CO_2 Fluxes over Plant Canopies and Solar Radiation: A Review

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I. SUMMARY

In this paper we try to assess the parameters determining the shape of the response of CO_2 flux over closed plant canopies (F) to photosynthetic photon flux density PPFD (Q). Over one hundred data sets relating CO_2 flux above canopies to radiation or PPFD have been compiled, digitized, put in standard units and statistically analysed. There is a lack of data for some vegetation classes, in particular coniferous forests, tropical grasslands and mixed vegetation. Linear regressions and rectangular hyperbolic functions have been fitted through the data sets. The parameters of importance that have been extracted are the slope at the origin (defined as the apparent quantum yield, α), the CO_2 flux at maximum irradiance of $1800\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$ or $80\,\text{mol}\,\text{m}^{-2}\,\text{d}^{-1}$ (defined as the photosynthetic capacity, F_m), the intercept on the y axis (defined as dark respiration rate, R), and the departure from linearity, calculated as the difference between the r^2 of the rectangular hyperbolic fit and the r^2 of the linear fit. The sensitivity of the F/Q relationship to various factors has been tested, using statistics on particular data sets that were obtained in similar conditions, and statistics applied to data sets for closed canopies grouped by classes, with respect to technique and vegetation class. Micrometeorological methods result in F/Q relationships closer to linearity than enclosure methods. Analysing data sets obtained with micrometeorological methods only has allowed us to distinguish between the F/Q relationships of crops and forests: the CO_2 fluxes of crops have a linear relationship with PPFD, while the CO_2 fluxes of forests have a curvilinear relationship with PPFD. The relationship between CO_2 flux corrected for dark respiration or soil respiration and PPFD is not clearly improved compared with the relationship between net ecosystem flux and PPFD. Although seasonality, nutrient availability, water availability, water vapour pressure deficit, CO_2 concentration and temperature certainly affect the F/Q relationship, we have not been able to illustrate quantitatively their role because of lack of suitable measured data. The best fit through all the data sets is a rectangular hyperbola. Scaling up in space (using aircraft mounted flux sensors) and time (daily integrated fluxes) seems to linearize the F/Q relationship.

II. SYMBOLS AND ABBREVIATIONS

CO_2 flux measurements (amount of CO_2 per unit ground area and time):

F: net ecosystem flux, with or without addition of some respiration terms (p. 13)
F_d: net ecosystem flux in the day
F_n: net ecosystem flux in the night
F_c: canopy or above-ground flux
F_s: soil flux

Terms of the carbon budget of the stand (amount of CO_2 or dry mass per unit area and time):

A_n: net photosynthetic rate or gross primary productivity
A: gross photosynthetic rate
R_l: leaf dark respiration rate
R_w: dark respiration rate of above-ground woody plant parts
R_r: root dark respiration rate
R_a: autotrophic respiration rate
R_h: heterotrophic respiration rate
P_n: net primary productivity
P_e: net ecosystem productivity
ΔS_c: variation of CO_2 storage in the canopy

Radiation (amount of photons or energy per unit area and time):

Q: photosynthetic photon flux density
S_p: photosynthetically active radiation
S_g: solar (global) radiation
S_n: net radiation
subscripts for radiation: 0, incident; int: intercepted; abs: absorbed; t: transmitted.
no subscript: incident, intercepted or absorbed radiation over closed canopies (see p. 16).

Parameters of statistical regressions:

n: number of data points
F_∞: CO_2 flux at saturating photosynthetic photon flux density
A_∞: net assimilation rate of a leaf at saturating photosynthetic photon flux density
α: apparent quantum yield, i.e. slope of the relationship at $Q = 0$
R: value of F at $Q = 0$
r^2: non-linear coefficient of determination
D: departure of the relationship from linearity, i.e. $r^2(\mathrm{H}) - r^2(\mathrm{L})$
F_m: photosynthetic capacity, i.e. F at $Q = 1800\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ for instantaneous data or F at $Q = 80\,\mathrm{mol\,m^{-2}\,d^{-1}}$ for daily data sets

Other symbols:

e: conversion efficiency of absorbed radiation into dry matter
e' : photosynthetic efficiency
f: radiation absorption efficiency
R: radiation extinction coefficient
C: atmospheric CO_2 concentration

Abbreviations for statistical treatments:

L: linear best fit
H: rectangular hyperbola best fit
N: no statistical relationship

Other abbreviations:

GPP: gross primary production
NPP: net primary production
NEP: net ecosystem production
NEE: net ecosystem exchange
PAR: photosynthetically active radiation
PPFD: photosynthetic photon flux density
LAI: leaf area index
VPD: vapour pressure deficit
CBL: convective boundary layer

III. INTRODUCTION

The first measurements of CO_2 fluxes over plant canopies are those reported by Thomas and Hill (1949) who used large plastic enclosures over fields of alfalfa, sugar beet and wheat. At the time they used a chemical method for measuring CO_2 concentration. However, this work remained isolated and it was only in the 1960s that new measurements were obtained with infra-red gas analysers. Beside canopy enclosures (e.g. Musgrave and Moss, 1961; Eckardt, 1966), micrometeorological methods were also developed, using vertical profiles of CO_2 concentration and associated measurements in the aerodynamic method and in the energy balance method (e.g. Lemon, 1960; Monteith and Szeicz, 1960; Monteith, 1962; Inoue, 1965; Saugier, 1970). Eddy correlation methods were first developed for measuring heat and water vapour fluxes, and extended to CO_2 fluxes when reliable fast response CO_2 sensors became available in the 1980s (e.g. Anderson *et al.*, 1984; Verma *et al.*, 1986). CO_2 flux measurements are useful in various fields:

(i) *Annual net carbon balance of ecosystems.* In the context of rising atmospheric CO_2 concentration as a result of the burning of fossil fuels and land use changes, the question of closing the carbon budget of the global biosphere has become critical. CO_2 flux between an ecosystem and the atmosphere is a direct indication of whether that terrestrial ecosystem is a source or a sink of CO_2 over a certain period. Based on measurements of net ecosystem flux, for example, Wofsy *et al.* (1993) measured carbon storage rates by a broadleaf, deciduous forest that are somewhat larger than those currently assumed in global carbon studies.

(ii) *Canopy and stand physiology*. CO_2 flux measurements provide insight into canopy and stand physiology, i.e. the response of gas exchange at the ecosystem scale to environmental variables. Similar to analyses at leaf scale, relationships between canopy photosynthetic rate or net ecosystem flux and absorbed photosynthetic photon flux density (PPFD), or respiration rate of the canopy or the ecosystem and temperature, have been established and the effect of environmental variables, such as atmospheric water vapour pressure deficit (VPD), on stand or canopy CO_2 flux have been investigated.

(iii) *Testing "bottom-up" plant production models*. Various models were developed in the 1960s to understand patterns of radiation penetration and of photosynthesis in homogeneous plant canopies (e.g. Saeki, 1960; Monteith, 1965; Duncan *et al.*, 1967) and were later extended to heterogeneous canopies (see Sinoquet, 1993, for a recent review). Computed PPFD reaching a given leaf level in the canopy, along with data on leaf photosynthetic rate, have been used to model canopy photosynthetic rate. Similarly, models of autotrophic respiration were developed (e.g. McCree, 1974). Before the availability of CO_2 flux measurements, the only data useful for testing these models were biomass increments of plants and vegetation. Canopy CO_2 flux data are intermediate in spatial and temporal scales between ecophysiological measurements of leaf photosynthesis over short periods, and measurements of plant production made over a whole growing season, and are suitable for the purpose. Flux measurements put a "lid" on the system and, therefore, provide a test of our understanding of processes within the system, and of "bottom-up" *process models* (e.g. Amthor *et al.*, 1994)

(iv) *Parameterizing "top-down" plant production models using remote sensing*. For many crops not short of water, the production of plant biomass is proportional to accumulated absorbed photosynthetically active radiation or PAR (Monteith, 1972; Monteith, 1977; Varlet-Grancher, 1982). The ratio between these two quantities has been called the conversion efficiency of absorbed radiation into dry matter, and is used in many simple models of crop growth, i.e. by-passing the complex processes of photosynthesis and of respiration known to depend on many environmental variables. A linear relationship between plant biomass production and absorbed PAR implies a linear relationship between canopy CO_2 flux and absorbed PPFD. In addition, the efficiency of radiation absorption by vegetation can be derived from remotely sensed vegetation indices. These coefficients are used in "top-down" *parametric models* (e.g. Kumar and Monteith, 1981).

The response of the CO_2 flux between a *leaf* and the atmosphere to PPFD can be described by a rectangular hyperbola. There is a respiratory flux in the dark; at low, limiting irradiance the CO_2 flux is proportional to PPFD, the slope being defined as the apparent quantum yield of photosynthesis; at high, saturating irradiance the response curve levels off, the asymptotic value being defined as photosynthetic capacity. The response of the CO_2 flux of a closed canopy is qualitatively similar. However, when the upper leaves are PPFD saturated, the lower leaves may still be PPFD limited, and the response of the CO_2 flux between a *canopy* and the atmosphere to PPFD saturates less rapidly than in the case of a single leaf, even being linear over the whole range of PPFD in some cases.

In this paper we aim to assess the possibility of obtaining general relationships between the CO_2 flux over canopies and absorbed PPFD. In particular, we aim to determine whether the relationship for a closed canopy is linear, consistent with the Monteith model, or curvilinear, consistent with the results of many mechanistic canopy models. Both general relationships and relationships for different vegetation classes are sought. Some methodology-related differences are also investigated, including comparison between micrometeorological and enclosure methods, the effect of taking into account respiration rate, and the effect of integrating measurements in time. For this we use, whenever possible, statistics on *similar data sets* (i.e., except for the variable under study, all environmental conditions were similar, and the data were obtained on the same site, with the same measuring technique, by the same scientific team), and statistics on *grouped data sets* (i.e. all the data sets on closed canopies satisfying the conditions described in the data analysis section are grouped by vegetation class or method of measurement or representation). Some effects of environmental variables are also investigated, but not quantitatively analysed because of lack of information in the original papers.

IV. STAND CO_2 BALANCE

The flux of CO_2 measured across a plane above a stand is the net result of all the CO_2 fluxes occurring within the system. In this respect the stand is analogous to a leaf. Within the stand there are photosynthetic organs and respiratory sources just as there are photosynthetic organelles and nonphotosynthetic, respiring tissues in a leaf. The net flux of CO_2 across the plane bounding the stand system is analogous to the net flux of CO_2 across the surface of a leaf through the stomata. The normal convention in micrometeorology is that fluxes downwards are negative and fluxes upwards positive. The convention we have followed in this paper is the convention used in ecophysiology, i.e. both photosynthetic and respiratory fluxes at the organ scale are treated as positive. At the stand scale, downward fluxes into the stand are treated as positive and upward fluxes as negative. The change in the amount of CO_2 stored in the column of air between the system boundaries, ΔS_c, is treated as either positive if S_c increases, or negative if S_c decreases.

