Simulation of Growth and Yield in Cotton:

Respiration and the Carbon Balance[1]

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ABSTRACT

Rates of respiration and dry matter accumulation were measured for growing squares (floral buds), bolls, and leaves of cotton, *Gossypium hirsutum* L. After assuming a "maintenance respiration" and a "growth respiration", it was possible to derive an equation whereby such components of respiration could be estimated from regression analysis of transformed experimental data. New values for the efficiency of conversion of photosynthate into dry matter were estimated for leaves, squares and bolls; such values ranged from 50 to 69%. The theory, experiments described, and results from cotton offer hope for better descriptions of respiration for growing organs of other plant species. Such information is urgently needed for the development of management models depending on predictions of effects of environment on plant growth.

Additional index words: Morphogenesis, Cotton bolls, *Gossypium hirsutum* L.

A CASE has been made for better descriptions of respiration in plant communities to develop better plant models (6, 5, 2, 1). A large fraction of gross photosynthate is necessary for respiration in growth (3); therefore, our understanding of primary productivity also depends upon better descriptions of the respiratory processes. We report here results of recent experiments and developments in theory concerning growth and respiration in cotton bolls and leaves (*Gossypium hirsutum* L.).

METHOD

Standard leaf chamber techniques (8) were used to measure rates of CO_2 evolution from detached squares, flowers, bolls and leaves at various stages of development. Air was flushed through the 8 by 20 by 20 cm^3 chamber at about 10 liters/min. For the field experiments a 1-ha stand of 'Stoneville 213' cotton (*Gossypium hirsutum* L.), was thinned to 100,000 plants with 1 m between rows. Greenhouse plants were grown in soil of the floor of the house about 60 cm apart. Air temperature in the field and in the chamber was usually 30 C; respiration rates at small deviations from this were corrected to 30 C using a relationship derived from earlier data (Fig. 1 in (1). About 100 unfolded leaves about the same size, 100 squares 3 mm on a side, or 100 flowers were tagged at one time and were sampled at later dates for the growth studies. Flowers were also tagged every few days, and samples were taken when the oldest bolls were open. The latter technique allowed measurements of rates of respiration on the same day for bolls of all ages.

RESULTS AND DISCUSSION

Respiration rates and dry matter values are given in Fig. 1, 2, and 3 for detached squares, bolls and

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leaves. As found earlier, square growth was logarithmic (1); boll growth was logarithmic for about 10 days and was linear thereafter to about 40 days. Leaf growth appeared to be logarithmic during the early part of the sampling period. The respiration rates were high for young tissue and decreased with time as the bolls and leaves acquired dry matter with age; however, rates did not decrease much as floral buds developed.

Theoretical Considerations

For analysis of the above-mentioned results, we use here a concept of maintenance respiration (R_o) for all cells and growth respiration (G_R) for cells undergoing division or synthesis of metabolites associated with growth (5). If we define R = respiration rate (g CH_2O/g CH_2O hr), W = dry weight (g), R_o = maintenance respiration rate (g CH_2O/g CH_2O hour), and G_R = respiration required to convert CH_2O to dry weight in some part of a plant (g CH_2O/g CH_2O), then

$$RW = R_oW + G_R \, dW/dt. \qquad [1]$$

Dividing through by W,

$$R = R_o + G_R \, (dW/dt) \, 1/W. \qquad [2]$$

Various forms of Equation [1] have been used by others (7, 9) with either gross photosynthetic rates or

