Crop Photosynthesis and the Flux of Carbon Dioxide Below the Canopy

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CROP PHOTOSYNTHESIS AND THE FLUX OF CARBON DIOXIDE BELOW THE CANOPY

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I. INTRODUCTION

The carbon dioxide assimilated by crops is supplied by downward transfer from the atmosphere and by upward transfer from the soil. Rates of gross photosynthesis may be estimated from the diurnal variation of the atmospheric flux alone (Monteith 1962) but to establish a complete carbon dioxide budget, the flux from the soil must be found separately. From measurements of carbon dioxide concentration within crop foliage, Lundegardh (1927) and Misra (1950) suggested that assimilation rates may be closely related to the rate at which carbon dioxide is evolved from the soil. This view was not supported by Moss, Musgrave & Lemon (1961) who found that the rate of soil respiration beneath maize was much smaller than the assimilation rate in bright sunshine.

To investigate the part played by soil respiration in the carbon dioxide balance of a field crop, the flux from an arable soil was measured at Rothamsted throughout the growing season. Later, a theoretical relationship between flux, concentration in the canopy, and rate of photosynthesis was established and was used to calculate possible increases of yield when additional carbon dioxide is given to crops outdoors or under glass.

At about 310 parts per million by volume (ppm), the mean carbon dioxide concentration of the atmosphere is buffered by the much larger amount of carbon dioxide dissolved in the oceans, but Bolin & Keeling (1963) detected a small annual cycle, with a range of about 4 ppm (at 50° N), which was in phase with plant activity and a secular increase of about 0·7 ppm per annum attributable to the burning of fossil fuels. Superimposed on these relatively small changes in the free atmosphere, the concentration immediately above a growing crop often decreases to 280 ppm during a sunny day and increases to about 400 ppm or more on a calm night (Tamm & Krzysch 1961). In the soil atmosphere, the concentration is usually an order of magnitude greater than in air just above the soil surface, implying that the upward diffusion of carbon dioxide is governed by the diffusive resistance of soil pores and is almost independent of atmospheric mixing.

II. THEORY

The exchange of carbon dioxide between soil, plant, and atmosphere can be represented by an electrical analogue in which concentrations are potentials and fluxes are currents. In Fig. 1, simplifying a previous model (Monteith 1963), $\varphi(z)$ is the potential in the atmosphere at height z; φ_s is the soil potential, here assumed independent of depth; and $\varphi(0)$ is the potential at the 'surface' of the crop. Let the diffusive resistance between air at height z and the crop surface be r_a depending on height, shearing stress, surface roughness and atmospheric stability.

A corresponding quantity r_b represents the resistance between the crop surface and

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sources of respired carbon dioxide in the soil. By definition, the downward flux of carbon dioxide from the atmosphere is then

$$F_a = \{\varphi(z) - \varphi(0)\}/r_a \qquad (1a)$$

and the upward flux from the soil is

$$F_b = \{\varphi_s - \varphi(0)\}/r_b \qquad (1b)$$

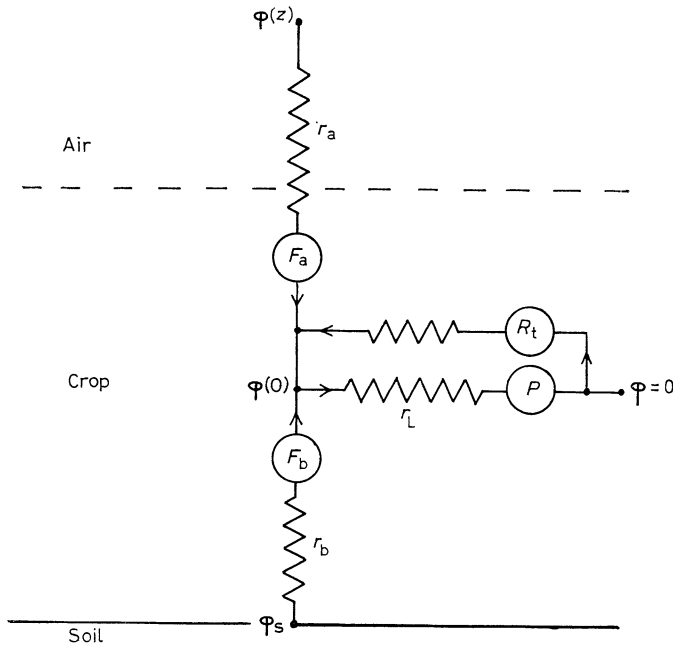In this model, the atmosphere maintains a fixed potential $\varphi(z)$ so that $\varphi(0)$ will vary in

Fɪɢ. 1. Electrical analogue of carbon dioxide exchange. Net uptake of carbon dioxide by tops is gross photosynthesis P less respiration of tops R_t. Across the total plant resistance r_L, the concentration drops from $\phi(0)$ in the canopy to zero at assimilating chloroplasts so r_L is defined by $P = \phi(0)/r_L$. Respiratory carbon dioxide is released in the canopy through an undefined resistance. Across the aerodynamic resistance r_a, a decrease in concentration from $\phi(z)$ in the air to $\phi(0)$ at the surface produces a downward flux F_a. Similarly, the decrease in concentration $\phi_s - \phi(0)$ across r_b is associated with the upward flux from the soil F_b.

response to changes of F_a and r_a. The soil generates a constant 'current' F_b so that φ_s will vary in response to changes of $\varphi(0)$ and r_b.

  Gaastra (1959) found that when the intensity of *visible* radiation exceeded about 0·2 cal cm^{-2} min^{-1}, equivalent to one third the maximum intensity of summer sunlight, rates of *gross* photosynthesis by crop leaves were nearly proportional to carbon dioxide concentration below 300 ppm. This proportionality will often hold in the field and may be written

$$P = \varphi(0)/r_L \qquad (2)$$

where P is a rate of gross photosynthesis and r_L is total plant resistance (Fig. 1). The

difference between the rate of gross photosynthesis and the respiration rate of tops (R_t) is equal to the total flux of carbon dioxide towards the canopy. In symbols,

$$P - R_t = F_a + F_b \tag{3}$$

and combining equations (2) and (3) gives

$$F_a + F_b + R_t = \varphi(0)/r_L \tag{4}$$

To show how $\varphi(o)$ and P vary with the soil flux F_b, F_a is eliminated from equations (1a) and (4) to give

$$\varphi(0) = \{\varphi(z) + r_a (F_b + R_t)\}/(1 + r_a/r_L) \tag{5}$$

$$P = \{\varphi(z) + r_a (F_b + R_t)\}/(r_L + r_a) \tag{6}$$

In equations (5) and (6), $r_a F_b$ is the amount by which a given soil flux increases the concentration of carbon dioxide at the crop surface. Photosynthesis will be insensitive to changes of soil flux unless $r_a F_b$ is comparable with $\varphi(z)$ ($\simeq 300$ ppm). The measurement of F_b is discussed in the next two sections and the estimation of r_a in Section VI.