Because the flux across the system is the algebraic sum of the fluxes within the system, if we consider instantaneous fluxes within the forest depicted in Figure 1, and assume a one-dimensional, horizontally uniform

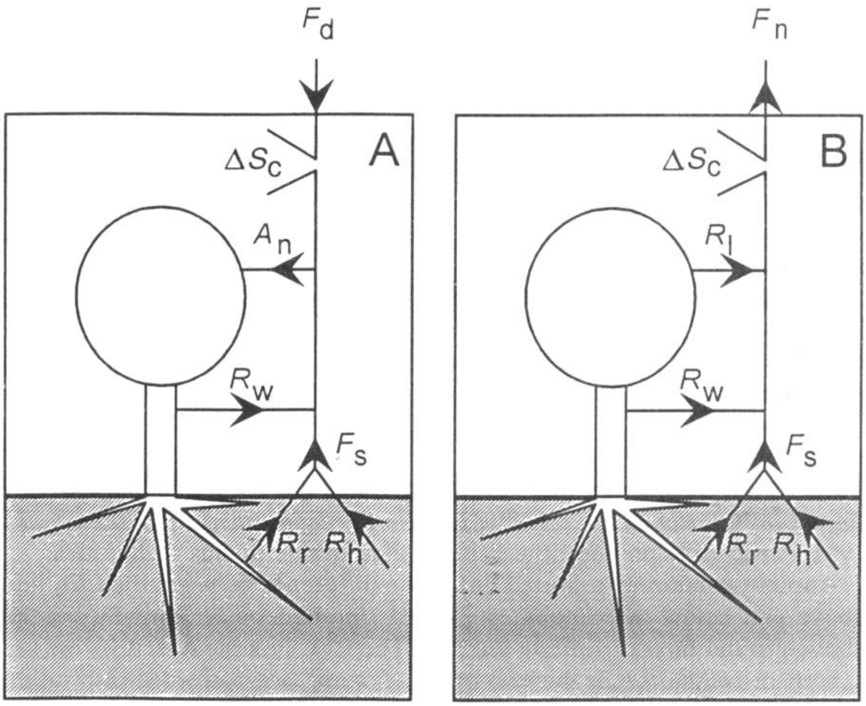

Fig. 1. CO_2 budget of a stand (A) during the day, and (B) during the night. F_d is the net ecosystem flux during daylight, F_n is the net ecosystem flux during darkness (night-time respiration), F_s is the soil CO_2 flux measured below the canopy assuming there is no photosynthesizing understorey vegetation, ΔS_c is the change of CO_2 stored in the canopy. The components of the carbon budget of the stand are: leaf net photosynthesis (A_n), leaf dark respiration (R_l), wood respiration (R_w), root respiration (R_r), and heterotrophic microbial decomposition (R_h).

system, then we can write

$$\begin{aligned} &\text{for the day:} && F_d = A_n - (R_w + R_r + R_h) + \Delta S_c \\ &\text{for the night:} && F_n = -(R_l + R_w + R_r + R_h) + \Delta S_c \end{aligned} \qquad (1)$$

where F_d is net CO_2 flux above the canopy during the day, F_n is net CO_2 flux above the canopy during the night, A_n is rate of net photosynthesis, R_l is respiratory flux from leaves, R_w from wood, R_r from roots and R_h from microorganisms in the soil and soil fauna.

From the point of view of the carbon balance of the system as a whole, the net flux across the upper system boundary, integrated over time, defines the gain or loss of carbon by the system, and thus determines whether the forest system is a sink or a source of carbon. The net flux, when integrated over time, gives the *Net Ecosystem Production*, NEP.

The physiological capability of the forest canopy to assimilate CO_2 in daytime in relation to weather and other environmental variables is determined by net photosynthetic rate, A_n. Assuming the above sign convention, rearrangement of equation (1) gives:

$$A_n = F_d + R_w + R_r + R_h - \Delta S_c \qquad (2)$$

This flux, integrated over time, is the *Gross Primary Production*, GPP. Although A_n depends on all the fluxes in the system and will only be approximated by F_d if all the other fluxes in respiration and storage are small by comparison, attempts to relate F_d alone to PPFD have been successful.

Subtracting the average CO_2 flux in the night from instantaneous CO_2 fluxes in the day (or adding the absolute values of these fluxes) gives a so-called *gross photosynthetic rate A*, which can be regarded as the sum of net photosynthetic rate and leaf mitochondrial respiration rate in the daytime:

$$A = A_n + R_l = F_d - F_n - \Delta S_c \qquad (3)$$

This, however, ignores the fact that dark respiration rate of leaves is significantly lower in the daytime than in the nighttime (e.g. Villar *et al.*, 1994). True gross photosynthesis is not measurable by flux techniques.

Another commonly reported flux is the difference between the CO_2 flux above and below the canopy, measured simultaneously. This flux is the above-ground flux, or *canopy flux*, F_c. The CO_2 flux measured below the canopy or *soil flux*, F_s is the sum of the root and heterotrophic respiration rates, and the net photosynthetic rate of the understorey vegetation. This latter term is usually neglected.

$$F_s = -(R_h + R_r) \qquad (4)$$

$$F_c = A_n - R_w = F_d - F_s - \Delta S_c \qquad (5)$$

F_c has also been successfully related to radiation, and has been regarded as *canopy net photosynthetic rate*, even though some wood respiration is included.

If one could easily separate roots and microorganisms in the soil respiration term, we could rearrange equation (1):

$$\begin{aligned} &\text{for the day:} && F_d + R_h - \Delta S_c = A_n - (R_w + R_r) \\ &\text{for the night:} && F_n + R_h - \Delta S_c = -(R_l + R_w + R_r) \end{aligned} \qquad (6)$$

This flux, integrated over time, is analogous to *Net Primary Productivity*, NPP.

Table 1 summarizes the correspondence between the CO_2 flux measurements terms and the components of the CO_2 budget of a stand, omitting the storage component.

Table 1

Equivalence between CO_2 flux measurements and terms of the carbon budget of a stand

Process	Flux measurement	Carbon budget
Leaf or canopy gross photosynthesis	F_d–F_n	A
Leaf respiration		R_l
Leaf or canopy net photosynthesis		$A_n = A - R_l$
Respiration of above-ground woody plant parts		R_w
Root respiration		R_r
Autotrophic respiration		$R_a = R_l + R_w + R_r$
Heterotrophic respiration		R_h
Net ecosystem flux in darkness or total respiration of the system	F_n	$R_a + R_h$
Soil flux, or root + microorganism respiration	F_s	$R_h + R_r$
Net primary production		$P_n = A - R_a$
Above-ground flux or canopy flux	$F_c = F_d - F_s$	$A_n - R_w$
Net ecosystem flux or net ecosystem production	F_d	$P_e = P_n - R_h$

V. STORAGE FLUX

A so-called *Net Ecosystem Exchange* NEE, defined as the flux of the biota, is usually calculated as:

$$\begin{aligned} &\text{for the day:} && F_d - \Delta S_c = A_n - (R_w + R_r + R_h) \\ &\text{for the night:} && F_n - \Delta S_c = -(R_l + R_w + R_r + R_h) \end{aligned} \qquad (7)$$

The difference from equation (1) is that the atmospheric storage term within the system, ΔS_c, is now on the left hand side, together with the net gain or loss of CO_2 by the system, F_d or F_n, and all the terms describing immediate biological activity are on the right hand side.

An increase in storage of CO_2 in the air column can be regarded as a measure of ecosystem activity if the concentration at the reference plane remains constant. This approach was used by Woodwell and Dykeman (1966) to estimate ecosystem respiration rate at night, under stable conditions generated by temperature inversion. The temperature inversion turns what was essentially an open system into a closed system and allows a straightforward treatment that cannot be easily applied in more general circumstances, when the concentration of CO_2 within the stand may change for several reasons, which are related to both the physiology of the canopy (photosynthetic and respiration rate of the different compartments), and the meteorology (growth of the convective boundary layer, CBL, and entrainment of air).

The flux in and out of storage can be particularly important at times. For example, after an overnight temperature inversion, when the CO_2 concentration within the stand may have reached 500 or 600 μmol mol^{-1}, the rapid reduction in CO_2 concentration at dawn is partly a result of the assimilation of CO_2 stored within the system. As the system warms in the early morning and an upward heat flux develops, the overnight inversion breaks down, warm air is convected upwards, the CBL grows, and the concentration of CO_2 within the stand falls as a result.

Some recent publications present results of NEE where ΔS_c was estimated by measuring the variations of CO_2 concentration with time at a reference height in or above the canopy (e.g. Wofsy *et al.*, 1993; Hollinger *et al.*, 1994). Both assimilation of CO_2 by the canopy and entrainment of air of lower CO_2 concentration contribute to the change in CO_2 storage within the canopy.

During the day, the CO_2 concentration within the mixed layer varies as the result of assimilation of CO_2 by vegetation at *regional* scale. This concentration may easily change by 100 μmol mol^{-1} from dawn to mid-afternoon. The column of air that arrives at a measurement point has usually travelled a substantial distance. Whilst the CO_2 concentration within the surface layer close to the vegetation surface is determined by a comparatively local process, the concentration of CO_2 in the mixed layer reflects both entrainment and physiological activity of vegetation on a much larger scale. This change in concentration of CO_2 within the CBL may be used to estimate CO_2 assimilation integrated over the day at the regional scale (McNaughton, 1988; Raupach *et al.*, 1992). The CO_2 concentration at the upper system boundary of a rough surface such as forest is closely coupled to the CO_2 concentration in the mixed layer and consequently reflects regional scale processes rather than local processes.

Figure 2A shows the idealized development of CO_2 concentration profiles through a canopy during the course of a day, in the absence of regional scale phenomena. The bulge to the left becomes more pronounced during the morning and retracts during the afternoon. At the same time, the CO_2 concentration profile as a whole moves to the left as a result of regional CO_2 assimilation modified by entrainment, as shown in Figure 2B, and moves back again in the evening. The locally attributable change in storage is represented only by the shaded area in Figure 2A and not by the entire shaded area in Figure 2B. Thus, assessment of the change in storage must be based on measurements of CO_2 concentrations down through the canopy. It is a basic premise of the flux measuring schemes in use that a steady state exists over the period of integration, as pointed out by Tanner (1968). It is also a basic assumption that transport is one-dimensional and that the area of vegetation is extensive and homogeneous: if advection occurs on a substantial scale then additional terms need to be added as shown by Tanner for water transport.