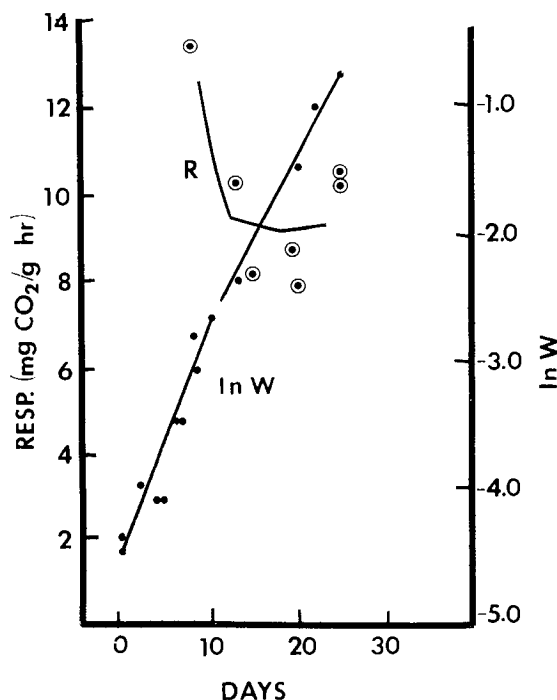Fig. 1. Respiration rates, R, and dry weight, W, against time for cotton squares on field-grown cotton. The date of the first measurement was set to 0.
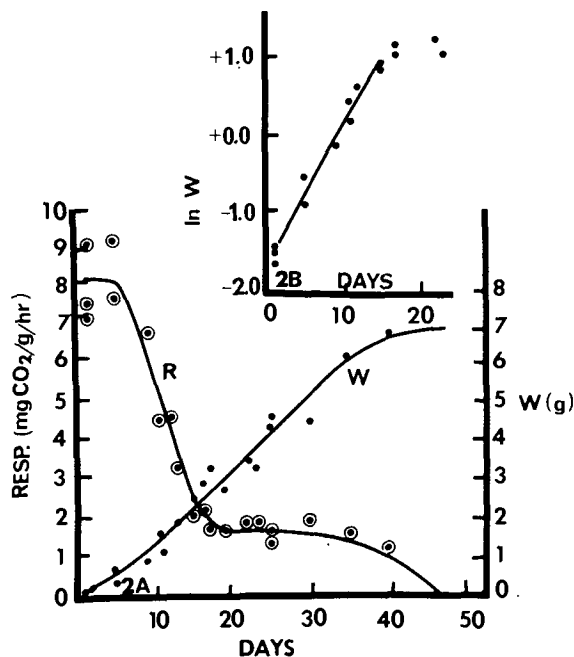
Fig. 2. A. Respiration rates, R, and dry weight, W, against time for bolls of different ages on field-grown cotton. Day 0 = day of flowering. B. Logarithm of dry weight, W, of bolls between 0 to 22 days.
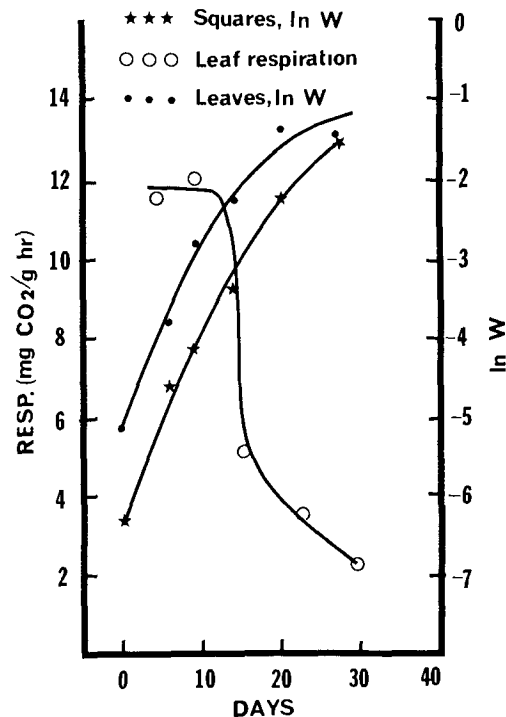

Fig. 3. Dry matter accumulation and respiratory demands of a growing leaf on the main stem, greenhouse, winter. T = 29.5 C. Respiration adjusted to 30 C. The date of the first measurement was set to 0. Data for squares in the axil of the leaf are also given.

net photosynthetic rates in the equation. Hiroi and Monsi (5), Sawada (10) and Thornley (11) also present a form of Equation [1] in their papers, which we will discuss later. Our Equations [1] and [2] appeared under comments by D. Baker in *Newsletter of the Work Conference on Crop Production Simulation, I (June):7. 1970.*

Where growth is perfectly logarithmic, i.e., $W = W_o e^{kt}$, then $d(\ln W)/dt = (dW/dt)1/W = k$. Since the differential is constant, R theoretically is constant. In Fig. 1, square growth is logarithmic and respiration is consistently high. In boll and leaf growth, Fig. 2B and 3, there is a logarithmic phase of growth associated with reasonably constant R values. From Equation [1] where growth is linear with time or $W = W_o + bt$, R_o and R_B can be estimated from two sets of experimental data by solving two equations for two unknowns. (This cannot be done directly from Equation [2] when growth is logarithmic and $(dW/dt)1/W$ is constant; hence, we cannot use data from Fig. 1 to estimate both constants.)

Setting $dW/dt = b$,

$$R = R_o + G_R b(1/W),\qquad [3]$$

and from plots of R vs. 1/W, one can estimate R_o and $G_R b$. Also b can be obtained from regression of W on time.

