown in the phytotron in the three temperature treatments 32/23, 26/26 and 23/20 are presented in Fig. 4. The three types of response shown were representative of all seven treatments. The 32/23 treatment showed a 50% lower respiration rate at night than in the daytime. The differences in day and night fruit respiration were as large for the 32/29 and 29/26 treatments. Differences in day and night fruit respiration at 26/23 and 20/17 were similar to those shown for 23/20. The 26/26 data are unique in that day and night respiration did not differ.

Initially the growth of the boll was exponential. Later it became linear. The time at which growth terminated depended upon temperature (6). Boll growth was twice as rapid at 32/23 as at 23/20. At 26/26 the growth was 16% slower than at 32/23. The growth rate at 26/23 was similar to that at 26/26. An increment of respiratory loss was obtained by multiplying the boll respiration rate at a given temperature by the number of hours at that temperature in each treatment. These data, then (converted to CH_2O) were added to the weight gains to show the effects of temperature and boll size on efficiency in conversion of available carbohydrate into dry matter by young bolls (Figs. 5 and 6). The amount of total carbohydrate required for respiration plus growth over the first 3 g of boll growth is graphed for various temperatures in Fig. 5. It is evident that efficiency increased with increasing temperature. Nine representative bolls 15- to 27-days old were harvested from plants in the 32/29 treatment and were found to be 50% lighter than bolls of a similar age grown at the lower temperatures. This suggests that respiratory losses at the high temperatures resulted in carbohydrate shortages. The 32/23 treatment which was very heavily loaded with fruit also had many stunted bolls. After boll weights of 3 g were reached, the rate of dry matter accumulation was slow for the 32/29 and 29/26 treatments. During this phase of boll growth these plants were loaded with fruit. Respiration rates at night were often considerably less than during the day in these treatments.

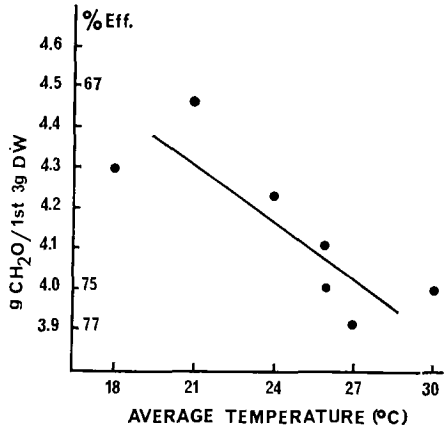

Fig. 5. Total carbohydrate (3 g + the respiratory loss) required to produce 1st 3 g dry weight in cotton bolls at various temperatures.

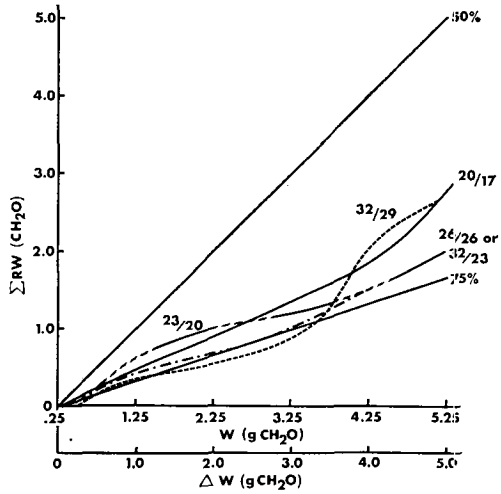

Fig. 6. Cumulative fruit respiratory loss vs. weight gained in cotton bolls grown at different temperatures.

Cumulative CH_2O respired by cotton bolls is plotted against growth in Fig. 6. The high efficiency in the young fruit at the higher temperature is quite evident. The curves for 32/29, 32/23, and 26/26 fall below those for 20/17 and 23/20. From 2 g on the efficiency was essentially constant and identical in the 26/26 and in the 32/23 treatments. At 3 g the 32/29 bolls apparently ran short of carbohydrate. Maintenance respiration became relatively large. These bolls were very small at maturity. The 20/17 bolls developed a fungus infection and their efficiency remained low.