Conclusions regarding storage:

(i) Change in storage is a component of the mass balance. Storage of CO_2 is important and relevant to a discussion on forest CO_2 fluxes. Unfortunately, most past studies have ignored this process. However, the fluxes in and out of storage are generally much smaller than the other fluxes, except in the early morning period after an inversion, and 24-hour storage in the airspace is generally zero or negligible.

(ii) Even in a simple situation with a constant ambient CO_2 concentration, the fluxes in and out of storage are a complex product of physiology and meteorology.

(iii) The apparent flux out of storage at a particular point in a region, based on a shift in the vertical profile of CO_2 concentration through the vegetation, may give a misleading impression of the physiological activity of the vegetation at that point.

(iv) When the atmospheric CO_2 concentration is changing on a regional scale, the flux out of storage throughout the whole of the mixed layer and the surface layer represents the net CO_2 exchange of the vegetation on a regional scale.

Fluxes measured over the canopy may or may not have been corrected for change in storage. Appendix 1 mentions if change in storage has been taken into account in the day or in the night, in each data set. What are referred to as CO_2 fluxes in the rest of this paper may represent somewhat different quantities for this reason.

VI. RESPIRATION FLUX

If we do ignore CO_2 storage within the air column, the flux over a plant canopy, F_d, is a balance between the photosynthetic and respiration rates

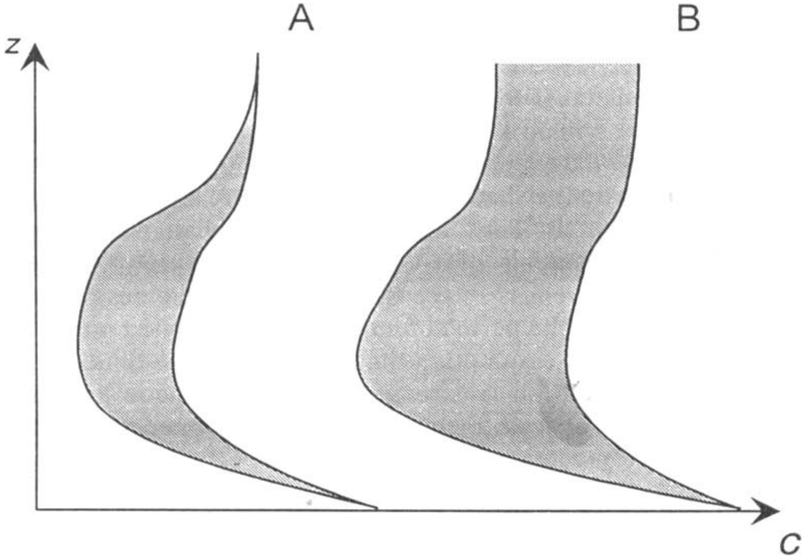

Fig. 2. Idealized development of CO_2 concentration profiles through a canopy, during the course of a day (A) in the absence of regional scale CO_2 depletion, (B) with regional scale CO_2 depletion. z is the height from the ground, C is the CO_2 concentration. The concentration profile moves from right to left within the shaded area during the morning, and moves back during the afternoon.

of the system. Total respiration rate may represent the sum of two or more of the individual respiration fluxes, depending on the definition of the system. Heterotrophic respiration depends on soil temperature and moisture content. Autotrophic respiration can be partitioned, following McCree (1974), into maintenance and growth respiration. Maintenance respiration rate depends on temperature and the protein content of organs; growth respiration rate depends on the fraction of assimilates allocated to growth and on the chemical composition of growing tissues. In considering the relationship between F_d and Q, we should bear in mind the following:

(i) In the dark, maintenance and heterotrophic respiration rates vary with air and soil temperature. This affects the dark respiration rate, i.e. CO_2 flux at $Q = 0$. For a given temperature, maintenance respiration rate depends principally on the biomass of the canopy.
(ii) In the light, maintenance and heterotrophic respiration rates follow the diurnal course of temperature. The time lag between the diurnal course of solar radiation and of air and soil temperature generates hysteresis in the response of F_d to PPFD.
(iii) Growth respiration rates vary during the day, therefore the time step and interval of measurements affect the value of F_d.

A. Soil Respiration

In the case of micrometeorological measurements, the system comprises vegetation and soil, and therefore measured F_d always includes soil CO_2 flux. In forest systems, it is possible to measure fluxes above ground level and below the canopy by placing eddy covariance sensors below the canopy (e.g. Baldocchi *et al.*, 1987). In this case the CO_2 efflux from the forest floor also includes the photosynthetic flux of the understorey vegetation.

In the case of enclosures, definition of the system depends on which parts are enclosed. In herbaceous vegetation, it is usually not easy physically to separate vegetation from soil, and therefore measured F_d includes soil respiration rate. Soil respiration rate can be measured separately with enclosures over areas where the vegetation has been removed (e.g. Puckridge and Ratkowski, 1971). In the rare cases of measurements with enclosures over areas of forests (Wong and Dunin, 1987; Mordacq *et al.*, 1991), the soil was not included in the enclosure.

B. Dark Respiration

Night time CO_2 flux, F_n, represents the rate of all the components of the system. Two ways of taking dark respiration rate into account in the calculation of CO_2 flux are to be found in the literature:

(i) The mean value of F_n has been subtracted directly from daytime CO_2 fluxes F_d, so that the PPFD response curve passes through the origin. In this case, the differences in respiration rate during the night and day, resulting from differences in temperature in particular, have been neglected.

(ii) F_n has been recorded at night with the corresponding air temperature. A respiration rate/temperature relationship has been established, used to calculate dark respiration rate at the appropriate temperature during the day, and then subtracted from daytime CO_2 flux. In this case the reported CO_2 flux is regarded as gross photosynthetic rate, A.

Appendix 1, describing the data sets, indicates whether soil flux or dark respiration rate was measured by the authors, and whether the daytime fluxes reported have had some respiration terms subtracted. In this study, there has been no attempt to standardize all the CO_2 fluxes compiled, in order to retrieve, for instance, the flux of CO_2 assimilated by the canopy, A_n. Therefore, what is referred to as CO_2 flux, "F", in the rest of this paper may represent very different quantities: net ecosystem flux alone, or net ecosystem flux plus the absolute value of some respiration terms.

VII. CANOPY PHOTOSYNTHESIS

Canopy net photosynthetic rate is determined by leaf photosynthesis, respiration of twigs and branches, and by radiative transfer through the canopy. The response of leaf photosynthetic rate to PPFD is asymptotic, the parameters depending on leaf photosynthetic properties and the environment. The result of radiative transfer is to linearize the response curves of CO_2 flux to PPFD at the canopy scale. This is achieved in canopies in three ways (Jarvis and Leverenz, 1983):

(i) Grouping of the foliage into shoots, branches and crowns results in efficient transmission of direct radiation through the canopy and effective scattering where it is intercepted.
(ii) Spatial distribution of the leaves, together with the distribution of their inclination angles, results in exposure of the majority of leaves to intermediate PPFD so that the leaves are not PPFD saturated.
(iii) Compensation in physiological and anatomical properties for the gradient of PPFD through the canopy as a result of "shade" acclimation: photosynthesis of shade leaves is more efficient at low PPFD, largely because of lower dark respiration rate (Osmond *et al.*, 1980).

Saugier (1986), Wong and Dunin (1987) and Jarvis and Leverenz (1983) show comparisons between the PPFD response curves of leaf and canopy photosynthetic rate for, respectively, a grass crop of *Dactylis*, a broadleaf forest of *Eucalyptus maculata*, and a needleleaf forest of Sitka spruce (*Picea sitchensis*). In the case of the Sitka spruce, a curve for an intermediate photosynthetic element, the shoot, was also presented. Figure 3 shows the response of photosynthetic rate to PPFD for a leaf (expressed per unit projected leaf area), a shoot (expressed per unit shoot silhouette area) and a canopy (expressed per unit ground area) of Sitka spruce. Visual analysis of the regression curves through the data points presented in these papers leads to the following conclusions:

(i) Dark respiration rate (CO_2 flux at $Q = 0$) is less for a leaf than for a shoot, and for a shoot than for the canopy. This results probably from the difference in the relative respiring biomass of these elements.
(ii) Maximum photosynthetic rate at high PPFD is lower for a leaf than for a shoot, and for a shoot than for the canopy.
(iii) The response curve of photosynthetic rate to PPFD departs further from linearity for a leaf than for a shoot, and for a shoot than for the canopy. Points (ii) and (iii) are the result of more efficient utilization of photons by groups of photosynthetic elements than by a single leaf.
(iv) The slope of the PPFD response curve at $F_d = 0$ shows no general trend: in the case of the grass crop, the initial slope was steeper for the

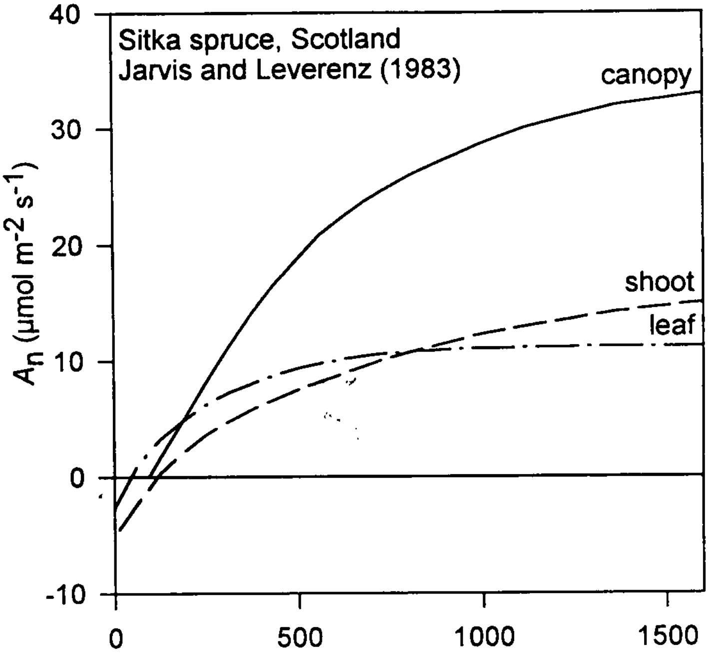

Fig. 3. The relationship between rate of net photosynthesis (A_n) and incident quantum flux density (Q_0) in Sitka spruce, for "sun" needles, a "sun" shoot and a forest canopy. Replotted from Jarvis and Leverenz (1983).

canopy than for the leaf, but the slope was less steep for the canopy than for the leaf in the case of the broadleaf forest, and all three slopes were almost identical for the needleleaf forest (Fig. 3). In all three cases, the slope is close to the quantum yield for a C3 leaf at normal CO_2 concentration, i.e. 0·05 µmol (CO_2) µmol^{-1} (photons) (Ehleringer and Pearcy, 1983).

