Equations for the Rate of Dark Respiration of White Clover and Grain Sorghum, as Functions of Dry Weight, Photosynthetic Rate, and Temperature[1]

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ABSTRACT

Equations were designed to be used in computer models of photosynthesis and respiration in crops. They were developed from new experimental data on the rates of CO_2 exchange of whole plants grown under constant conditions. The dark respiratory rate was separated into two components. The "maintenance" component was taken to be the efflux of CO_2 after more than 48 hours in the dark at constant temperature. This component was proportional to the dry weight of the plant (W), and was a strong function of temperature (T). The proportionality constant (c) was about twice as great for clover (*Trifolium repens* L.) as it was for sorghum (*Sorghum bicolor* L.), at the same temperature. The "growth" component was taken to be the difference between the "maintenance" component and the total efflux during a normal night period (N). This component was proportional to the total influx during the previous daytime period (D), and the proportionality constant (k) was independent of species and temperature. The values of c and k were in good agreement with values calculated by Penning de Vries, using the principles and equations of biochemistry.

The experimental data were best fitted by the following equations:

For clover at 30C: $N = 0.14\ D + 0.0143W$

For sorghum at 30C: $N = 0.14\ D + 0.0054W$

Temperature dependence of maintenance coefficient:

$$c_T = c_{30}\ (0.044 + 0.0019\ T + 0.0010\ T^2)$$

where N = night total of CO_2 evolved in $g \cdot 12h^{-1} \cdot plant^{-1}$,
D = daytime total of CO_2 taken up in $g \cdot 12h^{-1} \cdot plant^{-1}$,
W = CO_2 equivalent of dry weight in $g \cdot 12h^{-1} \cdot plant^{-1}$,
T = temperature in °C.

Additional index words: Computer models, Growth, Maintenance, CO_2 exchange.

IN early models of crop growth, the rate of respiration was assumed to be proportional to the standing biomass or the leaf area. Since the rate of photosynthesis reached its maximum at the point at which all of the incident light was absorbed, any increase in leaf area or biomass beyond this point resulted in a decrease in the net uptake of CO_2 over 24 hours.

This simple picture of an optimum leaf area for crop growth is demonstrably false. Measurements have shown that the rate of respiration is not proportional to the biomass, but is strongly dependent on the rate of photosynthesis (Ludwig, Saeki, and Evans, 1965; McCree and Troughton, 1966). The following empirical equation was developed to fit experimental data on the rates of exchange of CO_2 by whole clover plants (*Trifolium repens* L.) grown under constant conditions (McCree, 1970):

$$R = 0.25 + 0.015W \qquad [1]$$

where R is the 24-hour total of dark respiration for the whole plant, P is the 12-hour total of gross photosynthesis, and W is the CO_2 equivalent of the dry weight of the plant. This equation has been used in several models of crop growth (Wit, Brouwer, and Penning de Vries, 1970; Curry and Chen, 1971; Loomis, Williams, and Hall, 1971; Soribe and Curry, 1973).

In most models, and in crop ecology generally, the term respiration has been used to mean the loss of CO_2 from the plant, which is considered to be undesirable, but respiration is also the name of the process by which the high-energy compounds needed for essential metabolic reactions are produced from carbohydrates. During the same process, the carbon skeletons of many of the organic compounds which make up the permanent structure of the plant are produced as intermediates (Beevers, 1970). In this view, a high rate of evolution of CO_2 indicates a rapid synthesis of new material, which is obviously desirable. Undesirable loss of CO_2 would result only from a low efficiency of conversion to new material, or from synthesis of redundant compounds.

Thornley (1970) pointed out that equation [1] is analogous to that used by microbiologists to describe the growth of bacteria on exogenous substrate, if it is assumed that, in the steady state, 25% of the substrate formed by photosynthesis in unit time is lost during the conversion to new plant material, and 1.5% of the dry weight is lost per day in providing energy to maintain vital functions of the plant. A similar analysis could be applied to the equation developed independently by Hesketh, Baker, and Duncan (Hesketh et al., 1971; Baker et al., 1972) for cotton (*Gossypium hirsutum* L.). According to Pirt (1965), Duclaux (1898) was the first microbiologist to use this form of equation.