III. SIMPLE FLUX MEASUREMENT

A. Technique

Lundegardh (1927) estimated rates of carbon dioxide production by covering the soil with a metal cone. Small samples of the air enclosed in the cone were removed for volumetric analysis and the flux was calculated from the rate at which concentration increased initially. He assumed that while the concentration at the surface was much smaller than in the soil atmosphere, the rate of upward diffusion was governed by the porosity of the soil and was unchecked by the suppression of turbulence. Later workers devised more accurate or more convenient ways of measuring concentrations but the principle of Lundegardh's method has not been superseded and a simple variant is described here.

A glass Petri dish containing a layer of granulated soda lime is oven-dried in the laboratory and weighed. In the field, the dish is mounted a few centimetres above the soil within a large inverted glass tank whose edges are pressed below the soil surface. The tank is shielded with aluminium foil to minimize heating of the soil in bright sunshine. After several days, the soda lime dish is removed, oven dried, and re-weighed, and the carbon dioxide flux is found by dividing the weight increase per day by the cross-section of the tank. Preliminary tests showed that:

(i) To avoid edge effects, the tank should cover at least 400 cm². Below smaller tanks, the weight of absorbed carbon dioxide was not proportional to surface area.

(ii) For maximum uptake of carbon dioxide, the area of the Petri dish should be at least 150 cm² (14 cm diameter). With smaller dishes, the apparent flux was less, presumably because carbon dioxide was absorbed too slowly to keep the concentration low inside the cover.

(iii) The optimum drying time for the soda lime is about 2 h at 100° C. The amount of carbon dioxide absorbed in the oven is negligible because soda lime is inactivated by drying, but when the dried granules are exposed in the field they are usually re-activated quickly by the absorption of moisture diffusing from the soil.

(iv) Over a uniform surface, the standard deviation of flux measured with a single

tank is about ± 10 to $\pm 20\%$ of the mean flux determined with a set of five tanks a few feet apart.

As a check on the validity of the method, a metal tank fitted with inlet and outlet tubes was inverted on the soil beside a glass tank covering the same area. The air below the metal tank was circulated continuously through a solution of barium hydroxide and the amount of carbon dioxide absorbed per day was found by titration. Below the
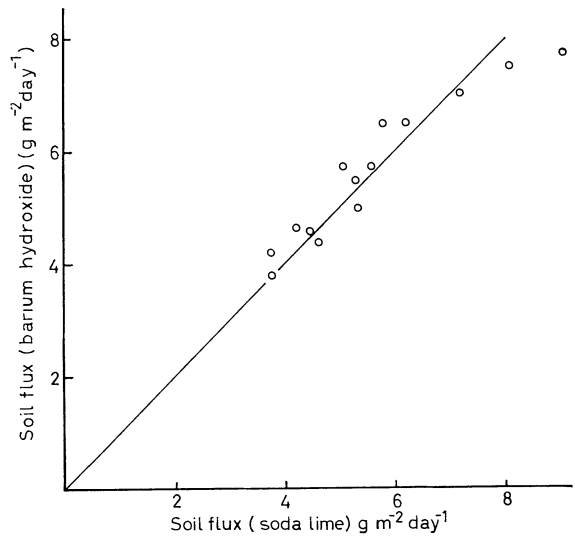

FIG. 2. Comparison of soil carbon dioxide flux estimated volumetrically with a solution of barium hydroxide and gravimetrically with granules of soda lime.

glass cover, carbon dioxide was absorbed in a 14 cm diameter Petri dish holding about 40 g of soda lime. Fig. 2 shows that the volumetric and gravimetric determinations of the soil flux agreed within the limits of experimental error, although the barium hydroxide solution may have become saturated at large fluxes.

Table 1. *Cropping scheme for plots on Great Field II*

Plots on which flux measurements were made are in italics.

1959		grass (first year)	mustard	
1960	oats	grass and *fallow*	beans	fallow
1961	beans	*grass* and *fallow*	kale	potatoes
1962		wheat		beans
1963	*barley* and *fallow*			*kale* and *fallow*

B. Sites

All the measurements of soil flux were made in Great Field II, a field of about 12 ac which was under grass from 1872 to 1942 and again from 1944 to 1951. Table 1 shows the cropping of this field from 1959 to 1963: plots on which measurements were made are in italics. The kale was grown on a small plot of about $\frac{1}{12}$ ac and the other crops on larger areas of several acres. For the first measurements on fallow soil, in 1960, when most of the field was in its second year of grass, foliage and surface roots were removed from several sites about a metre square. The cover was moved to a new site every few