VIII. RADIATION

In the literature, CO_2 fluxes have originally been reported in relation to photosynthetically active radiation (S_p), photosynthetic photon flux density (Q), solar radiation (S_g), or net radiation (S_n). Radiation is either incident (subscript: 0), intercepted by the canopy (subscript: int) or absorbed by the canopy (subscript: abs). For a review and a definition of these terms, see the articles by Varlet-Grancher *et al.* (1989) or Goward and Huemmrich (1992). Intercepted and absorbed PPFD, for instance, are defined as follows:

$$\begin{aligned} Q_{\mathrm{int}} &= Q_0 - Q_{\mathrm{t}} \\ Q_{\mathrm{abs}} &= Q_{\mathrm{int}} - Q_{\mathrm{r}} + Q_{\mathrm{rs}} \end{aligned} \tag{8}$$

with Q_{t}, PPFD transmitted through the canopy, Q_{r}, PPFD reflected by the canopy and Q_{rs}, PPFD reflected by the soil or understorey, and reabsorbed by the canopy. Q_{rs} is small compared with the other fluxes, and is usually neglected.

The relationships between solar radiation, PAR, PPFD and net radiation are variable, depending on several environmental variables, such as the proportions of diffuse and direct radiation (see for instance McCree 1972) and on the canopy structure and optical properties. To transform radiation ($\mathrm{W\,m^{-2}}$) into PPFD ($\mu\mathrm{mol\,m^{-2}\,s^{-1}}$) in this paper, the following assumptions have been made (Varlet-Grancher *et al.*, 1981):

$$\begin{aligned} S_{\mathrm{p}} &= 0{\cdot}48\ S_{\mathrm{g}} \\ Q &= 4{\cdot}6\ S_{\mathrm{p}} \end{aligned} \tag{9}$$

One single, statistical relationship has also been used to transform the few data expressed in net radiation into solar radiation:

$$S_{\mathrm{n}} = 0{\cdot}7\ (S_{\mathrm{g}} - 30) \tag{10}$$

We have focused our review on *closed canopies*, for which we consider that all the incident photon flux is intercepted, and we have neglected the difference between absorbed and intercepted photon flux. Leaf area index (LAI) is the primary factor determining the absorption of photon flux by a canopy. However, variations in the extinction coefficient can be important at times: e.g. Breda (1994) reports extinction coefficients of solar radiation varying from 0·46 to 0·32 for thinned oak stands. Another issue is that absorption or interception of radiation by photosynthetic organs is different for different expressions of radiation: for example, photosynthetically active radiation is more atttenuated through the canopy than solar radiation: Hutchison and Baldocchi (1989) report extinction coefficients for an oak-hickory forest of 0·65 for PAR and 0·51 for solar radiation. The absorbed PPFD depends on the albedo of the canopy, and albedo varies with vegetation class and structure: Sellers (1965) reported albedos for solar radiation of 5–15% for coniferous forests, 10–20% for deciduous forests, and 15–25% for crops. Albedos for PPFD are less than 5%.

In this study, these discrepancies have been neglected, and there has been no attempt to standardize the radiation flux compiled, in order to retrieve, for instance, PPFD absorbed by the canopy. Therefore, what is referred to as photosynthetic photon flux density, "Q", in the rest of this paper may represent incident, absorbed or intercepted PPFD in closed canopies. Appendix 1, describing the data sets, indicates the expression of radiation that was originally reported by the authors.

IX. RADIATION USE EFFICIENCY

Part of this study is intended to define whether, and on what time and space scales, a linear relationship between CO_2 fluxes over closed plant canopies and absorbed PPFD exists. In these cases, we can calculate a *photosynthetic efficiency*, as the slope of the linear regression between F and Q.

Usefulness of a linear relationship. A linear relationship between absorbed PPFD and canopy photosynthetic rate would be very useful in doing "biology from space". Kumar and Monteith (1981) derived a "top-down" plant production model for remote sensing of crop growth. This model has been used to estimate NPP over various surfaces, ranging from the field scale to the whole biosphere:

$$P_n = e\, f\, S_p, \mathrm{o} \qquad (11)$$

where P_n is net primary productivity, f is the efficiency of absorption of incident PAR, and e is the efficiency of conversion of absorbed PAR into dry matter.

The coefficient f can be related to combinations of reflectances obtained by remote sensing, called vegetation indices. The most commonly used are the Normalized Difference Vegetation Index, NDVI, and the Simple Ratio, SR, both of them being combinations of reflectances in the red and near infra-red channels of the NOAA-AVHRR radiometer. Monteith (1977) found that the shape of the relationship of annual NPP versus absorbed PAR integrated over a year is linear, and that the slope, e, is constant over a wide range of crops and climatic conditions in England. This constant slope of 3 g of dry matter produced per MJ of PAR absorbed has been used by Heimann and Keeling (1989) to estimate seasonal variations of global NPP.

Ruimy *et al.* (1994) showed that e is much more variable between different natural vegetation types, and used a conversion efficiency varying with vegetation class for global NPP estimates. One of the factors with which e varies is the proportion of asssimilates lost by autotrophic respiration. Monteith (1972) expressed NPP as:

$$P_n = \epsilon_r\, \epsilon_q\, \epsilon_d\, f\, S_{p,0} = \epsilon_r\, A_n \qquad (12)$$

where ϵ_q is quantum efficiency, ϵ_d efficiency of diffusion of CO_2 molecules from the atmosphere to the sites of photosynthesis in the leaves, and ϵ_r fraction of assimilates not used for respiration.

A linear relationship between annual NPP and integrated absorbed PAR requires that there is a linear relationship between GPP and absorbed PPFD, at least on an annual time-scale. In this case, we can define a *photosynthetic efficiency* e', so that

$$A_n = e' f Q_0 \tag{13}$$

Linear relationships imply that, on a seasonal time-scale, i.e. weekly or monthly, mean solar radiation can be multiplied by mean absorption efficiency and mean conversion efficiency (respectively photosynthetic efficiency) to retrieve NPP (respectively GPP), whereas a curvilinear relationship implies that NPP (respectively GPP) has to be computed instantaneously or hourly, and this dramatically increases computing time.

Are linear relationships artefacts? Three arguments may lead to the suggestion that linear relationships between F and Q are artefacts.

(i) Model computations of canopy photosynthesis, ranging from instantaneous to daily scale, when plotted versus radiation always show curvilinear relationships, however far from photon saturation (e.g. Baldocchi, 1994; Sellers, 1985; Oker-Blom, 1989; Wang *et al.*, 1992).
(ii) The mean initial slopes of regressions through data sets for which the best fits are curvilinear are often higher than the slopes of linear regressions through data sets for which the best fits are linear (see Appendix 2).
(iii) Some linear best fits are poorly defined or the result of environmental stresses: a large amount of scatter in the data characterized by low r^2 below 0·40 (e.g. Allen and Lemon, 1976); a small number of data points, fewer than 10 (e.g. Desjardins *et al.*, 1985); relatively low maximum PPFD, below 1000 μmol photons m^{-2} s^{-1} (e.g. Valentini *et al.*, 1991); water-stressed vegetation (e.g. Kim and Verma, 1990).

X. TECHNIQUES FOR MEASURING CO_2 FLUX

A. Energy Balance or Bowen Ratio Method

This method was first used to measure water vapour fluxes over a surface (Bowen, 1926), and has then been applied to the measurement of CO_2 fluxes (see Jarvis *et al.*, 1976 for examples). The method is based on the energy balance at a surface:

$$S_n = G + H + LE \tag{14}$$

where G is sensible heat flux into the ground, H, sensible heat flux into the air, and LE, latent heat flux into the air (L, latent heat of vaporization of water; E, rate of evaporation at the surface). S_n and G are measured quantities. To partition between the two other quantities, the Bowen ratio, β, can be measured as:

$$\beta = \frac{H}{LE} = \frac{c_p \, \Delta T}{L \, \Delta q} \tag{15}$$

where c_p is specific heat of air at constant pressure, ΔT, difference of air temperature between two reference heights and Δq, difference of specific humidity of the air over the same height interval above the vegetation. Then:

$$E = \frac{S_n - G}{(\beta + 1)\, L} \tag{16}$$

Knowing the evaporation rate E, we can calculate CO_2 flux F from:

$$\frac{F}{E} = \frac{\Delta C}{\Delta q} \tag{17}$$

where ΔC is the difference of specific CO_2 concentration over the same height interval.

B. Aerodynamic or Profile Method

The theory of this method and some applications were given by Monteith and Szeicz (1960). The method is based on the assumption of similarity of the turbulent transfer of mass and momentum, i.e. equality of the turbulent transfer coefficients for CO_2, K_c, and for momentum, K_M. The CO_2 flux can be written with our sign convention as:

$$F = \rho_c K_c \frac{\Delta C}{\Delta z} \tag{18}$$

where ρ_c is the density of CO_2 and K_c the turbulent transfer coefficient for CO_2.

K_M is calculated from the logarithmic profiles of wind speed through the canopy as follows:

$$K_M = \frac{k^2 z \Delta u}{\ln\left(\frac{z_2}{z_1}\right)^2} \tag{19}$$

where k is von Karman's constant, Δu the difference in horizontal wind speed between the two measurement heights, z_1 and z_2. If z is measured from the ground, it is necessary to subtract from z the displacement height of the wind-speed profile, d. Substituting the expression for K_M in equation

(19) for K_c in equation (18), incorporating d and integrating yields the final equation:

$$F = \frac{\rho_c k^2 (u_2 - u_1)(C_1 - C_2)}{\ln \left(\frac{z_2 - d}{z_1 - d}\right)^2} \qquad (20)$$

Equation (20) assumes that the atmosphere is in neutral equilibrium. Various corrections have been proposed for unstable or stable conditions (e.g. Monin and Yaglom, 1971).

C. Eddy Correlation or Eddy Covariance

This method was first used to measure water vapour fluxes, and has been extended to CO_2 fluxes only recently (Anderson *et al.*, 1984; Verma *et al.*, 1986). The time average of the vertical flux of CO_2 at a fixed point above a surface can be expressed as:

$$F = \overline{\rho_c w' C'} \qquad (21)$$

where $C' = C - \overline{C}$ is the instantaneous deviation from the mean CO_2 concentration measured at a reference height and w' is the instantaneous deviation of vertical wind speed from the mean wind speed.