Penning de Vries and his colleagues (Penning de Vries 1972, 1974a, 1974b; Penning de Vries, Brunsting, and van Laar, 1974) have recently published a series of theoretical analyses of the use of assimilates in plants. They showed how the maximum efficiency of conversion to new material can be calculated from basic biochemical equations, if the chemical composition of the end product is known. For young whole plants, the calculated efficiencies agreed closely with measured values (Penning de Vries, 1974a), and with the value from equation [1]. Maintenance, transport, and other losses were treated in a similar manner, again with good agreement with experimental values. These analyses supply a much-needed general framework for experimental studies of respiration in plants.

The experiments reported here were planned as an extension of the work on clover (McCree, 1970) to a species with a contrasting genetic background, grain sorghum (*Sorghum bicolor* L.). The effects of temperature were studied with both species. The results

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are interpreted in the light of the new theoretical treatments.

MATERIALS AND METHODS

New Zealand white clover (*Trifolium repens L.*, 'C-1852') and grain sorghum (*Sorghum bicolor* L. Moench, 'RTX 412') were grown in a growth chamber at constant air temperature (20 and 30C in 2 different experiments), 500 μeinsteins$\cdot s^{-1} \cdot m^{-2}$ of photosynthetically active radiation (400 to 700 nm) (McCree, 1972) from fluorescent and incandescent lamps, a 12-hour day, and uncontrolled CO_2 and H_2O concentrations. The plants were grown in vermiculite and nutrient solution. The surface of the vermiculite was covered with opaque plastic to reduce the growth of algae.

At suitable intervals, individual plants were transferred to a whole-plant assimilation chamber. In this chamber, the air temperature was the same as in the growth chamber, but the irradiance at the top of the plant was 1500 to 200 μeinsteins$\cdot s^{-1} \cdot m^{-2}$ of photosynthetically active radiation (solar levels). The light source was a single 400 W Metalarc lamp (Sylvania) in an aluminum reflector (Steber HB 200) with a sheet of glass between the lamp and the chamber to reduce the thermal radiation load.

The air in the chamber was rapidly circulated, with a fan (air speed 3 $m \cdot s^{-1}$), through a temperature-controlled radiator coil, the temperature of which was set to achieve the desired leaf temperature ($\pm$ 1C), as measured by a thermocouple pressed against the leaf surface. The leaf temperature was about 5C above the coil temperature in the light, and 2C above in the dark. The dewpoint temperature was equal to the coil temperature.

The chamber was operated on the open system. Compressed air from the laboratory supply (350 to 400 ppm CO_2) was bubbled through water to humidify it and also to remove oil, then passed through the chamber at 5 to 10 liters$\cdot min^{-1}$, depending on the size of the plant. The volume of the chamber was 35 liters (base area 0.025 m^2). A sample of the air in the chamber was passed at 0.5 liters$\cdot min^{-1}$ through one cell of an infrared gas analyzer (Beckman Model 315A). A sample of the air coming into the chamber was passed through the other cell of the analyzer. Both streams were first passed over saturated solutions of sodium chloride, to bring them to the same relative humidity (75%), and thus eliminate interference from water vapor. The analyzer was calibrated with gas mixing pumps (Wösthoff type M300). The overall accuracy of CO_2 flux measurements is estimated to be $\pm$ 10%.

Measurements were started 24 hours after transferring a plant from the growth chamber. Various combinations of light, darkness, and temperature were used to determine the coefficients of equation [1]. To emphasize the fact that CO_2 exchange rates measured in this way cannot be identified with rates of "photosynthesis" or "respiration" (however defined), and still less with rates of production or use of specific "substrates for growth" (Thornley, 1970), the results will be presented simply as measured CO_2 fluxes, into or out of the whole plant, in light or darkness.

When a plant is placed in darkness, it uses up its reserves of substrate, and growth eventually stops. At this point, the efflux of CO_2 is entirely due to maintenance. This flux is assumed to be a function of the dry weight of the plant and temperature. During growth under normal conditions, the efflux in the dark is greater than this. The difference is the growth component, which is assumed to be proportional to the influx in the light, in the steady state. Since the plant is able to store substrate, the growth component of the efflux will lag behind the influx, but if the lag time is much less than 24 hours, and the influx and efflux are integrated over the respective day or night periods, a steady state can be assumed.