days when the soda lime was changed. For the measurements on grass in 1961 and on barley in 1963, the cover was placed over plants cut close to the soil surface. It was assumed that the total respiratory flux from the soil was much greater than the possible changes in the rates of respiration in the root and that the net carbon dioxide exchange of the remaining foliage could be neglected. The beans and kale grew in rows far enough apart for the cover to be sited between them. This made it unnecessary to remove the tops but the contribution of root respiration to the total soil flux may have been some-what underestimated. In 1963, the fallow sites were surrounded by barley and kale
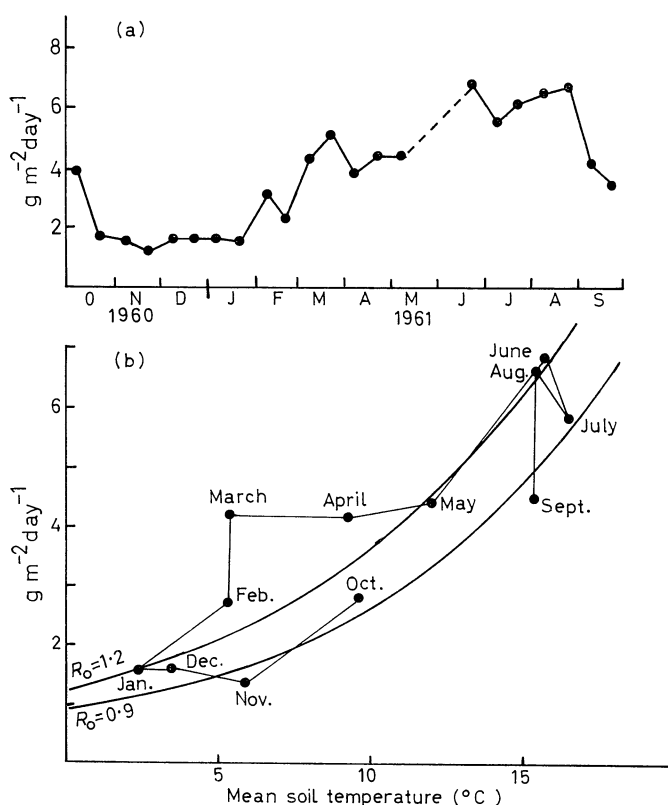
FIG. 3. (a) Variation of carbon dioxide flux from bare soil from October 1960 to September 1961; (b) monthly averages from (a) plotted against mean soil temperature at 4 in. The curves are $R(0)\,Q^{T/10}$ with $Q = 3$ and two values of $R(0)$.

which were cleared when the plants were young and weeded afterwards. These sites were about 3×3 m, allowing the cover to be moved to a new position within the site each time the soda lime was changed.

IV. RESULTS

A. Bare soil

Fifteen-day averages of the flux from fallow soil were calculated from measurements of uptake by the soda lime dish over periods of from 3 to 6 days, Fig. 3(a) shows that

the flux varied seasonally from 1·5 to 6·7 g m^{-2} day^{-1} during the year October 1960 to September 1961. The mean monthly fluxes were plotted against the corresponding mean soil temperatures (at 10 cm depth) and the loop formed by the points in Fig. 3(b) shows how far flux and temperature were out of phase. Over periods shorter than a month, the flux values were too scattered for useful analysis.

The change of respiration rate with temperature may be written

$$R = R(0) \ Q^{T/10}$$

where $R(0)$ is respiration at 0° C and Q is a factor for the increase of respiration per 10° C increase of temperature. In Fig. 3(b) the points from September to January fall
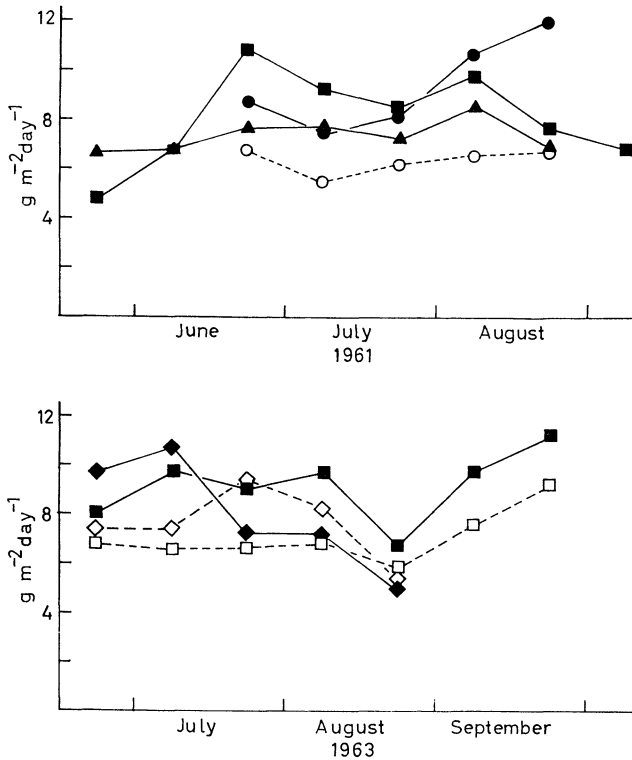

FIG. 4. Flux of carbon dioxide from cropped and fallow soil. ▲, Beans; ■, kale; ●, grass; ◆, barley. Bare soil surrounded by kale (□), grass (○) or barley (◇).

near the curve with $R(0) = 0·9$ g m^{-2} day^{-1}, $Q = 3$, whereas the points from February to August (excluding March) are close to the curve $R(0) = 1·2$ g m^{-2} day^{-1}, $Q = 3$. Laboratory determinations by Koepf (1953) gave Q between 2 and 3, depending on the initial temperature of the sample.

The flush of carbon dioxide in early spring (Fig. 3b) suggests that, when temperature began to rise, fresh substrate material became available to a rapidly growing bacterial population. This material could be provided by grass roots and stubble added during the previous autumn and preserved during the period of low winter temperatures. As the substrate became exhausted, the rate of decomposition would decrease and the biomass may then have reached an equilibrium size which persisted from May to June

to give a constant value of $R(0)$. In September, a further decrease of $R(0)$ may have followed the exhaustion of nutrients available to zymogenous bacteria.

For the year from September 1960 to August 1961, the total production of carbon dioxide was $1\cdot44$ kg/m^2 (c. 6 tons/ac) equivalent to a mean flux of 4 g m^{-2} day^{-1}.