CO_2 concentration is measured with a fast-response CO_2 gas analyser and wind speed with a sonic anemometer. Because this method requires observations at only one reference height, instruments can be placed on an aircraft as well as on a tower.

D. Enclosures

Details on this method were given by Musgrave and Moss (1961). A portion of the vegetation is enclosed from the outside environment in a large chamber. The chamber may or may not include the soil surface. In a *closed system*, the change of CO_2 concentration in the chamber with time is used to calculate CO_2 flux as:

$$F = V\frac{\Delta C}{\Delta t} \qquad (22)$$

where V is chamber volume, and $\Delta C/\Delta t$ the rate of decrease of CO_2 concentration.

In the case of *open systems*, there is a constant flow rate of air (d) through the enclosure, and the difference in concentration of the air entering and leaving the system ($\Delta C''$) is monitored and used to calculate CO_2 flux:

$$F = d\,\Delta C'' \qquad (23)$$

E. Models

The shape of the response of canopy GPP to intercepted PPFD can be modelled knowing the PPFD response curve of a leaf and the attenuation of PPFD through the canopy (e.g. Monteith, 1965). There are several models that combine leaf photosynthesis and radiative transfer through a canopy (e.g. de Wit *et al.*, 1978; Wang and Jarvis, 1990; Wang *et al.*, 1992). PPFD response curves of leaves can be modelled with a rectangular hyperbola:

$$A_n = \frac{\alpha Q_0 A_\infty}{\alpha Q_0 + A_\infty} - R \qquad (24)$$

where A_∞ is leaf assimilation rate at saturating PPFD, α is apparent quantum yield and R is dark respiration rate.

In closed canopies with randomly distributed leaves, the curve of PPFD attenuation versus LAI is asymptotic, and PPFD interception efficiency can be simply modelled with a Beer-Lambert law:

$$f = 1 - \exp^{-KL} \qquad (25)$$

where K is radiation extinction coefficient of the canopy and L is leaf area index.

Models can be effectively used to investigate, for example, the effect of stand structure on radiation interception (e.g. Oker-Blom, 1989), of soil warming on soil respiration rate (e.g. Baldocchi, 1994), of leaf photosynthetic properties on canopy photosynthesis (e.g. Jarvis and Leverenz, 1983), and of all variables affecting the relationship between canopy photosynthetic rate and absorbed PPFD.

XI. DATA SETS, DATA ANALYSIS

A. Data Set Compilation

This study is intended first to be an exhaustive collection of data sets on CO$_2$ fluxes over plant canopies in relation to the radiation environments. However, because of the relatively large number of data sets on crops, not all data on crops have been reviewed. As eddy correlation measurements develop and become more widely used, especially in large field campaigns such as BOREAS (BOReal Ecosystem Atmosphere Study), many more data sets will become available and the conclusions of this study may be altered. We compiled only original data; the following data sets were not compiled in this study:

(i) data sets on photosynthetic conversion efficiency already calculated as the ratio of CO_2 flux integrated over a certain period to integrated radiation (e.g. Rauner, 1976);
(ii) data sets where canopy photosynthetic rate was modelled and not measured (e.g. Oker-Blom, 1989);
(iii) curves given in original papers as fitted curves with no data points (e.g. Uchijima, 1976).

Appendix 1 lists the data sets collected and digitized, along with relevant information for each data set that was available in the original paper. Data sets are identified by the authors and year of publication, plus a digit identifying the data sets obtained in different treatments or conditions within the same article: for instance, "Hollinger *et al.*, 1994 −1 to −5" are data sets published by Hollinger *et al.* (1994) obtained at five different times of year.

B. Vegetation Classification

The following simple functional classification of vegetation classes has been applied to the data sets: broadleaf forests, coniferous forests, C3 grasslands, C4 grasslands, C3 crops, C4 crops and mixed vegetation. Because of the disproportionate number of data sets for some vegetation classes, for some statistical procedures the data sets are also grouped into *broad vegetation classes*: forests (broadleaf and coniferous), grasslands (C3 and C4), crops (C3 and C4) and mixed vegetation. Some vegetation classes have received more attention than others: the most numerous studies are on crops, followed by forests, grasslands, and mixed vegetation. Among the crops studied, there are more C3 than C4 types; among the grasslands there are about the same amount of each; and among the forests there are more broadleaves than conifers. Overall, there is a lack of data for some vegetation classes, in particular coniferous forests, tropical grasslands and mixed vegetation.

C. Statistical Analysis of Instantaneous Data Sets

All the radiation response curves were digitized, using a digitizing table (ALTEK), and converted into the following standard units: CO_2 flux density in $\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$ and photon flux density in $\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$. Statistical regression analysis has been applied to all the resulting files, using the SIGMA-PLOT ® curve fitter. In all cases, the following two models have been fitted:

$$F = \alpha Q - R \qquad \text{(model L)} \quad (26)$$

$$F = \frac{\alpha Q F_\infty}{\alpha Q + F_\infty} - R \qquad \text{(model H)} \quad (27)$$

where F_∞ is F at saturating Q, α is apparent quantum yield (i.e. dF/dQ at $Q = 0$), and R is dark respiration rate (i.e. F at $Q = 0$).

We have applied the following constraints to these models: $0 < \alpha < 1$, $F_\infty > 0$, $R > 0$. If a value of R is given in the original paper, this value is used to constrain R in the statistical model. For all the regressions, the non-linear coefficient of determination, r^2, was calculated using the SIGMA-PLOT iterative procedure. The *best fit* has been defined as follows:

(i) if the r^2 of the two models (L and H) are different at 1%, the relationship having the highest r^2 is the best fit;
(ii) if the two r^2 are identical at 1%, the best fit is the simplest relationship, i.e. L;
(iii) if F_∞ is "unrealistically" high (i.e. $F_\infty > 100\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$ for ambient atmospheric CO_2 concentration), L is regarded as the best fit.

To facilitate comparison among the data sets, some derived parameters have also been calculated. The *departure of the relationship from linearity* has been expressed as:

$$D = r^2\,(\text{H}) - r^2\,(\text{L}) \qquad (28)$$

The *photosynthetic capacity* (F_m) of the vegetation has been defined as the calculated value of F at $Q = 1800\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$.

The results of the statistical regressions for all individual data sets are shown in Appendix 2.

D. Statistical Analysis of Grouped Data Sets

The statistical analysis described above has also been applied to *grouped data sets*, i.e. to all the data sets obtained in given conditions (for example, all the data sets obtained with micrometeorological methods; all the data sets obtained with enclosures), that satisfy the following criteria.

(i) The canopy is *closed*: forests are considered as closed canopies, unless otherwise stated; grasslands, both natural and cultivated, are considered as having closed canopies if the paper explicitly mentions a leaf area index $L > 3$. This arbitrary convention may not be valid for

Table 2

Statistics on the relationship between CO_2 flux (F) and PPFD (Q).

2.1. Instantaneous data sets, F_∞, R and F_m are in μmol $m^{-2}s^{-1}$

Description	n	F_∞	α	R	r^2 (best fit)	D	F_m	best fit
			mean					
All data sets (Fig. 10)	1362	43·35	0·044	4·29	0·57	0·06	23·72	H
			effect of vegetation class					
Broadleaf forest	593	39·35	0·037	3·34	0·59	0·05	21·39	H
Conifer forest	125	32·37	0·024	0·00	0·34	0·10	18·50	H
C3 grasslands	68	/	0·017	0·00	0·59	0·00	30·60	L
C4 grasslands	280	84·13	0·028	8·11	0·88	0·02	23·41	H
C3 crops	476	42·85	0·062	4·03	0·65	0·14	26·93	H
C4 crops	83	88·84	0·036	4·45	0·77	0·01	33·02	H
All forests (Fig. 8A)	718	35·25	0·040	3·46	0·57	0·08	20·20	H
All grasslands (Fig. 8C)	348	82·92	0·025	5·39	0·80	0·02	23·78	H
All crops (Fig. 8B)	560	46·87	0·056	3·94	0·66	0·10	28·05	H
			effect of respiration					
Net ecosystem flux (F_d) (Fig. 7A)	978	56·79	0·034	5·17	0·70	0·03	24·29	H
Canopy flux ($F_c = F_d - F_s$) (Fig. 7B)	614	34·60	0·066	4·24	0·50	0·15	22·55	H
			effect of technique					
Micrometeorological (Fig. 5A)	1120	58·27	0·030	4·48	0·70	0·03	23·79	H
Enclosure (Fig. 5B)	478	44·44	0·060	2·42	0·60	0·20	29·08	H

Table 2—*cont.*

Description	n	F_∞	α	R	r^2 (best fit)	D	F_m	best fit
effect of technique and vegetation class								
Micrometeorological, forests (Fig. 9A)	654	39·13	0·035	3·90	0·61	0·06	20·23	H
Micrometeorological, crops (Fig. 9B)	225	/	0·023	3·21	0·84	0·00	37·26	L
envelope (10% upper values)								
All data sets (Fig. 10)	159	55·78	0·081	1·62	0·58	0·27	38·72	H
effect of vegetation class								
Forests	70	47·36	0·071	0·00	0·89	0·43	34·55	H
Grasslands	35	70·09	0·044	2·90	0·85	0·07	34·28	H
Crops	56	57·30	0·084	0·00	0·68	0·44	41·55	H
effect of respiration								
Net ecosystem flux (F_d)	94	71·13	0·046	0·00	0·90	0·14	38·26	H
Canopy flux ($F_c = F_d - F_s$)	59	51·48	0·100	0·89	0·65	0·50	39·14	H

2.2. Daily data sets, F_∞, R and F_m are in mol m^{-2} d^{-1}

Description	n	F_∞	α	R	r^2 (best fit)	D_∞	F_m	best fit
mean								
All data sets (Fig. 13)	66	/	0·020	0·02	0·54	0·00	1·58	L

Data sets are grouped by the variable described in column 1. Statistics were applied on full data sets ("mean") or on the 10% upper boundary values ("envelope"). n is number of data points. A rectangular hyperbola (H) and a linear model (L) are tested and best fit is defined by the relationship having the highest coefficient of determination (r^2). The parameters of the statistical models are initial slope (α), intercept on the y axis (R), and for the hyperbolic model value of F at saturating Q (F_α). Derived parameters are departure from linearity (D), defined as r^2(H)–r^2(L), and photosynthetic capacity (F_m), defined as F at maximum Q (1800 μmol m^{-2} s^{-1} for instantaneous data sets, 80 mol m^{-2} d^{-1} for daily data sets). R = 0·00 indicates that the intercept would be positive (therefore the value of R negative), but is constrained by the model.

some erectophile crops such as corn, where PPFD is not fully intercepted even at $L = 3$, or for vegetation with highly clumped foliage such as some forests.