If the equation for the steady state is of the general form (McCree, 1970):

$$N = k\,D + cW \qquad [2]$$

where N = night total of CO_2 evolved by the plant,
D = daytime net total of CO_2 taken up by the plant,
W = dry weight of the plant, in CO_2 equivalents,
k = "growth" coefficient (dimensionless), and
c = "maintenance" coefficient (dimension:$time^{-1}$),

then the rate of change of dry weight is

$$dW/dt = D - N$$
$$= (1 - k)\,D - cW. \qquad [3]$$
$$\text{Also, } kdW/dt = (1 - k)\,N - cW. \qquad [4]$$

Thus, if cW is small, dW/dt is simply proportional to N (Penning de Vries et al. 1974).

N and D were obtained by integrating the instantaneous value of the flux (F). To obtain W, the vermiculite was washed from the roots, and the whole plant was oven-dried to a constant weight at 85C. Each gram of dry weight was taken to be equivalent to 1.43 g of CO_2, as previously determined (McCree and Troughton, 1966). Protein contents were determined as Kjeldahl N $\times$ 6.25.

RESULTS AND DISCUSSION

Figure 1 is an example of a continuous recording of the CO_2 flux into or out of a plant during one experiment. During the first 24 hours the conditions were constant, and both the influx in the light and the efflux in the dark were constant throughout their respective 12-hour periods. During the second light period (24 to 36 hours), the light was switched off for half an hour, at 3-hourly intervals. The efflux in the dark was constant and equal to that measured during the normal night period. One hour into the third light period (at 49 hours), the light was switched off permanently. The efflux decayed rapidly, reaching a steady level after approximately 48 hours (Heichel, 1970; Ryle et al., 1973).

Typical decay curves are shown in Fig. 2. In all cases there was an exponential decay during the first 12 hours in the dark, followed by a break, and then another decay. When the second night period was simply extended, so that the plants received no light signal at the beginning of the third "light" period (Fig. 3), the decay started at the same time as before. The simplest way to explain the results shown in Fig. 2 and 3 is to assume that the plants were using two separate pools of substrate, one of them being available during the light period and the other during the night period, and that the switch between the two pools was under the control of an endogenous rhythm.

The decay constants for the two species and temperatures are given in Table 1. The constants at 20 C were about 70% of those at 30 C (half-life of 5.8 hours at 20 C and 4.2 hours at 30 C). There was no significant difference between species.

In the ELCROS simulation of crop growth (Wit et al., 1970) the growth component was assumed to be proportional to the quantity of substrate present, up to a limit of 4% of the dry weight, and constant above that level. The total quantity of CO_2 evolved from our plants during the 48-hour decay period was between 1 and 3% of their dry weights (in CO_2 equivalents). An additional 2 to 4% was evolved during the preceding night. Thus with some adjustment of the 4% cutoff level, the simple model used in ELCROS should explain the constant efflux during a normal night period and the exponential decay when the dark period was extended (Fig. 1). However, it would not explain the complex kinetics of Fig. 2.

Once the decay kinetics had been established, the efflux was routinely measured after 48 hours in the dark, the final steady-state value being obtained by

Table 1. Decay Constants. Initial slope of the plot of ln (F — F∞) against time (Fig. 2), in h^{-1}. Mean of four replications.