B. Cropped soil

Fig. 4 shows 15-day averages of carbon dioxide output from cropped soils in 1961 and 1963. The seasonal variation, with maximum values about 10 g m^{-2} day^{-1}, is similar to that found by Koepf (1954) and, in the first year at least, there are no consistent differences between the fluxes in different crops. Except for barley in 1963, the flux from cropped soil was about 2–3 g m^{-2} day^{-1} more than from fallow, a difference which
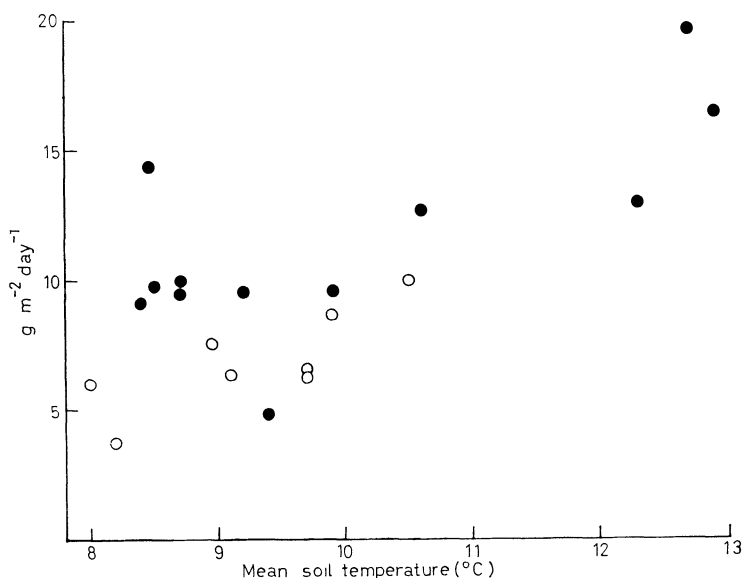

Fig. 5. Flux of carbon dioxide from soil below barley, 1963. ●, Soil moisture deficit less than 9 cm; ○, soil moisture deficit more than 9 cm.

may be attributed to root respiration and to the stimulation of microbial activity in the rhizosphere. The respiration of the roots of plants growing in sterile sand was measured by Newton (1923), who found that the mean rate for several species shortly before harvest was about $1\cdot3$ mg CO_2 per g dry weight of whole plant per day. The crops in Table 1 reached maximum dry weights of 1–2 kg m^{-2}, from which Newton's data would suggest values of root respiration of $1\cdot3$–$2\cdot6$ g CO_2 m^{-2} day^{-1}. These are consistent with the observed difference in flux between bare and cropped soils.

In 1963, the production of carbon dioxide from soil under barley decreased from the beginning of July until harvest in August and was smaller for several weeks than the corresponding flux from the area of bare soil surrounded by the crop. This reversal of the flux difference between cropped and fallow soil which was found in the other comparisons may be associated with the separate effects of soil moisture and soil temperature shown in Fig. 5. In this soil, the moisture deficit in a fallow profile rarely exceeds 2 cm

even after a long period of drought. Under the barley, the deficit (measured with a field balance (Morris 1959)) increased from 7 cm on July 1 to 13 cm on August 1. The mean temperature at 10 cm depth in bare soil in the Rothamsted meteorological enclosure rose from about 15° C at the beginning of June to about 19° C at the beginning of August. During the same period, the barley grew to shade the soil surface from direct sunshine, and the mean temperature at 10 cm below the soil surface within the crop (measured by I. F. Long), fell from about 12° C to 9° C. When the mean soil temperature was between 8 and 11° C, the mean rate of output of CO_2 was about 10 g m^{-2} day^{-1} as long as the soil moisture deficit was less than 9 cm; and it decreased to a mean rate of about 7 g m^{-2} day^{-1} when the deficit exceeded 9 cm (Fig. 5).

Over very dry soil, re-activation of the soda lime (by the absorption of soil moisture) may proceed too slowly for complete absorption of carbon dioxide while the granules are exposed. The effect of soil moisture on the apparent flux of carbon dioxide may therefore be overestimated by this method.

V. CARBON BALANCE

A. Vegetation

Profile measurements (Tamm & Krzysch 1959) show that all the carbon dioxide released from the soil during daylight is assimilated by the leaves of a growing crop. Ignoring a possible diurnal variation of soil flux with temperature such as was demonstrated by Koepf (1952), the amount of soil carbon dioxide available for photosynthesis is nF_b where n is the number of hours of daylight as a fraction of 24 h and F_b is the mean daily soil flux. As P is the gross uptake of carbon dioxide per day, the fraction of the total CO_2 uptake which is supplied by the soil is nF_b/P. The quantity P, which is difficult to measure in the field, can be related to the net uptake of carbon dioxide W by assuming that $P = \alpha W$ where α is a constant exceeding unity. Then the fractional assimilation of soil carbon dioxide is $nF_b/\alpha W$ and the ratio $(P - W)/P = (\alpha - 1)/\alpha$ represents the fraction of the assimilated carbon which is translocated to plant roots or respired by the whole plant. Assuming that 10 % of the total carbon assimilated is stored in the roots, and that 25 % of it is lost in respiration, $\alpha = 1 \cdot 5$.

To follow seasonal changes in W, grass and beans were sampled weekly in 1961 and barley and kale in 1963. The oven-dry weight of tops was plotted against time and weekly increments of dry matter were read from a smooth curve. Assuming that all dry matter was carbohydrate of the form $(CH_2O)_x$, the equivalent net weight of carbon dioxide assimilated per day was 44/30 times the corresponding increase in dry matter. The amounts of carbon dioxide evolved from the soil over the same periods were also derived from a smoothed curve. Table 2 gives mean values of F_b and W in g CO_2 m^{-2} day^{-1}, and the ratios nF_b/W and $nF_b/\alpha W$ as percentages.

In the grass crop, growing rapidly in early spring, the soil supplied about 6 % of the total carbon assimilated, but for other crops the mean supply from this source over the main period of growth is about 20 %. Because F_b is relatively independent of weather whereas W varies with solar radiation, instantaneous values of F_b/W will be smaller than the mean in bright sunshine and larger under an overcast sky or at dawn and dusk. Moss *et al.* (1961) found that on a clear day F_b/W for a stand of maize varied in phase with radiation with a minimum of 5 % at noon and a mean of about 10 % during the hours of daylight. On a very cloudy day, F_b/W was about unity.

Table 2. *Daily means of net carbon dioxide uptake by crops* (W) *and soil flux* (F_b) *in g* m^{-2} *day^{-1}*

n, hours of daylight as fraction of 24 h; nF_b/W, uptake of soil CO_2 as percentage of *net* assimilation; nF_b/aW, uptake as percentage of estimated *gross* assimilation with $a = 1.5$; long period means in italic.