(ii) *Instantaneous* data sets: the data are half or one hour average values. Data sets where F and Q are expressed as daily means are analysed separately.

(iii) *Local* data sets: the data apply to a stand with a scale of metres to hundreds of metres. Data sets obtained with aircraft-mounted eddy correlation instruments over a large region have been analysed separately.

(iv) The following data sets have been arbitrarily discarded: data sets showing no statistical relationship (best fit with a coefficient of determination $r^2 < 0{\cdot}4$); data sets obtained in non-ambient CO_2 concentrations; data sets obtained on water-stressed vegetation; data sets obtained in artificial environments; and data sets where F is negative in high PPFD (i.e. $Q > 1000\,\mu mol\,m^{-2}\,s^{-1}$) (Hollinger *et al.*, 1994; Price and Black, 1990).

When instantaneous data sets are integrated over time (usually a day), they have been analysed independently, using the same procedure, in standard units for F, R, F_∞, Q of $mol\,m^{-2}\,d^{-1}$. Photosynthetic capacity F_m is then defined as F at $Q = 80\,mol\,m^{-2}\,d^{-1}$.

Mean statistics on grouped instantaneous data sets are summarized in Table 2.1. Mean statistics on grouped daily data sets are summarized in Table 2.2.

One must note that grouped data sets have nothing in common except for the variable under study. They are not *similar*, in the sense that, generally, environmental conditions were different, and the data were obtained on different sites, with different measuring technique, by different scientific teams.

E. Boundary Value Analysis

For grouped data sets, the *upper boundary values* of the data have been determined as follows: a histogram has been made of the distribution of data in eight equal size classes of PPFD: 0–250, 250–500, 500–750, 750–1000, 1000–1250, 1250–1500, 1500–1750, 1750–2000 $\mu mol\,m^{-2}\,s^{-1}$ (points above $2000\,\mu mol\,m^{-2}\,s^{-1}$ have been discarded), and in each class the highest 10% of the CO_2 flux values have been retained. The resulting data sets have been analysed using the statistical procedures described above, the resulting equation being the *upper envelope* of each data set. Statistics on boundary values of grouped data sets are summarized in Table 2.1.

XII. EFFECTS OF VARIOUS FACTORS ON THE RESPONSE FUNCTION OF CO_2 FLUX TO PPFD

A. The Micrometeorological and Enclosure Techniques

Denmead (1991) has noted that the relationship between F and Q departs further from linearity when using enclosure methods than when using micrometeorological methods. The hypotheses to explain this are:

(i) The enclosure methods increase the amount of diffuse radiation in the canopy, so that maximum assimilation is obtained at lower PPFD (Denmead, 1991). This is supported by the finding that micrometeorological methods result in a lower initial slope, whereas photosynthetic capacity determined with the two methods is similar.

(ii) Enclosures usually isolate a plant, a few plants or a mini-ecosystem, allowing more PPFD onto the sides of the canopy than in natural conditions, so that more leaves become PPFD saturated in the enclosure than in nature, especially at low solar elevation.

(iii) Micrometeorological methods integrate CO_2 fluxes over larger areas than enclosures, and spatial integration could lead to more linear PPFD response curves (see XIV.A).

Example 1. Eucalyptus forest in Australia (Denmead, 1991). Figure 4 shows that the linear model gives the best fit to the micrometeorological data, while the hyperbolic model fits the enclosure measurements best, with $r^2 = 0{\cdot}96$ and $0{\cdot}94$, respectively. Denmead suggests that enclosures

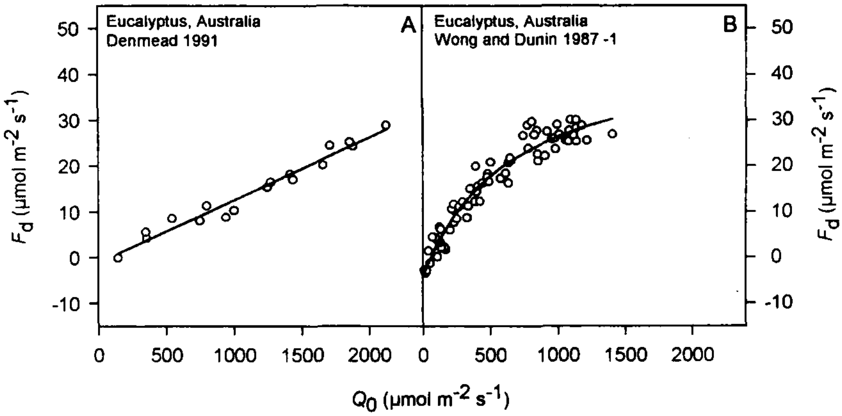

Fig. 4. Effect of CO_2 flux measurement technique: relationship between net CO_2 flux (F_d) over a Eucalyptus forest in Australia and incident quantum flux density (Q_0) measured with (A) a micrometeorological method and (B) an enclosure. The lines through the data points are the lines of best fit. Replotted from Denmead (1991) and Wong and Dunin (1987).

diffuse radiation, so that 90% of the assimilation rate is obtained at about half of the saturating PPFD. This is supported by the finding that at Q = 1800 μmol m^{-2} s^{-1}, the CO_2 flux is similar in the two cases (F_m = 24·1 for the micrometeorological method and 22.4 μmol CO_2 m^{-2} s^{-1} for the enclosure). This is the only linear PPFD response function that we found for forests that is unlikely to be an artefact (i.e. r^2 too low, or maximum Q not saturating).

Statistics on grouped data sets. We plotted all data sets on closed canopies, for all vegetation classes, distinguishing between data sets obtained using micrometeorological methods and sets obtained using enclosures (Fig. 5). The micrometeorological regression curve is closer to linearity than the enclosure one: the parameter D representing the departure from linearity is much higher for enclosures than for micrometeorological methods (0·20 versus 0·03). The initial slope α is higher for enclosure methods (0·060 versus 0·030), but photosynthetic capacities at 1800 μmol m^{-2} s^{-1}, F_m, are fairly similar (23·8 for micrometeorological versus 29·1 μmol m^{-2} s^{-1} for enclosures). Scatter of the data is lower for micrometeorological methods than for enclosures (r^2 = 0·70 versus 0·60), but this may not be significant as there are many more points for the first case. In fact, when we look closer at Figure 5B, a large number of points seem to be concentrated further from linearity than the line of best fit, saturating at PPFD approximately 1000 μmol m^{-2} s^{-1} at a value of CO_2 flux around 25 μmol m^{-2} s^{-1}. However, some points are way off this tendency, and this increases the variability and lowers D.

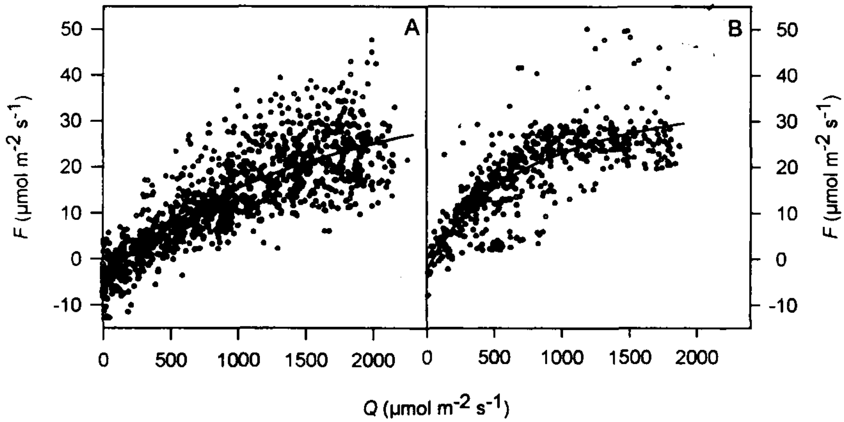

Fig. 5. Effect of CO_2 flux measurement technique: relationship between CO_2 flux (F) and quantum flux density (Q) for all data sets on closed canopies obtained (A) using micrometeorological methods and (B) using enclosures. The line through the data points are the lines of best fit.

In conclusion, both Example 1 and the statistics on grouped data sets show that micrometeorological methods lead to a relationship between CO_2 flux and PPFD closer to linearity than enclosures.

Artificial environments. When the environment is controlled, high PPFD can be obtained artificially, independently of other variables which are usually correlated in the field, e.g. high PPFD is usually associated with high temperature and high VPD, both of which tend to reduce CO_2 flux by either reducing photosynthetic rate or increasing respiration rate. The response of CO_2 flux to PPFD by these canopies is an indication of what the *potential* PPFD response of canopy photosynthetic rate would be.

Among the compiled data sets, several come from crops cultivated in artificial environments (Sheehy, 1977; Jones *et al.*, 1984; Baker *et al.*, 1990; Warren-Wilson *et al.*, 1992). All the curves obtained on forage grass species from Sheehy (1977) are curvilinear, but there is no indication of LAI in the paper. The relationship for a rice crop in an early stage (Baker *et al.*, 1990 -1) is also curvilinear. For the other data sets, LAI was above three and relationships are linear. Slopes of these linear relationships are fairly high (α = 0·048 mol mol^{-1} for Baker *et al.*, 1990, -2, 0·041 for Warren-Wilson *et al.*, 1992), i.e. of the same order of magnitude as the quantum efficiencies determined from rectangular hyperbolic fits, and similar to the effective quantum efficiency for a C3 leaf (α = 0·05). In natural environments, linear relationships are usually found with lower slopes (α around 0·02). These findings suggest that firstly the response of F to PPFD for closed canopies would be close to linearity with an initial slope similar to the quantum efficiency for a leaf, if it were not for other limitations that occur at high PPFD. In natural conditions, distance from linearity could result partly from the fact that high temperature and high VPD usually occur together, so that F is further limited by both high soil respiration rate and stomatal closure. Secondly linear response functions with a slope much smaller than the leaf quantum efficiencies may be artefacts (for instance because of large data scatter).

Because data sets obtained in artificial environments are obtained in conditions that may be far from the conditions encountered in the field, they are not comparable to the field data, and have not been included in the grouped data sets.