Temperature	Clover	Sorghum
°C		
30	0.18	0.16
20	0.13	0.11
20/30	0.71	0.73

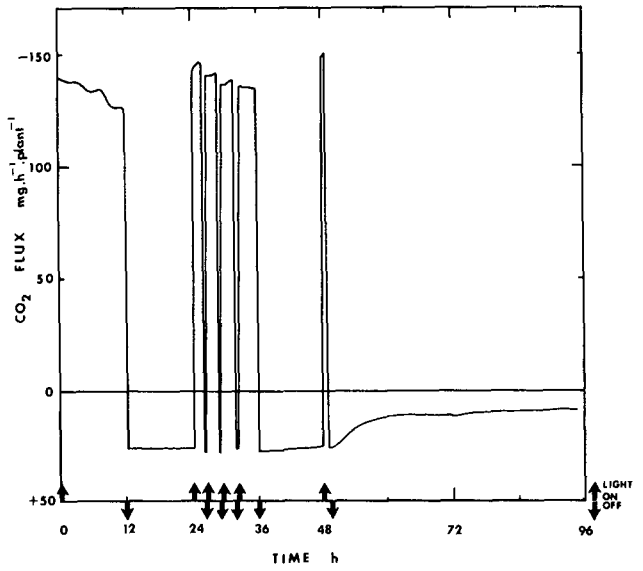

Fig. 1. CO_2 flux into (—) and out of (+) a clover plant at 20 C.

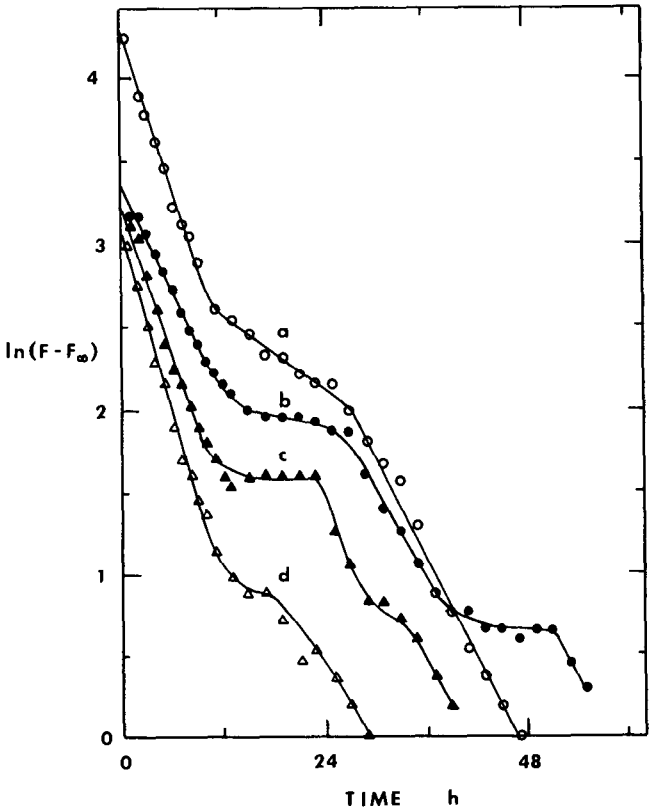

Fig. 2. Decay of efflux in the dark (F), minus final steady-state rate (F∞), with time after switching off the light (preceding light period, 1 hour, see Fig. 1 at 49 hours). (a) sorghum 30C, (b) sorghum 20C, (c) clover 20C, (d) clover 30C.

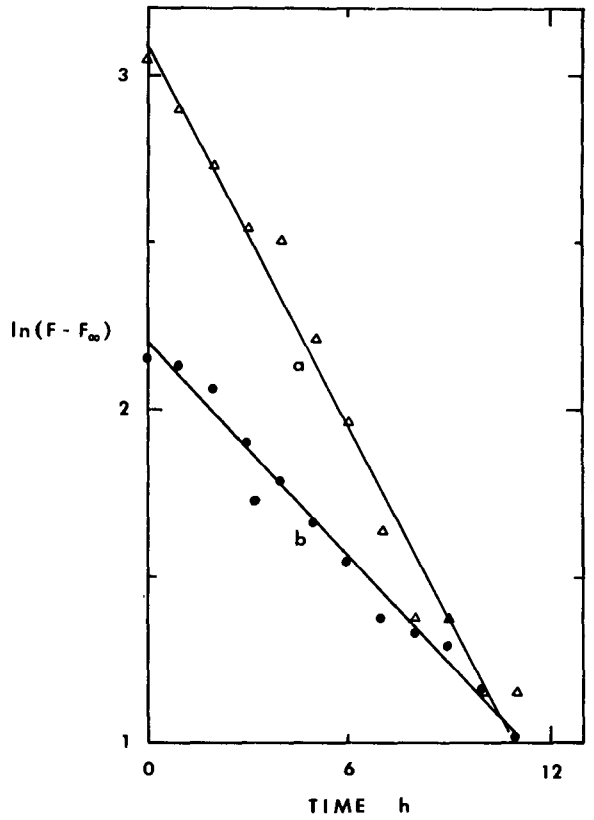

Fig. 3. Decay of efflux in the dark (F) minus final steady-state rate (F∞), with time in the dark (no preceding light period; time zero is the start of the normal light period). (a) clover 30C, (b) sorghum 20C.