Period	W	F_b	n	nF_b/W	nF_b/aW
GRASS 1961					
18 April to 24 April	50	7·1	0·60	9	
24 April to 1 May	40	4·5	0·61	7	
1 May to 8 May	33	4·0	0·63	8	
8 May to 16 May	28	6·9	0·65	16	
16 May to 24 May	24	9·5	0·66	26	
18 April to 24 May	*35·0*	*6·4*	*0·63*	*11*	*8*
cut on 31 May 1961					
24 July to 31 July	12	7·7	0·65	42	
31 July to 8 Aug.	18	7·9	0·64	28	
8 Aug. to 14 Aug.	15	8·6	0·62	35	
14 Aug. to 23 Aug.	11	11·0	0·61	61	
24 July to 23 Aug.	*14·0*	*8·8*	*0·63*	*40*	*26*
BEANS 1961					
16 June to 23 June	29	7·6	0·69	18	
23 June to 30 June	26	7·8	0·69	21	
30 June to 7 July	26	7·0	0·69	19	
7 July to 14 July	16	8·2	0·68	35	
14 July to 21 July	13	7·8	0·67	40	
21 July to 28 July	10	7·2	0·66	48	
16 June to 28 July	*20·0*	*7·6*	*0·68*	*26*	*17*
BARLEY 1963					
30 May to 6 June	7	12·8	0·69	126	
6 June to 14 June	12	16·5	0·69	95	
14 June to 20 June	29	11·0	0·69	26	
20 June to 27 June	34	9·5	0·69	19	
27 June to 4 July	29	10·5	0·69	25	
4 July to 11 July	26	12·0	0·69	32	
11 July to 18 July	20	7·5	0·68	26	
18 July to 25 July	22	8·0	0·67	24	
25 July to 1 Aug.	26	7·5	0·65	24	
30 May to 1 Aug.	*22·1*	*10·6*	*0·68*	*33*	*22*
KALE 1963					
7 Aug. to 14 Aug.	19	8·5	0·65	29	
14 Aug. to 21 Aug.	30	8·5	0·60	17	
21 Aug. to 28 Aug.	21	4·8	0·58	13	
28 Aug. to 4 Sept.	15	5·0	0·57	19	
4 Sept. to 11 Sept.	8	6·5	0·55	45	
11 Sept. to 18 Sept.	2	10·5	0·53	279	
18 Sept. to 25 Sept.	2	11·5	0·51	294	
7 Aug. to 25 Sept.	*13·9*	*7·9*	*0·57*	*32*	*22*

B. Soil

The carbon content of Great Field II measured in February 1964 was 2·7% of air dry weight in the plough layer (0–23 cm) and 1·1% in a sub-soil layer from 23 to 46 cm. Taking a mean bulk density of 1·4 g cm^{-3}, the total carbon in the 46 cm layer was $X = 12·2$ kg m^{-2}.

APP. E   H

Assuming that crop residues return the equivalent of A kg carbon m^{-2} year^{-1}, and that a fraction γ of total carbon is lost annually by decomposition, then

$$\delta X / \delta t = A - \gamma X \tag{7}$$

If X_0 is the weight of carbon at $t = 0$, then

$$X = (X_0 - A/\gamma)e^{-\gamma t} + A/\gamma \tag{8}$$

Putting $A = 0$, the half life of organic matter added to the soil is $\tau = 0.69/\gamma$. After a long period with constant A and γ, the equilibrium carbon content is A/γ. Values of γ describe the behaviour of the soil organic matter in bulk and represent an average rate for many different processes of decomposition. Jenkinson (1964) showed that when uniformly labelled ryegrass was incubated with soil, only about one third of the radioactive material remained after 1 year, and this residue decayed more slowly with a half-life of about 4 years. The decay of (unlabelled) humus was slower still with a half-life of about 25 years.

To find a mean value of γ for Great Field II under its present management, the small amounts of carbon gained from rainfall and lost by leaching will be ignored, so that γX will be equal to the carbon equivalent of the annual soil flux F_b measured at the surface. From Section IVA (p. 327) the flux is 0·39 kg C m^{-2} year^{-1}, and if this were produced by the decomposition of organic matter in the 0–46 cm layer, γ is 0·031 per year. The half-life is about 22 years and, considering the uncertainties of the flux measurements, agreement with the longest half-life found by Jenkinson is fortuitously close. On the basis of these figures, the soil flux from Great Field II may decrease to about half the present rate after 36 years.

Since 1951, the estimated annual supply of carbon from plant residues is $A = 0.1$ kg m^{-2} equivalent to about 1 ton of dry matter per acre. Because this is only one quarter of the present annual loss, the carbon content of the field would seem to be decreasing from a maximum reached after 80 years under permanent grass. Putting $\gamma = 0.031$ in equation (8) and taking $t = 10$ years for the period 1951–1961, the estimated carbon content in 1951 is 15·4 kg m^{-2}. Before 1951, the dry matter production of grass roots was probably less than 2 tons/ac/year (Russell 1961) giving $A = 0.2$ kg m^{-2} at most. Assuming that the estimated carbon content in 1951 was the equilibrium content A/γ, the half-life of organic material under permanent grass was at least 50 years.

VI. PHOTOSYNTHESIS AND SOIL FLUX

In Section V is has been shown that 10–20 % of the carbon assimilated by beans, barley and kale was supplied by the decreasing reserves of carbon in an old grassland soil. If the predicted decrease in soil flux lowers the mean concentration of carbon dioxide at the assimilating surfaces of the leaves, then yields will decrease too. But if the mean concentration there remains constant, crops will derive a smaller fraction of their carbon from the soil without any change in their gross rates of photosynthesis. The possible variation of assimilation rate with soil flux can be found by solving equation (6).

$$P = \{\varphi(z) + r_a \, (F_b + R_t)\}/(r_L + r_a)$$

For the biological components, representative values of F_b, R_t and r_L will be used, based on previous experience. The only weather component is the aerodynamic resistance r_a depending on surface roughness and atmospheric stability. For neutral stability (no

heat transfer between surface and atmosphere) the variation of wind speed u with height is given by

$$u = u^* \ln (z/z_0)/k \qquad (9)$$

where u^* is the friction velocity,

             k is a constant (0·41)

             z_0 is a roughness length characteristic of the surface.