The equation $dW/dt = P — RW$ (see Ref. 5, 9, 10) (P = gross photosynthetic rate or rate of translocation of carbohydrate into a growing organ) can now be modified by substituting for RW from Equation [1] as follows:

$$dW/dt = [1/(1+G_R)] (P — R_o W) \text{ and}\qquad [4]$$

$$W = (P/R_o) \{1 — \exp [(—R_o t)/(1+G_R)] \},\qquad [5]$$

assuming P, G_R, and R_o are constant and $W = 0$ at $t = 0$ (see Ref. 5 for a form of Equation [4].)

The efficiency by which CH_2O or gross P is converted into W becomes

$$W/Pt = 1/R_o t \{1 — \exp [—R_o t)/(1+G_R)] \}.\qquad [6]$$

Estimates of G_R and R_o

Rate of respiration was measured as mg CO_2/g dry weight per hour whereas growth was determined as g dry weight per day. To use the above equations, both must be in the same units for both mass and time. From earlier day and night respiration data (Table 1, Ref. 1) at 31.5 C day and 20.5 C night temperatures, night respiration was 33% of day res-

Table 1. Budget for carbohydrate needs of a maturing cotton boll at 26.5 C (average), calculated from theory and estimated constants from data in Figs. 1, 2, and 4.

Growth phase	W_0, g CH_2O	R, g CH_2O/ g CH_2O/day	k*	Time, days	∫RWdt, g CH_2O /day	W, g CH_2O	Efficiency
Squaring							
Phase I (early)	0.0114	0.1614	0.187	10	0.054	0.062	.53
Phase II (late)	0.074	0.114	0.125	13.7	0.3066	0.336	.52
Flowering: Florial parts lost and RW = 0.207 g†							
Boll growth							
In phase	0.21	0.096	0.171	10	0.534	0.96	.64
Linear phase	1.17	R_0:0.0032 G_R:0.375(g/g)	0.1826	30 ·	2.43	5.48	.69
Maturing phase					0.254	0.17	
	Total dry weight of boll	7.0 g					
	Total CH_2O used	10.61 g					
	Average conversion	.66					

* The slope of W or ln W with time. (g CH_2O/day or 1/day)   † This dry matter disappears during the day of flowering and doesn't add to the total CH_2O required. In 1969, for four sets of determinations, 0.207 g W was lost the day of flowering; 0.126 g of this was in shed floral parts. After accounting for the boll weight left, 0.08 g W must have been used up in respiration. When growth of the square was extended one day, 0.1 g CH_2O was required. Estimates of RW the day of flowering suggest about 0.11 g CH_2O was required. From these figures, we can estimate that 0.02 to 0.03 g of CH_2O must have been translocated into the boll or flower the day of flowering. This additional requirement wouldn't have much effect on the Average Conversion calculated above.

piration. Respiration values as determined in this study over a short time period during the day (Fig. 1, 2, and 3) were converted to 24-hour CH_2O values by multiplying by (16.6 hour/day) (30/44 g mole CH_2O/ mole CO_2) where one mole of CO_2 is equivalent to one mole CH_2O dry matter. McCree and Troughton (7) found the latter to be true for white clover plants; we also found this to be true for cotton bolls where 1 gram of boll dry matter made up of protein, fat, fiber, N-free extract and mineral matter had the carbon equivalent of 1 gram of CH_2O. The 16.6 factor comes from 13 hours of daylight with respiration proceeding at the full rate, and 11 hours with respiration at 0.33 the full rate, or $13 + 11(0.33) = 16.6$ hours of respiration at the full rate.

When one considers the effect of temperature on the days required to grow a boll to maturity (4), about 76% of the growth would occur during the daylight hours because of the higher temperatures. To convert boll growth per day to an hourly basis during daylight hours, 24-hour values were multiplied by 0.76/13, 13 being the hours of daylight. Needless to say, the greatest potential for errors in our estimates will be in such factors as are necessary to convert R and dW/dt to the same units.

Using the transformation as given in Equation [4] (see Fig. 4 where the square of the correlation coefficient was 0.98), R_o was calculated to be 0.0032 g CH_2O/g CH_2O day and G_Rb was 5.944 mg CO_2/hour. From regression of Boll W on time, $b = 0.1826$ g CH_2O/day (the linear phase of growth, Fig. 2). An adjusted b value per hour would be 0.76 (0.1826)/13 = 0.0107 g/hour. G_R then = (30/44 × 0.005944) /0.0107 = 0.379 g/g.

As an independent approach, respiration rates were converted to 24-hour values by multiplying by 16.6 × 30/44; G_R was then calculated to be 16.6 × 30/44 × 0.005944/0.1826 = 0.368 g/g.