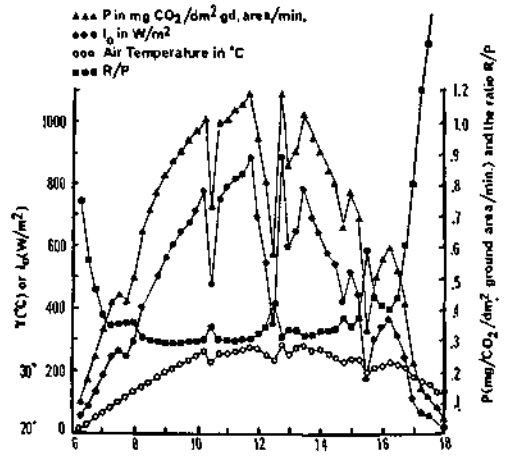

Fig. 7. Typical day's time course (0600 to 1800 local standard time) of solar radiation, air temperature, and gross photosynthesis and the ratio respiration/gross photosynthesis. Computed according to the model discussed in this paper.

In the seedling experiment the efficiency of conversion of photosynthate to dry matter was 33 ± 2.3% (n = 4) for the first 0.3 g accumulated. For the next 0.5 g dry weight, the efficiency was 53.5 ± 3.5%. These values were similar for plants from four temperature regimes and the mean with its standard error is given here. The 53.5% value is the same as that reported earlier (5) for growing leaves. Some of the respiration rates measnred, with three replicates combined for each valne, were extremely high, being about 50 mg CO_2/g dry weight/hr. The highest valnes we had measnred in other experiments were 30 mg CO_2/g dry weight/hr for flowers that had been open only a few hours. Obviously, the type of organ and its age are important in determining the efficiency with which carbohydrate is fixed.

The R/P Ratio

The fraction of gross photosynthate respired by the plant has long been of interest to the physiologist. Quantitative information is demanded in any growth modeling effort. In Fig. 7 we have graphed a typical day's light and temperature data. We computed the photosynthesis (P) and respiration rates (R) for the crop in the first setup. The ratio of these values (R/P) ranges from infinity in the dark down to 0.29 under intense sunlight at 0900. Fig. 7 demonstrates the variation in (R/P) with temperature and sunlight. For example, at 0730 the light intensity was 260 W/m² and R/P was .34. At 1545 with a similar light intensity (240 W/m²) the R/P value was 0.50. For this reason the use of an expression such as that of McCree (8) which defines respiration as a function of photosynthesis would appear to be rather hazardons.

REFERENCES

1. Baker, D. N. 1965. Effects of certain environmental factors on net assimilation in cotton. Crop Sci. 5:53-56.
2. Baker, D. N., and J. D. Hesketh. 1969. Respiration and the carbon balance in cotton (*Gossypium hirsutum* L.). Proc. 1969 Cotton Prod. Res. Confs. 60-64.
3. Forrester, M. L., G. Krotkov, and C. D. Nelson. 1966. Effect of oxygen on photosynthesis, photorespiration and respiration in detached leaves. I. Soybean. Plant Physiol. 41:422-427.
4. Kramer, P. J., H. Hellmers, and R. J. Downs. 1970. SEPEL: New phytotrons for environmental research. Bio. Sci. 20: 1201-8.
5. Hesketh, J. D., D. N. Baker, and W. G. Duncan. 1971. Simulation of growth and yield in cotton: Respiration and the carbon balance. Crop Sci. 11:394-398.
6. ———, and A. Low. 1968. Effect of temperature on components of yield and fiber quality of cotton varieties of diverse origin. Cotton Growing Review 45:248-257.
7. Ludwig, L. J., T. Saeki, and L. T. Evans. 1965. Photosynthesis in artificial commnnities of cotton plants in relation to leaf area. I. Experiments with progressive defoliation of mature plants. Aust. J. Biol. Sciences. 18:1103-18.
8. McCree, K. J. 1969. An equation for the rate of respiration of white clover plants grown under controlled conditions. Preliminary texts of invited papers. IBP/PP Technical Meeting. Productivity of Photosynthetic Models and Methods. Sept. 14-21, 1969. pp. 70-76.
9. Mnramoto, H., J. D. Hesketh, and C. D. Elmore. 1967. Leaf growth, leaf aging, and leaf photosynthetic rates of cotton plants. 1967 Beltwide Cotton Production Research Conferences, Jan. 10-11, 1967. Dallas, Texas, pp. 161-170.