In turbulent flow, the ratio of flux to gradient may be assumed the same for diffusion of momentum and carbon dioxide. It follows that

$$\rho u^{*2}/\rho u = F_a/\{\varphi(z) - \varphi(0)\} \qquad (10)$$

where ρu^{*2} is momentum flux and $\varphi(0)$ is now identified as the concentration at $u = 0$.

Combining equations (1a), (9) and (10) gives

$$r_a = \{\ln (z/z_0)\}^2/k^2 u \qquad (11)$$

In non-neutral conditions u^{*2}/u assumes a more complex form which is given in the Appendix.

By definition, $r_a(z)$ is the diffusive resistance between a crop surface and the atmosphere at height z. If equation (9) is to be valid, z should be small, not exceeding the depth of the friction layer in which the vertical momentum flux is almost constant. On the other hand, it is convenient to choose a reference height where $\varphi(z)$ is independent of diurnal changes of concentration at the surface. As a compromise, the concentration at 30 m is assumed constant at 300 ppm, although real concentrations vary diurnally up to 150 m at least (Chapman, Gleason & Loomis 1954) and seasonally to much greater heights. The following representative parameters are assumed:

     $z_0 = 5$ cm (farm crops growing to heights between 50 and 100 cm)

     $R_t = 0\cdot5$ g m^{-2} h^{-1}

     $P = 3$ g m^{-2} h^{-1} $\left.\right\}$ in bright sunshine

     $r_L = 7$ sec cm^{-1}

     $P = 1\cdot5$ g m^{-2} h^{-1} $\left.\right\}$ under overcast skies

     $r_L = 14$ sec cm^{-1}

The variation of P with radiation intensity is based on hourly measurements of carbon dioxide exchange over a field crop (Monteith 1962). Corresponding values of r_L were found from equation (2), assuming $\varphi(0) = 0\cdot57$ g m^{-3} (300 ppm). When r_a is zero, the predicted rate of photosynthesis is equal to the rate at a standard concentration of 300 ppm. For finite values of r_a, surface concentrations and rates of photosynthesis were calculated for three types of weather, specifying sensible heat transfer C (positive downwards):

(1) Bright sunshine, unstable atmosphere, representative of morning and early afternoon over a non-irrigated crop receiving adequate natural rainfall; $r_L = 7$ sec cm^{-1} $C = -0\cdot2$ cal cm^{-2} min^{-1}.

(2) Bright sunshine, stable atmosphere, representative of late afternoon over a non-irrigated crop or whole day over an irrigated crop in dry surroundings; $r_L = 7$ sec cm^{-1}, $C = 0\cdot05$ cal cm^{-2} min^{-1}.

(3) Dull, neutral stability, representative of an overcast day; $r_L = 14$ sec cm^{-1}, $C = 0$.

To relate the resistance of the 0–30 m layer to the wind speed at a convenient height

of 2 m, corresponding values of r_a (30 m) and u (2 m) were calculated for the above values of C and for a range of u^*. Values of u at 2, 4 and 8 m/sec were then found graphically.

Table 3 shows values of 'surface' concentration $\varphi(0)$ for zero soil flux and also for $F_b = 10$ g m^{-2} day^{-1}. At each concentration, $\Delta P/P$ is the fractional decrease in photosynthesis from the rate at 300 ppm. The salient features of Table 3 are:

(a) For the weather conditions chosen, r_a varies from 0·2 to 2 sec/cm and is usually much smaller than r_L. With $F_b = 10$ g m^{-2} day^{-1}, the increase of surface concentration attributable to soil flux varies from 1 to 10 ppm and is therefore a trivial fraction of the mean atmospheric concentration.

(b) Except with a stable atmosphere and light wind, the rate of photosynthesis is only 1–4% less than the rate at 300 ppm. It is almost independent of wind speed and of the flux of carbon dioxide from the soil.

(c) The resistance of the atmosphere is relatively large for the stable Case 2 with light wind (2 m/sec). The assumed downward heat flux $C = +0·05$ cal cm^{-2} min^{-1} may

Table 3. *Calculated 'surface' concentration of carbon dioxide $\varphi(0)$ for different weather conditions and soil fluxes (see text)*

—100 $\Delta P/P_{300}$ is percentage decrease of photosynthesis from standard rate at 300 ppm.

	u (m/sec)	C (cal cm^{-2} min^{-1})	r_a (sec/cm)	r_L	$F_b = 0$		$F_b = 10$ g m^{-2} day^{-1}	
					$\phi(0)$ ppm	$\dfrac{-100\Delta P}{P_{300}}$	$\phi(0)$ ppm	$\dfrac{-100\Delta P}{P_{300}}$
Case I	2	—0·2	0·35	7	288·1	4	290·1	3
	4	—0·2	0·28	7	290·4	3	292·0	3
	8	—0·2	0·17	7	294·1	2	295·1	2
Case II	2	+0·05	2·00	7	244·7	19	254·1	15
	4	+0·05	0·39	7	286·7	4	289·0	4
	8	+0·05	0·18	7	293·9	2	294·9	2
Case III	2	0	0·70	14	290·6	3	294·7	2
	4	0	0·35	14	295·2	2	297·3	1
	8	0	0·18	14	297·7	1	298·1	1

often be exceeded in practice; a flux of +0·3 cal cm^{-2} min^{-1} was reported over irrigated cotton by Lemon, Glaser & Satterwhite (1957) and over grass by Brooks (1963). There are other reports of surface concentrations as small as 200 ppm that may be associated with stable conditions, and starvation of carbon dioxide may be a common feature of irrigated crops in a dry environment. It is dangerous to extrapolate equation (15) (Appendix) to extreme oasis conditions where there is little assimilating vegetation outside the irrigated area. The concentration may then approach 300 ppm at the top of the boundary layer within a few metres of the crop surface so that the effective value of r_a will be smaller and the rate of photosynthesis larger than the prediction from equation (6).

From flights over Scandinavia, Bischof (1962) found that the mean concentration varied seasonally from 300 to 335 ppm in the layer between the surface and 200 m. At 30 m, the amplitude of this variation will be comparable with the drop in concentration from 30 m to the surface of a crop on a summer day. The amount of carbon dioxide available for photosynthesis is therefore governed as much by exchange and circulation on a global scale as by local rates of assimilation and turbulent transfer.