Similar values were obtained from two sets of data and by solving two equations for two unknowns. From numerous W determinations, we are certain that accumulation of W is linear over the time period involved.

From leaf data, Fig. 3, R_o was estimated to be 0.0264 g CH_2O/g day, and G_R to be 0.54 g/g. For such estimates, three sets of values were taken from a time period where dry matter accumulation in leaves was fairly linear. Respiration associated with leaf photosynthesis probably biased these estimates once photosynthate was exported from the leaf.

If one assumes R_o values during the logarithmic phase of growth to be similar to those during linear growth, the G_R becomes much larger, varying from 0.7 to 0.8 for leaves, bolls and squares, as contrasted to values of 0.3 to 0.4 during linear growth. The higher G_R values may be associated with synthesis of protein and other complex compounds, whereas the lower G_R may be associated with deposition of cellulose.

Hiroi and Monsi (5) and Sawada (10) present estimates of R_o and G_R. Their R_o values would seem to be estimated from actual measurements of respiration by gas exchange methods, which would have included a large G_R(dW/dt) component. Hiroi and Monsi's equivalent of a G_R factor of 0.25 is used to account for the discrepancy between their dW/dt, estimated from a function based on photosynthetic-
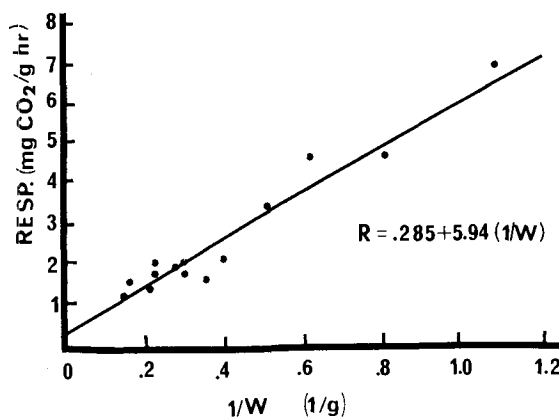

Fig. 4. Boll respiration as a function of the reciprocal of dry weight (W) (age 9 to 40 days).

light response curves of individual leaves minus the measured respiration, and their dw/dt actually measured from growth analysis. By making some gross assumptions, it was possible to estimate from Sawada's data R_o and G_R values that were similar to the ones we report.

McCree (7), using a form of Equation [1] with gross photosynthetic values, estimates a maintenance respiration value that includes a G_R(dW/dt) component after 24 hours of darkness. His k_1P is equivalent to our G_R(dW/dt) (except we use different units.) Combining this fact with dW/dt = P — R and his $R = k_1P + R_oW$,

$$G_R = k_1P/[(1-k_1)P - R_oW.]$$ [7]

He estimated k_1 to be 0.25 g CO_2/g CO_2 and R_o to be 0.15 g CO_2/g CO_2 × day. Selecting P and W values at 50 days from his experiment b, Fig. 4 where his theory best fits facts, we calculated G_R to be 0.46. Using our R_o values which were 1/3 his (0.0032 × g CO_2/g CO_2 × day), G_R becomes 0.36. For his entire experiment, such G_R values only varied between 0.34 and 0.36, values similar to our 0.375, Table 1. Using our Equation [1] and estimates of his R and W values at 30 and 40 days, G_R calculated to be 0.33 (two equations, two unknowns).

In Thornley's form (11) of our equation [1], his $(1 — Y_G)/Y_G$ is equivalent to our G_R term, his P_n to our dW/dt and his m = our R_o. We have used the N.A.R. (Net Assimilation Rate of dry matter per unit leaf area) notation as much as possible, for reasons discussed below.

The Carbon Balance for Growth of Bolls and Leaves

One use of the theory and experimental data reported above can be in the development of budgets for CH_2O needs of a boll from a pinhead square to opening or for a growing leaf. In such a budget we now can account for respiratory needs.

The integral of RW over time where $W = W_oe^{kt}$ is RW_oe^{kt}/k and can be estimated by knowing values for W_o, k, t, and R. Values and the integral are given in Tables 1 and 2 with $W—W_o$ values for the appropriate time interval. The efficiency for conversion of gross CH_2O to W becomes $(W—W_o)[(W—W_o) + \int RW \, dt]$; the values are similar for squares and leaves.

Table 2. Budget for carbohydrate needs of a leaf at 29.5 C, calculated from theory and constants estimated from data in Fig. 3.