extrapolation. This value was multiplied by 12 to obtain N∞, which was plotted against the dry weight, W, of the plant (Fig. 4). As before (McCree, 1970), there was a linear relationship between N∞ and W. The intercept is the residual rate of respiration of "soil" organisms and can be neglected. The slope is the maintenance coefficient c of equation [2]. This was considerably smaller for sorghum than for clover, at the same temperature (Table 2). The difference was statistically significant at the 1% level. The coefficient for sorghum at 30 C was about the same as that for clover at 20 C. There are two reasons for the coefficient for clover at 20 C (5.5 $mg \cdot g^{-1} \cdot 12\ h^{-1}$) being less than that given in equation [1] (15 $mg \cdot g^{-1} \cdot 24\ h^{-1}$): the time unit is 12 hours instead of 24 hours, and the decay period was increased from 24 hours to more than 48 hours.

The values in Table 2 can be compared with other published values. Penning de Vries (1974a, 1974b) using a similar technique, found values of 15 $mg \cdot g^{-1} \cdot 24\ h^{-1}$ for maize (*Zea mays* L.) and 47 $mg \cdot g^{-1} \cdot 24\ h^{-1}$ for sunflower (*Helianthus annuus* L.), at 25 C, and approximately half of these values at 18 C. In a simulation of the growth of barley (*Hordeum vulgare* L.) in a growth chamber at 23 C (day) and 18 C (night), an average maintenance coefficient of 30 $mg \cdot g^{-1} \cdot 24\ h^{-1}$ was adopted (Ryle et al., 1973). This value was based on the measured losses of ^{14}C during the period starting after the incorporation into new material (assumed to take place during the first 24 hours after assimulation) and ending with the

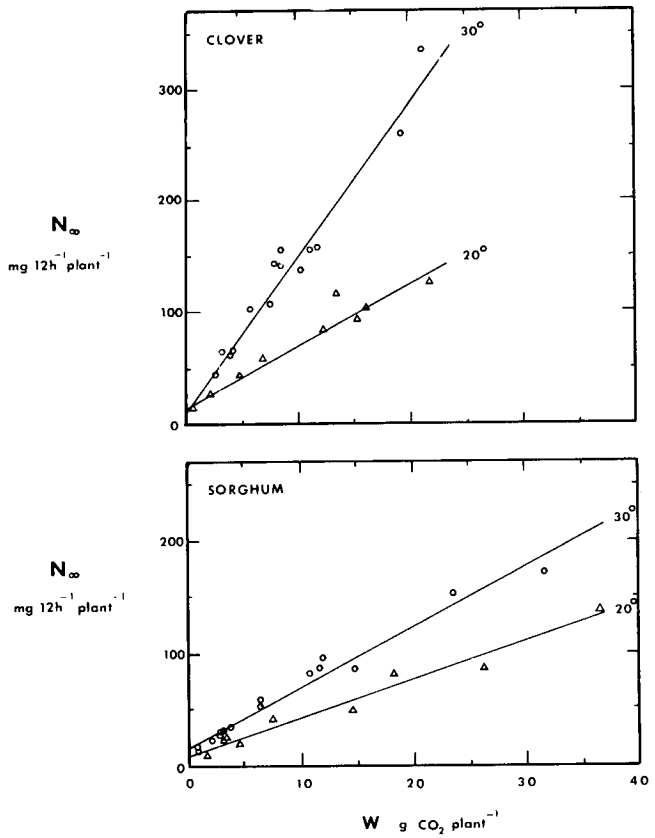

Fig. 4. Night total of CO_2 evolved at final steady-state ($N\infty$) plotted against the CO_2 equivalent of the dry weight of the plant W(1.43 × dry weight). The slopes of the regression lines (c of equation 2) are given in Table 2.