VII. PHOTOSYNTHESIS AND SUPPLEMENTARY CARBON DIOXIDE

A. Farmyard manure

It has been suggested without experimental evidence that carbon dioxide from decomposing farmyard manure may increase the assimilation rate of field crops. Lundegardh (1927) applied FYM to sand and loam soils at rates up to 65 kg/m² (260 tons/ac) and measured increases in soil respiration of about 0·4 g CO_2/day per kg FYM. If the carbon content of the FYM was 10%, then $\gamma = 0·4$/year and $\tau = 1·7$ years. At this rate of decomposition, the heavy dressing of 14 tons/ac applied to several of the plots in the 'classical' experiments at Rothamsted might increase the soil flux by 1·4 g m⁻² day⁻¹, about one fifth of the flux from unmanured soil on Great Field II during the summer. From Table 3, the evolution of carbon dioxide from FYM at practical rates of application will have a negligible effect on rates of photosynthesis by crops.

B. Glasshouses

Wittwer & Robb (1964) report many recent attempts to increase crop yields by the addition of carbon dioxide to glasshouse atmospheres. In experiments by Yabuki and others at the University of Osaka Prefecture, an increase from 300 to 6000 ppm increased the yield of spinach beet by five times in summer and doubled it in winter. By contrast, Marshall (1964) found no increase in the growth rate of young tomato plants in winter. Stories of success and failure will probably continue until the technique is made less empirical by a better understanding of the factors that control the diffusion of carbon dioxide among glasshouse plants.

For glasshouse crops, the effective value of the aerodynamic resistance depends on two quantities. First, there is a resistance $r_a{}^*$ between the crop canopy and the glasshouse atmosphere corresponding to the resistance between an outdoor crop and the air a few feet above it. Second, there is a resistance to air flow through windows, doors and ventilators, and this can be calculated from the bulk ventilation rate. Because the circulation of air within a glasshouse is usually too complex for formal analysis, Morris, Postlethwaite & Edwards (1954) assumed that each parcel of air passing through the glasshouse lost the same amount of carbon dioxide by crop assimilation. If air enters the glasshouse with concentration φ and leaves with concentration φ' then the uptake of carbon dioxide per unit floor area is

$$F_a = (\varphi - \varphi')/hN \qquad (12)$$

where h is mean glasshouse height and N is ventilation rate in consistent units. Assuming that φ' is close to the mean concentration in the glasshouse atmosphere, the uptake of carbon dioxide can also be written

$$F_a = \{\varphi' - \varphi(0)\}/r_a{}^* \qquad (13)$$

and the elimination of φ' from equations (12) and (13) gives

$$F_a = \frac{\{\varphi - \varphi(0)\}}{r_a{}^* + 1/hN} \qquad (14)$$

For a Dutch light glasshouse with closed ventilators, N is about one air change per hour. Then if $h = 2·4$ m, the ventilation resistance $1/hN$ is 15 sec cm⁻¹. The value of $r_a{}^*$ is less readily calculated. According to Businger (1963), the transfer coefficient for

heat exchange between glasshouse crops and surrounding air varies between 1 and 4 kcal m^{-2} h^{-1} °C^{-1}. The corresponding range of resistances for heat exchange is 2·5–10 sec cm^{-1}. Assuming resistances for carbon dioxide exchange to be of the same order, a representative value of $r_a = 20$ sec cm^{-1} will be adopted for the total resistance ($r_a* + 1/hN$) with closed ventilators. Because this resistance is much greater than values of r_a outdoors, the concentration of CO_2 in the canopy will be less for a given rate of photosynthesis and CO_2 flux from the soil. Conversely, there are much greater increases of CO_2 concentration and of assimilation rate when soil flux increases or when carbon dioxide is supplied artificially.

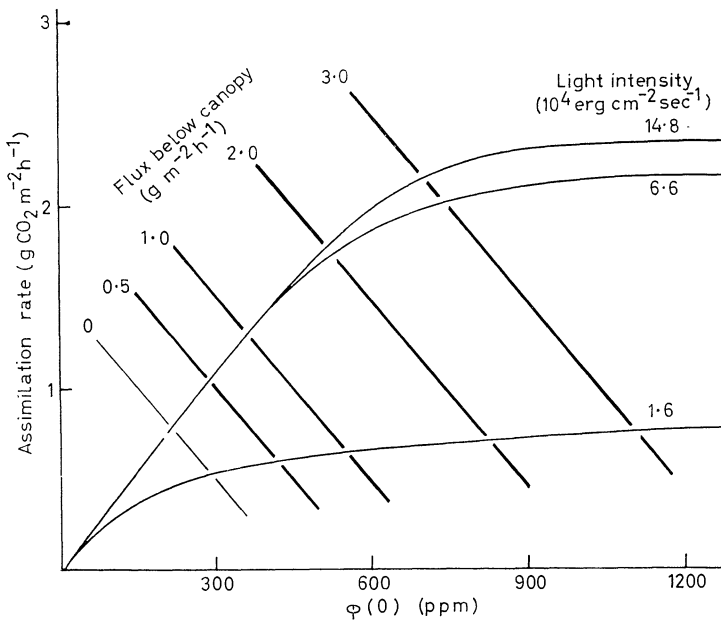At concentrations much greater than 300 ppm, the simple proportionality of photo-

FIG. 6. Assimilation rates of single tomato leaves in glasshouses with total aerodynamic resistance $r_a* + 1/hN = 20$ sec cm^{-1}. The curves are from measurements by Gaastra (1959) at three light intensities. Straight lines give variation of assimilation rate with concentration $\phi(0)$ for different values of carbon dioxide flux below the canopy. The flux for field soils is of order 0·5 g m^{-2} h^{-1}, and for artificial application of carbon dioxide, 3 g m^{-2} h^{-1} is approximately 27 lb ac^{-1} h^{-1}.

synthetic rate and concentration no longer holds because the plant resistance r_L varies with concentration as well as with light intensity. The solution of equations (1a) and (2) may now be found graphically as shown in Fig. 6. The three curves (from measurements by Gaastra 1959) show how the gross assimilation rate of tomato leaves increased with CO_2 concentration and light intensity in the laboratory. The straight lines show how $\varphi(0)$ varies with P according to equations (1a) and (3) with $r_a = 20$ sec cm^{-1}; $R_t = 0·5$ g m^{-2} h^{-1} and F_b varying from zero to 3 g m^{-2} h^{-1}. For given values of the light intensity and of the upward flux below the canopy, values of $\varphi(0)$ and P are defined by the intersection of the appropriate curve and straight line.