Growth phase	Time, days	W_0, g CH$_2$O	k*	R, g CH$_2$O/g CH$_2$O/day	∫RWdt, g CH$_2$O /day	W, g CH$_2$O	Effi- ciency
In phase	10	0.0064	0.228	0.192	0.047	0.056	.54
Linear phase	13	0.0626	0.014	R$_0$:0.0264	0.151	0.182	.55
				G$_R$:0.54			
	Total leaf dry weight			0.245 g			
	Total CH$_2$O needed			0.443 g			
	Average conversion			.55			

* The slope of W or ln W with time. (g CH$_2$O/day or 1/day)

Where $W = W_0 + bt$, $dW/dt = b$ and the integral of RW over time using $R_0W + G_R$ dW/dt becomes $R_0W_0t + R_0bt^2/2 + G_Rbt$. Appropriate values for the various symbols are given in Tables 1 and 2. During this linear phase of boll growth, the efficiency values were much higher.

Given a photosynthate supply rate of 0.228 g CH$_2$O/day to a boll for 45 days, from Equations [4] and [5], where $G_R = 0.375$ g/g and $R_0 = 0.0034$ g/g day, W becomes 7.1 g. W/total P = (7.1/0.228 × 45) = 0.69. The efficiency value for a mature boll as determined in Table 1 was 0.66. These values are higher than 0.56 calculated earlier (1) from a cruder set of data.

Biochemical Aspects of G$_R$

CH$_2$O is condensed into fats and is built into other large molecules using high energy compounds generated from CH$_2$O via glycolysis, in the citric acid cycle, and cytochrome systems. The efficiency in synthesizing and utilizing these high energy compounds determines G$_R$, along with the energy state of 1 g of synthesized product. G$_R$ would also include energy requirements for translocation as well as other growth-associated metabolic processes.

Modeling Considerations

Equations [4], [5], and [6] can be used as general models for simulating plant growth, provided P or gross photosynthate per day per plant is available from another model. (See Ref. 1, where net P was iterated from a model of multiple regression equations including light, temperature, light interception, and other environmental parameters). Models giving estimates of maintenance and growth respiration are useful in estimating the relative fraction of each in measured respiration rates per g dry weight at various stages of growth. Also, as pointed out earlier (1), the total respiratory demand can become quite large when the fruit load is heavy, and may be even greater than available gross photosynthate on cloudy days. Such information coupled with real plant responses (shedding of fruit) may help greatly in understanding the physiology of yield in cotton.

The following observations may be useful in future modeling efforts. From equation [4] when 1/W(dW/dt) is constant, P/W, theoretically, must remain constant. When W is linear on time, P — R$_0$W, theoretically must remain constant. In the logarithmic case, $dA/dt = \partial A/\partial W$ $(\partial W/\partial t)$ provides a model for leaf area (A) expansion in plants; $\partial A/\partial W$ changes greatly in early growth because of transformation of seed reserves (W$_0$) into leaf area. For time course plots of $\Delta A/\Delta W$, see (5).

Where N.A.R. or the Net Assimilation Rate of dry matter as grams CH$_2$O, is defined as 1/A (dW/dt),

$$N.A.R. = (1/A)[1/(1+G_R)] (P—R_0W). \quad [8]$$

This involves estimates of gross photosynthates per plant per day. Equation [8] also represents an instantaneous net photosynthetic rate, as is often measured using standard gas exchange techniques.

This plant growth model is similar to that of McCree in that all photosynthate is converted into dry matter without consideration of a reserve. Such a model would be useful for warm-climate plants such as cotton growing at very warm temperatures.

Future papers will deal with rates of leaf and square initiation. Once a new organ is known to be available, then CH$_2$O can be budgeted to it according to needs outlined in Tables 1 and 2. In a final model, supply of gross photosynthate will be balanced with such needs.

Such models offer methods whereby relationships between photosynthesis, respiration, and growth can be studied using measurements made at the same time of all three processes in the same system. The model then becomes an experimental tool, such as the statistical models that have been available for some time for analysis of variation associated with measurements.

CONCLUSIONS

A technique is described whereby respiration can be separated into maintenance and growth components. This involves a theoretical model for respiration and dry matter accumulation. The theory and calculations hopefully present a better understanding of why respiration changes as plant parts grow.

The estimates depended upon the behavior of growth and respiration at night; two independently derived factors yielded similar estimates for the growth components of respiration. The estimates involved some rather complex calculations utilizing respiration and dry matter data. The relationships between rates of respiration or dry matter and time seem fairly clear; however, both kinds of experimental determinations are fraught with difficulties, and subtle changes in these relationships can greatly affect estimates of G$_R$. Despite these limitations, quantitative information about respiration is needed for models simulating plant growth, and our estimates at least offer a base upon which to build better models and study various components of respiration.

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