B. Respiration

As shown above, soil respiration rate or dark respiration rate can be measured and subtracted from daily CO_2 flux to give an estimate of canopy net or gross photosynthetic flux. The expected effects on the F/Q relationship are:

(i) an upward shift of the F/Q relationship;

(ii) an increase in r^2, because hysteresis between photosynthetic and respiration rates generates scatter in the data;

(iii) a relationship further from linearity if temperature, and therefore respiration rate, increased with increasing PPFD; but a relationship closer to linearity, if hysteresis between photosynthetic and respiration rates increased the data scatter on each side of the regression curve.

Example 2. Tundra in Alaska (Coyne and Kelley, 1975) (Figure 6).

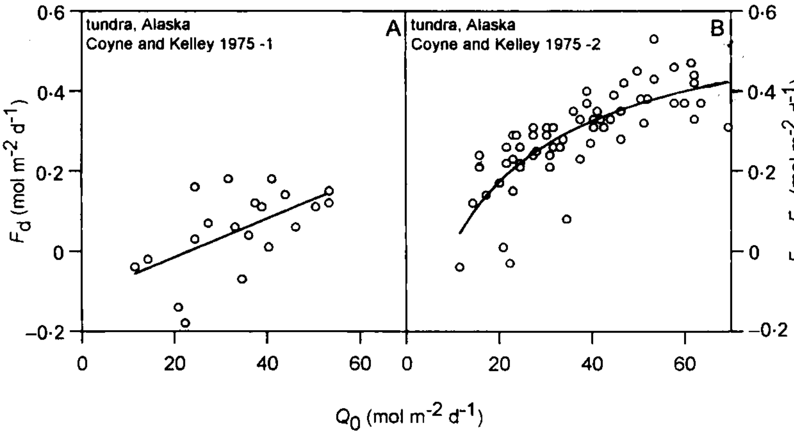

Fig. 6. Effect of dark respiration: relationship between daily CO_2 flux over tundra in Alaska, measured with a micrometeorological method and daily incident quantum flux density (Q_0). (A) net daytime ecosystem flux (F_d), (B) gross canopy photosynthesis, $A = F_d - F_n$ for daytime hours. The lines shown are the lines of best fit. Replotted from Coyne and Kelley (1975).

Daily net ecosystem flux, F_d, was measured, and dark respiration rate, F_n, was calculated from the CO_2 flux in the dark and an exponential relationship between respiration rate and temperature. Analysis of the resulting statistics indicates that subtracting F_n from F_d to get the "gross canopy photosynthesis" improves the statistical relationship (r^2 = 0·61 versus 0·34), transforms a linear best fit into a rectangular hyperbola, and increases the CO_2 flux (R = 0·11 versus 0·32, F_m = 0·44 versus 0·24 mol m^{-2} d^{-1}).

Statistics on grouped data sets (Figure 7). We plotted all data sets for closed canopies, for all vegetation classes, distinguishing between data sets in which F_d, the ecosystem CO_2 flux, and F_c, the canopy CO_2 flux, were reported. Analysis of the statistical parameters leads to the following conclusions.

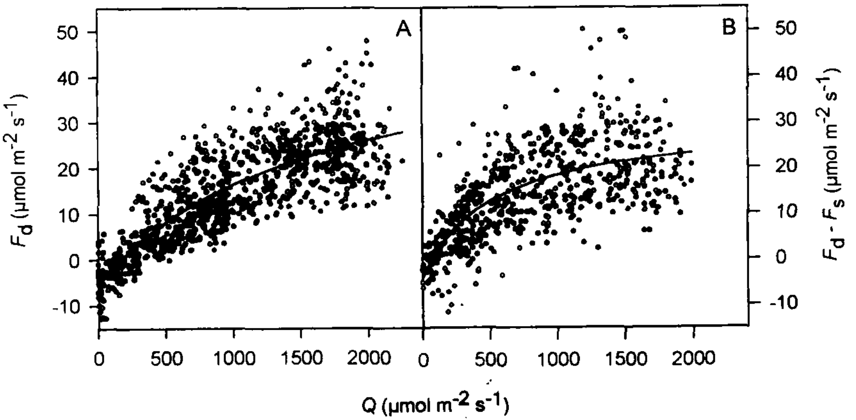

Fig. 7. Effect of soil respiration: relationship between CO_2 flux (F) and quantum flux density (Q) for all data sets on closed canopies. (A) net ecosystem flux (F_d), (B) above-ground flux or canopy flux, $F_c = F_d - F_s$ for daytime hours. The lines shown are the lines of best fit.

(i) The relationship between F_d and PPFD is less scattered than for F_c ($r^2 = 0{\cdot}70$ against 0·50). This contradicts the idea that F_d, being not wholly dependent on PPFD, would create errors in PPFD response curves, as seen in Example 2.

(ii) CO_2 flux at 1800 μmol m^{-2} s^{-1}, as well as CO_2 flux at 0 μmol m^{-2} s^{-1}, is not significantly different in the two cases (for F_d, F_m = 24·3 and R = 5·2; for F_c, F_m = 22·6, and R = 4·2 μmol m^{-2} s^{-1}).

(iii) The relationship between F_d and Q is closer to linearity than the relationship between F_c and Q (D = 0·03 versus 0·15), in agreement with Example 2.

In conclusion, subtracting respiration rate from the net ecosystem CO_2 flux has effects on the F/Q relationship that are difficult to analyse. In both Example 2 and the grouped data sets, subtracting respiration rates generates data sets further from linearity. In Example 2, the linearity of the response of net ecosystem flux to PPFD seems to be an artefact caused by large data scatter. For grouped data sets, however, there is more scatter in the F_c than in the F_d data. In Example 2, the effect of respiration is to lower both apparent dark respiration rate and photosynthetic capacity, while the differences are not significant for the grouped data sets. The reasons for these seemingly inconsistent findings could be that CO_2 flux measurements at night time and below the canopy are technically problematic and therefore not reliable, or that, for grouped data sets, made up of data sets that are not similar, comparisons are biased.

C. Vegetation Class

Looking through the data sets compiled, we note that there are more linear relationships between *F* and *Q* for crops than for forests. This may be for the following reasons.

(i) PPFD is the overwhelming factor controlling CO_2 assimilation in well-watered crops, the CO_2 flux of forests being also limited by other factors such as stomatal conductance, or much larger losses of CO_2 from the boles of the trees and particularly from soils at high temperature and hence at high PPFD.

(ii) Photosynthetic capacity of leaves is higher in general for herbaceous crops than for forest species (Larcher, 1975; Saugier, 1983), leading to higher photosynthetic capacity for crops than for forests and a relationship with PPFD closer to linearity.

(iii) The structure of grassland canopies is more erectophile, whereas canopies for most broadleaf forest species are more planophile: erectophile leaves enable the transmission of photons to the lower layers of the canopy, distributing them more evenly through the canopy, so that the canopy behaves more like a single leaf and saturates at lower PPFD.

Statistics on data sets grouped by vegetation class (Fig. 8). Because of the small number of data sets for certain vegetation classes (especially coniferous forests, C3 grasslands, C4 crops, see Table 2) the resulting statistics for these vegetation classes are less reliable than for the other vegetation classes. The data sets have, therefore, been grouped in broader vegetation classes of forests, grasslands and crops. Even so, the statistics on grasslands are less robust than for forests and crops, as there are fewer points in the data set despite the grouping of C3 and C4 vegetation classes ($n = 348$ for grassland versus 718 for forests and 560 for crops). Analysis of the regression parameters (Table 2.1) indicates that:

(i) Values of F_m decrease in the following order: crops 28·0, grasslands 23·8, forests 20·2 $\mu mol\ m^{-2}\ s^{-1}$. This agrees with our *a priori* idea that forests have higher respiration rates than stands of herbaceous vegetation because of higher respiring biomass, and that herbaceous crops have higher photosynthetic rates than forests and natural grasslands. However, this idea is not supported by the values of *R*, which are similar for forests and crops, and higher for natural grasslands.

(ii) Forests have a more curvilinear relationship between CO_2 flux and PPFD than grasslands (departure of relationship from linearity, $D = 0{\cdot}08$ and 0·02, respectively), which is in accordance with our *a priori* knowledge on the differences between forests and grasslands, but the relationship for crops is as curvilinear as for forests ($D = 0{\cdot}10$), which is surprising.

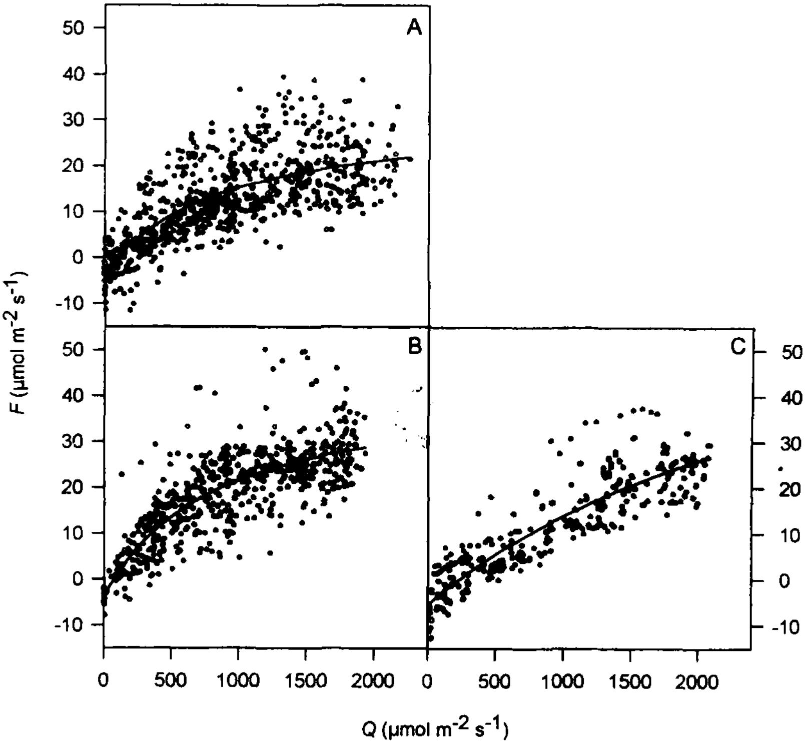

Fig. 8. Effect of vegetation class: relationship between CO_2 flux (F) and quantum flux density (Q) for all data sets on closed canopies of (A) forests, (B) crops, and (C) grasslands. The lines shown are the lines of best fit.

(iii) Grasslands have a relatively low initial slope: $\alpha = 0{\cdot}025$, while forests and crops have similar apparent quantum yields, closer to $0{\cdot}05$ mol-mol^{-1}.