At a visible light intensity of $1·6 \times 10^4$ erg cm^{-2} sec^{-1}, corresponding to mean winter sunshine under glass at latitude 50–55° N, the photosynthetic process is limited by

available energy. Because carbon dioxide is not limiting, the assimilation rate is almost independent of additional carbon dioxide supplies and this may be the main reason why the addition of CO_2 did not increase the growth rate of tomato seedlings in the winter months in Marshall's experiments (1964). At light intensities between 6·6 and $14·8 \times 10^4$ erg cm^{-2} sec^{-1}, corresponding to mean spring and summer sunshine under glass, the leaves are almost light saturated, carbon dioxide is limiting, and assimilation rates are more than doubled as the flux of applied carbon dioxide increases from zero to 3 g m^{-2} h^{-1} (27 lb ac^{-1} day^{-1}). For natural soil fluxes of the order of 10 g CO_2 m^{-2} day^{-1}, the assimilation rates increase by about 3 % per g m^{-2} day^{-1} (cf. about 0·3 % outdoors).

The curves of Fig. 6 give the assimilation rates of single leaves. Corresponding curves for a whole crop will have similar shapes but the uptake of carbon dioxide per unit floor area will exceed the uptake per unit leaf area. For more exact analysis a theoretical relationship must be determined between rates of photosynthesis and light interception (Monteith 1964).

The straight lines on Fig. 6 are valid only for natural soil fluxes or for supplementary carbon dioxide injected *below* the canopy. Gas released from a central burner or from pipes suspended above the plants meets an additional diffusive resistance (r_a*) before reaching the canopy and cannot be used so efficiently.

VIII. CONCLUSIONS

In most weather conditions, atmospheric mixing is vigorous enough to maintain carbon dioxide concentrations close to 300 ppm at the assimilating leaves of a field crop. The assimilation rate is dictated by light intensity, by the amount and distribution of foliage, and by its photosynthetic efficiency. An increase of soil carbon dioxide flux is met by an almost equal decrease of atmospheric flux keeping the carbon dioxide concentration and hence the assimilation rate almost constant. When the atmosphere is stable and the wind speed near the ground falls below 2 m/sec, turbulent mixing is much less effective and theory predicts that the concentration may drop to 250 ppm or less at the surface of a crop in bright sunshine. The possibility of serious carbon dioxide deficits in irrigated crops needs field investigation, but in general it is not feasible to increase the yield of field crops by supplying supplementary carbon dioxide.

In glasshouses, the increase of assimilation rate with carbon dioxide supply can be estimated from the measured response of single leaves and from parameters that specify rates of ventilation and diffusion. These estimates support experimental claims that the dry matter production of glasshouse crops can be greatly increased if additional carbon dioxide is supplied provided the rate of photosynthesis is not limited by low levels of light intensity.

SUMMARY

The upward flux of carbon dioxide at the soil surface was calculated from the weight

increase of soda lime granules exposed inside a glass tank covering 400 cm^2 soil. Over bare soil, the flux varied annually with a summer maximum of about 7 g CO_2 m^{-2} day^{-1}, a winter minimum of 1 g m^{-2} day^{-1}, and a Q_{10} of 3. The contribution of root respiration, calculated from the difference between the fluxes over fallow and cropped soil, was usually about 1–3 g m^{-2} day^{-1}.

From dry matter determinations, the amount of soil carbon assimilated by crops was about 6% of the net carbon uptake for rapidly growing grass in spring and about 20% for other crops during the summer. The top 46 cm of the soil profile contained 12 kg carbon m^{-2} and lost 0·4 kg m^{-2} annually by respiration. The corresponding half-life of soil organic matter is 22 years.

The variation of carbon dioxide concentration and rate of photosynthesis with soil flux depends on wind speed and atmospheric stability. In most weather, atmospheric mixing is so vigorous that the concentrations in the canopy and in the free atmosphere are very similar (*c.* 300 ppm), and photosynthesis is independent of soil flux. In glass-houses, where mixing is less, the concentration may be much less than 300 ppm. In chosen conditions gross photosynthesis increased by 30% when the upward flux of carbon dioxide below the canopy increased by 10 g m^{-2} day^{-1}.

APPENDIX

The form of (u/u^*) in non-neutral stability

The logarithmic wind profile (equation 9) is strictly valid only when there is no exchange of sensible heat between surface and atmosphere. In the presence of a heat flux C (positive downwards), departure from the logarithmic form was related by Webb (1960) to a scale length

$$z_f = -0·03 \, u^{*3} \, \rho cT/kgC$$

where ρc is the volumetric specific heat of air, g is gravitational acceleration, T is absolute temperature and other symbols have their usual meanings defined in the main text. From Webb's analysis, the non-dimensional quantity (u/u^*) can be expressed as a function of the ratios of height z, scale length z_f, and roughness length z_0.

When
$$z_0 < z \leqslant z_f$$

$$u/u^* = k^2 \{\ln(z/z_0) + (z - z_0)/7 \, z_f\}^2 \tag{15}$$

(This is the log + linear form of the Monin–Obukhov wind profile with an arbitrary constant of 5.) Below an inversion, measured wind profiles support the validity of equation (9) for large negative values of z_f but as $|z_f|$ becomes smaller with increasing stability, r_a approaches zero at a finite windspeed and the validity of equation (9) becomes more doubtful.

When
$$z_0 < z_f < z$$

$$u/u^* = k^2 \{3 \, [1-(z_f/z)^{1/3}] - (3/28) \, [1 - z_f/z]^{4/3} + \ln (z_f/z_0) - (1/7) \, [1 - z_0/z_f]\} \tag{16}$$

Assuming the identity of transfer coefficients of carbon dioxide and momentum irrespective of stability, r_a was calculated from equations (15) and (16) using $r_a = u/u^{*2}$.

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