death of the organ. In field-grown maize labeled 15 to 18 days after fertilization, about 20% of the ^{14}C incorporated was lost in 5 weeks (Palmer et al., 1973). This represents an average rate of 10 mg g^{-1} 24 h^{-1}. Soybean plants (*Glycine max* (L.) Merr.) lost about 20% of their ^{14}C in a week, a rate of 30 mg·g^{-1} ·24 h^{-1} (Hume and Criswell, 1973). No allowance for growth respiration losses was made in either of these two experiments. A maintenance coefficient of 14 mg·g^{-1}·24 h^{-1} was deduced from CO_2 exchange data obtained on a sward of perennial ryegrass (*Lolium perenne* L.) grown under constant conditions (22.5 C day, 12.5 C night) (Robson, 1973). Coefficients of 26.4 mg g^{-1} 24 h^{-1} for cotton leaves and 3.2 mg·g^{-1}·24 h^{-1} for bolls were determined by Hesketh et al. (1971). In bacteria, the values are about 100 times greater (Thornley, 1970). Theoretical values of 15 to 25 mg·g^{-1}·24 h^{-1} for plants were derived by Penning de Vries (1974b). The exact value depends on the protein turnover rate, and on the definition of "maintenance".

In the ELCROS model, maintenance losses are assumed to be proportional to the protein content of the material. The protein content of the plants used in these experiments was uniformly high, and only slightly lower for sorghum than for clover (Table 3). When the maintenance coefficients in Table 2 were converted to unit dry weight of protein (Table 4), the values for clover remained considerably higher than those for sorghum. The temperature effects were slightly more similar in the two species after conversion to unit protein.

Table 2. Maintenance Coefficient c. Slope of linear regression of $N\infty$ against W (Fig. 4), in: mg g^{-1} 12 h^{-1}.

Temperature	Clover	Sorghum	Clover/Sorghum
°C			
30	14.3	5.4	2.6
20	5.5	3.4	1.6
20/30	0.38	0.63	

Table 3. Protein contents (N × 6.25) in percent dry weight.

Temperature	Clover			Sorghum		
°C	Tops	Roots	Whole plant	Tops	Roots	Whole plant
30	28	18	26	23	8	19
20	28	8	23	29	10	21

Table 4. Maintenance coefficients from Table 2, converted to mg CO_2. g protein^{-1}. 12 h^{-1}.

Temperature	Clover	Sorghum	Clover/Sorghum
°C			
30	79	41	1.9
20	34	23	1.5
20/30	0.43	0.56	

Table 5. Growth Coefficient k. Slope of the linear regression of (N_o — $N\infty$) against D (Fig. 5) (dimensionless).

Temperature	Clover	Sorghum
°C		
30	0.13	0.17
20	0.14	0.12
	Mean value 0.14	

The growth component was assumed to be the difference between the total efflux and the maintenance component, and calculated as the difference between the night total at the start of the decay period (N_o) and that at the end ($N\infty$). This difference was plotted against the uptake of CO_2 during the last daytime period (D) (Fig. 5).

The relationship between (N_o — $N\infty$) and D was linear, with a slope of 0.14, independent of species and temperature, and the differences were not significant at the 5% level (Table 5). This slope is equivalent to that found in the original clover experiments, when the proper allowances are made for the changes from "gross" to "net" daytime totals, and from 24-hour to 12-hour periods (P = D + N, R = 2 N). It is very close to the theoretical value calculated from the chemical composition of the plant [(0.14 for maize, 0.12 for sunflower, from the calculations of Penning de Vries, (1974a), converted to a 12-hour day)], and to values found using a ^{14}C tracer technique (Ryle et al., 1973 Ryle and Powell, 1974) in which the growth coefficient was taken to be the fraction of labeled assimilates which was lost by the plant in the first 24 hours after feeding a leaf with ^{14}C. In maize plants, no losses of ^{14}C were detected in the first 24 hours (Palmer et al., 1973). A growth coefficient of 0.2 was deduced from CO_2 exchange and dry matter production data obtained with ryegrass (Robson, 1973).

To determine the effects of temperatures other than 30 and 20C on the maintenance coefficient, plants which had been grown at 30C were first kept in the dark for 48 hours, then the efflux was measured while the leaf temperature was reduced in steps, from 30 down to 5C. The results are shown in Fig. 6b.

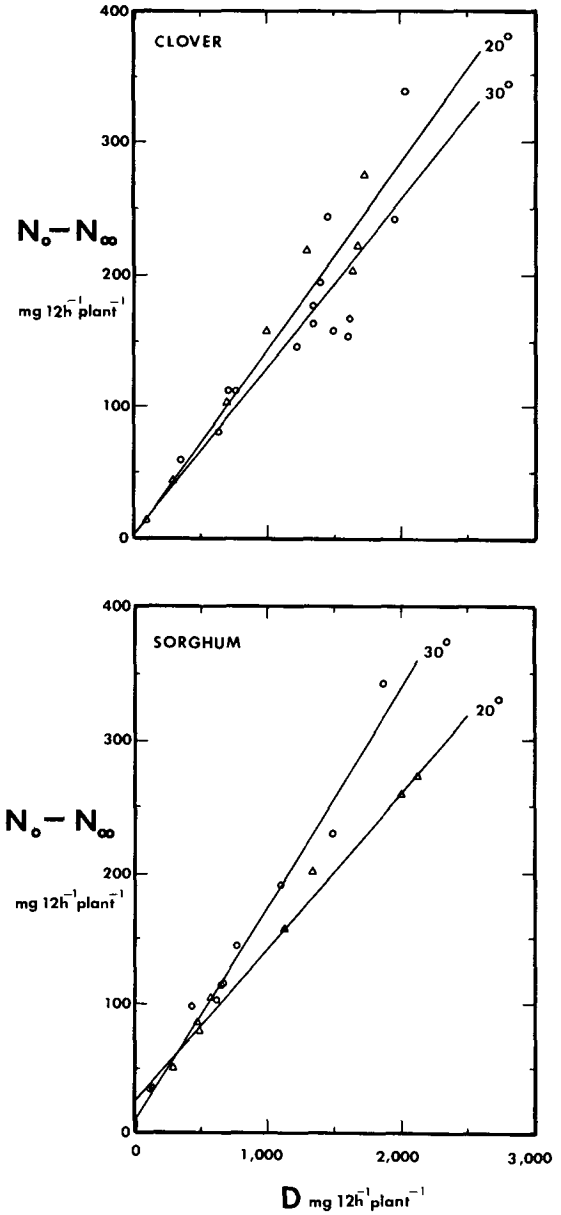

Fig. 5. Growth component of night total of CO_2 evolved (night total at start of decay period N_o minus final value $N\infty$) plotted against the net quantity of CO_2 taken up in the previous light period (daytime total, D). The slopes of the regression lines (k of equation 2) are given in Table 5.

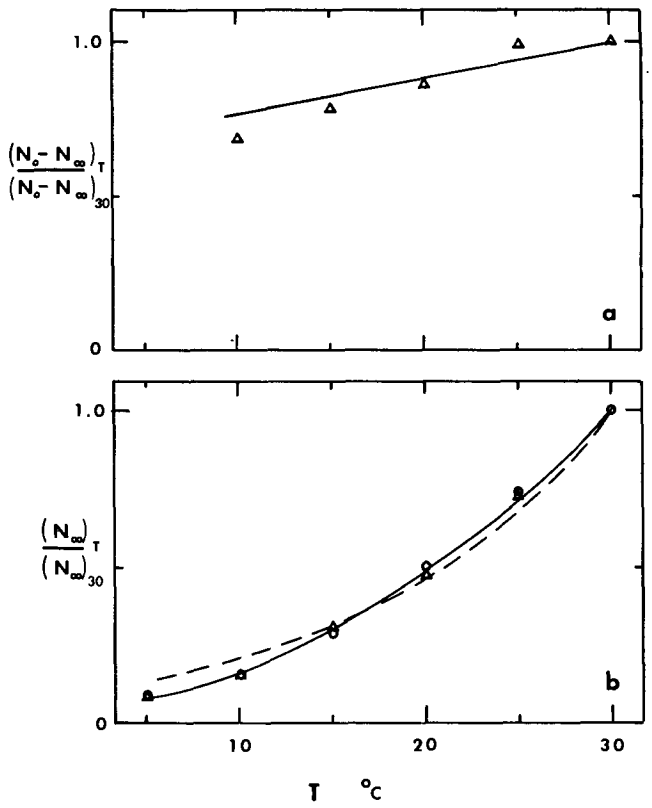

Fig. 6. Effect of night temperature (T) on (a) the growth component and (b) the maintenance component, for sorghum plants (circles) and clover plants (triangles). Day temperature 30C. Equations of lines: (a) y = 0.65 + 0.011x, (b) Broken line, ln y = 0.079(x—30), Q_{10} = 2.2. Solid line, y = 0.044 + 0.0019x + 0.0010x^2.

The temperature effect was the same in the two species. An approximate value of $Q_{10} = 2.2$ was obtained by least squares fitting to this response curve. A much better fit was obtained with a quadratic equation (solid line in Fig. 6b). The ratio of the maintenance coefficient at 20C to that at 30C was the same in these plants, which had been grown at 30C, as it was in plants which had been grown and tested at the same temperature (Table 4), within the limits of experimental error. Thus there was no "preconditioning" effect, at least over the range of 20 to 30C.

Once the temperature effects on the maintenance coefficient are known, the effects on the growth coefficient can be determined by differences, provided *that the daytime total* D can be kept constant. The technique used was to set the night temperature at different levels in 5 successive nights, keeping the daytime temperature constant at 30C. In sorghum plants and in young clover plants, this still did not result in a constant D, because the photosynthetic leaf area increased during the experiment. However, good data were obtained with older clover plants, in which the natural replacement of senescent leaves kept the leaf area constant (McCree and Troughton, 1966).

The dry weight, W, of the plant at any time during the experiment was obtained by adding the known gains and losses of CO_2 during each 12 hour period to the dry weight at the end of the experiment. The maintenance component for any night temperature was then calculated by multiplying W by the maintenance coefficient for clover at 30C (Table 2), and by the appropriate temperature factor (Fig. 6b). Finally, the growth component was calculated by subtracting the maintenance component $N\infty$ from the measured total N_o. The data (Fig. 6a) showed only a slight dependence on temperature of the growth coefficient calculated in this way. No dependence would be expected if the system was in a steady state, and the same compounds were being synthesized, at all temperatures (Penning de Vries, et al., 1974).

CONCLUSIONS

The maintenance coefficient was clearly smaller for the grain sorghum plants than for the white clover

plants, at the same temperature. The growth coefficient was the same for both species. At 30C, the results fit the following linear equations, of the form of equation [2]:

For clover: $N = 0.14\ D + 0.0143\ W$

For sorghum: $N = 0.14\ D + 0.0054\ W.$

The growth coefficient can probably be assumed to be independent of night temperature, but the maintenance coefficient was strongly dependent on temperature. The following equation best describes this temperature dependence, for both species:

$$c_T = c_{30}\ (0.044 + 0.0019T + 0.0010T^2) \quad [5]$$

where T is the temperature in °C.

There could be several limitations in applying these equations to field-grown plants. In the field, steady-state conditions would seldom ocur. The chemical composition of the plant would change with time, producing changes in the coefficients. All of these are subject to test, either directly or through the continued development and testing of computer simulations of crop growth.

There is a possibility that maintenance coefficients vary within a species, as well as between species. The technique used here, which involves simply putting a plant in the dark for 48 hours or more, then measuring the efflux of CO_2 at constant temperature, is well suited to mass use in plant breeding programs. In mature plants, the maintenance component can be quite large. Reducing this component would be an advantage to the plant, if the difference represented "idling" respiration which was of no use to the plant, and not true "maintenance" respiration which was necessary if the plant was to remain healthy (Beevers, 1970; Penning de Vries, 1974b). In an actively growing plant, the growth component, which certainly represents useful respiration, very often predominates. It can be reduced only by increasing the efficiency of conversion to new material.

The important distinction between a reduced rate of respiration and a true increase in the efficiency of use of substrate has often not been made in the past. Analyses of the type shown here may help to point up the distinction, while at the same time providing data for computer simulations of crop growth.

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