In conclusion, forests and grasslands have similar photosynthetic capacities, but the relationship between CO_2 flux and PPFD is further from linearity for forests than for grasslands. Crops have a higher photosynthetic capacity than both natural vegetation classes, but do not seem to have a more linear relationship with PPFD than forests, in contradiction with the individual examples.

Statistics on data sets grouped by vegetation class and technique used to measure CO_2 flux (Fig. 9). Because the technique used to measure CO_2 flux has an effect on the shape of the F/Q relationship (see Section A), and because the CO_2 fluxes of forests have mostly been studied using micrometeorological methods, while the fluxes of crops and grasslands have more often been studied using enclosures, the statistics on data sets

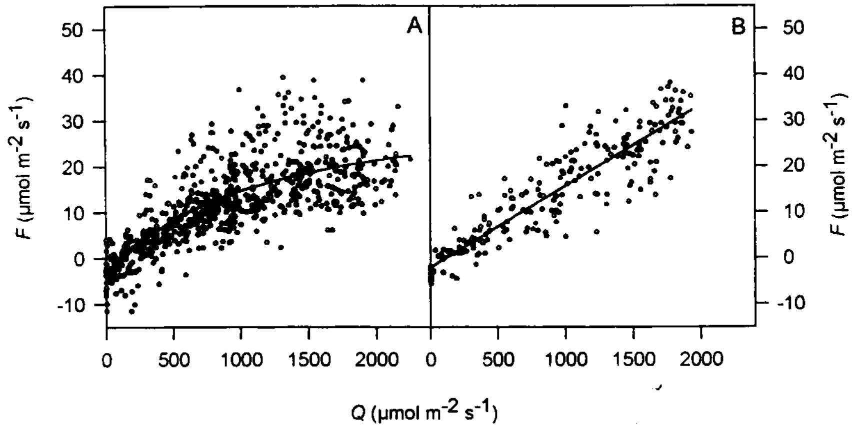

Fig. 9. Effect of vegetation type and CO_2 flux measurement technique: relationship between CO_2 flux (F) and quantum flux density (Q) for all data sets on closed canopies obtained with micrometeorological methods for (A) forests, (B) crops. The lines shown are the lines of best fit.

grouped by vegetation class could be biased. Hence, to investigate F/Q relationship independently of method of measurement, we have included only data sets obtained with micrometeorological methods and compared forests and crops. The resulting relationships are very different, with a curvilinear best fit for forests ($D = 0{\cdot}06$) and a linear best fit for crops. The apparent quantum yield is higher for forests than for crops (0·035 for forests, 0·023 mol mol^{-1} for crops). The intercepts on the y axis are quite similar (3·9 for forests, 3·2 μmol m^{-2} s^{-1} for crops): but despite forests having a higher biomass and more soil organic matter dark respiration rates are similar. However, an effect of nutrient fertilization on autotrophic and heterotrophic respiration in crops could compensate for the effect of higher carbon content of the forests. The r^2 is much higher for crops (0·84) than for forests (0.61), indicating that the forests may have been more limited than the crops by other variables besides PPFD.

In conclusion, analysing data sets obtained with micrometeorological methods only has allowed us to distinguish between the F/Q relationships of crops and forests: the CO_2 fluxes of crops have a linear relationship with PPFD, while the CO_2 fluxes of forests have a curvilinear relationship with PPFD. There are too few data sets on grasslands to analyse their behaviour in this way.

D. Other Variables

In this section we address other identified sources of variation influencing net ecosystem flux in natural conditions. Since F is largely the algebraic sum of photosynthetic and respiratory fluxes (equation 1), it is affected by all the variables affecting the individual processes. These variables have not been studied in detail in this review: whenever possible an example is given but no statistical analyses on grouped data sets have been made.

1. Seasonality

There are two classes of seasonal effects on F. Changes in leaf area index affect the amount of photons absorbed by the canopy, and the phenology of growth affects canopy CO_2 flux independently of LAI. Leaf area index determines firstly the area of leaves available to absorb photons, and secondly the canopy structure (i.e. arrangement of the canopy leaves), both of which determine radiation reaching the soil, multiple scattering within the canopy and the PPFD absorbed.

(a) Effect of LAI on absorption of PPFD. As LAI increases during a growing season, the fraction of incident PPFD absorbed by the canopy increases in a hyperbolic manner. The relationship between canopy fluxes (measured throughout a season with changing LAI) and absorbed PPFD is closer to linearity than the relationship between F and incident PPFD.

Example 3. Salt marsh in New York state, USA (Bartlett *et al.*, 1990). F was measured at intervals of three weeks over a whole growing season, together with PPFD transmitted by the canopy (Q_t) and incident PPFD (Q_0). The relationship between F and intercepted PPFD was linear, whereas the relationship between F and incident PPFD was curvilinear: e' defined as the ratio F/Q_0 decreased linearly with Q_0.

(b) Effect of canopy structure on CO_2 flux. Example 4. Baldocchi (1994) compared CO_2 fluxes measured over a closed canopy C3 (wheat) crop and an open canopy C4 (*corn*) crop, in Oregon, USA, on the same site and with similar techniques. Plotting F versus Q_{abs} led to apparent quantum yields of 0·026 for wheat and 0·020 for corn, in contradiction with other studies in which photosynthetic efficiency was significantly higher in C4 crops than in C3 crops. Baldocchi hypothesized that there was a bias because of the effect of LAI on radiative transfer and photosynthetic rate, which could be normalized by plotting F/L against Q_{abs}. The resulting slope of the linear relationship between CO_2 flux per unit leaf area and PPFD was 17% higher for the corn than for the wheat, as expected.

LAI also affects the ratio between canopy assimilation and respiration rates, because canopy closure leads to lower soil temperatures, and therefore to lower soil and root respiration rates. This effect can be taken into account by modelling respiration as a function of temperature.

(c) Phenological effects other than variations in LAI. Example 5. Wheat in

Australia (Puckridge and Ratkowski, 1971 −1, −3, −5, −7 and −10). *F* and *Q* were measured at different times throughout the season. As LAI increased steadily (0·8, 0·9, 1·2, 1·4, 1·7), photosynthetic capacity and departure of the relationship from linearity changed in an unpredictable way (F_m = 9·6, 16·0, 13·4, 14·4, 21·2 μmol $m^{-2} s^{-1}$, respectively, and D = 0·09, 0·40, 0·00, 0·22, 0·48, respectively).

In conclusion, to compare CO_2 fluxes measured at different times of year, it is better to relate *F* to absorbed PPFD rather than to incident PPFD. In order to compare CO_2 fluxes across different vegetation classes having different LAI, or CO_2 fluxes over the same vegetation class in different phenological stages having different LAI, it may be helpful to normalize *F* by dividing it by the LAI, i.e. express *F* on a leaf area basis. For simplicity this study has concentrated on closed canopies.

2. *Nutrient Availability*

Carbon assimilation rates of leaf and canopy depend very closely on nutrient availability. Rubisco accounts for a significant fraction of the nitrogen content of a leaf, and thus the Rubisco content of leaves is very closely related to leaf nitrogen content. Schulze *et al.* (1994) have related canopy CO_2 assimilation rate to leaf nitrogen content in an indirect way: they established linear relationships between maximum stomatal conductance and leaf nitrogen concentration, between canopy conductance and stomatal conductance, and between canopy photosynthetic rate and canopy stomatal conductance, all relationships having relatively high linear determination coefficients. Although nutrient availability is almost certainly one of the most important variables determining canopy photosynthetic rate, we have not been able to illustrate its role because of lack of suitable measured data.

3. *Water Availability*

Example 6. Tallgrass prairie in kansas, USA (Kim and Verma, 1990). *F/Q* relationships were given for three ranges of VPD, and for non-limiting and limiting soil water. When soil water was non-limiting, F_m was 25.5 μmol $m^{-2} s^{-1}$ for VPD of 0 to 1·5 kPa, and 20·9 for VPD of 1·5 to 3 kPa; when soil water was limiting, F_m was 21·1 and 7·4, respectively. For the low ranges of VPD, with limiting soil water and VPD between 3–4·5 kPa, there was strong hysteresis in the *F/Q* relationship, some *F* values in high PPFD even being negative. Similar results were found by Price and Black (1990) with Douglas-fir. Jarvis (1994) described negative values of *F* with Sitka spruce in high PPFD and VPD, even when soil water was non-limiting.

In conclusion, soil water shortage and high VPD can reduce canopy photosynthetic rate to almost zero, particularly when acting together. An additional effect of VPD is to increase scatter in the data, because of hysteresis generated by the daily course of VPD.

In the grouped data sets, we have eliminated data sets on canopies limited by water shortage in the soil, whenever stated by the authors. However, we have not been able to investigate a possible strong VPD effect in the variability of the *F*/*Q* relationships, as most studies have not segregated their data into VPD classes.

4. *Temperature*

Besides the effects of temperature on both autotrophic and heterotrophic respiration, air temperature can affect the CO_2 flux over an ecosystem through effects on canopy photosynthesis, and particularly photorespiration (e.g. Long, 1991). Not many studies report the effect of temperature on canopy photosynthesis, and when reported, the effects are not significant. For example, Mordacq *et al.* (1991) report no temperature effect on the response of canopy CO_2 flux of chestnut coppice to PPFD, with mean air temperatures ranging from 19 to 30 °C.

XIII. MEAN STATISTICS, RESIDUALS AND BOUNDARY VALUE ANALYSIS FOR THE COMPLETE DATA SET

Figure 10 shows the *F*/*Q* relationships for the *complete* data set, i.e. all data sets on closed canopies satisfying the conditions for grouping data sets (see above). The resulting best fit is curvilinear:

$$F = \frac{0{\cdot}044Q \times 43{\cdot}35}{0{\cdot}044Q + 43{\cdot}35} - 4{\cdot}29 \qquad (n = 1362, r^2 = 0{\cdot}57) \qquad (29)$$

The residual variability can be explained in two alternative ways: either the *mean* relationship represents the response of CO_2 fluxes over canopies to PPFD, variation around the mean being attributable to experimental errors and natural variability amongst study sites, or the *upper envelope* of the points represent the response of CO_2 flux in *optimal* conditions, all the points below this envelope being the result of reductions of net ecosystem exchange by various stresses such as shortage of water or nutrients, and high temperature and VPD.

The variability in the mean *F*/*Q* relationship is strong, but not excessive, with a r^2 of nearly 0·6. Visual analysis of the figure shows that maximum *F* lies between 10 and 40 $\mu mol\,m^{-2}\,s^{-1}$, whereas maximum leaf photosynthetic rate per unit leaf area in optimum temperature and low VDP conditions generally lies between 2 and 25 $\mu mol\,m^{-2}\,s^{-1}$ in tree species

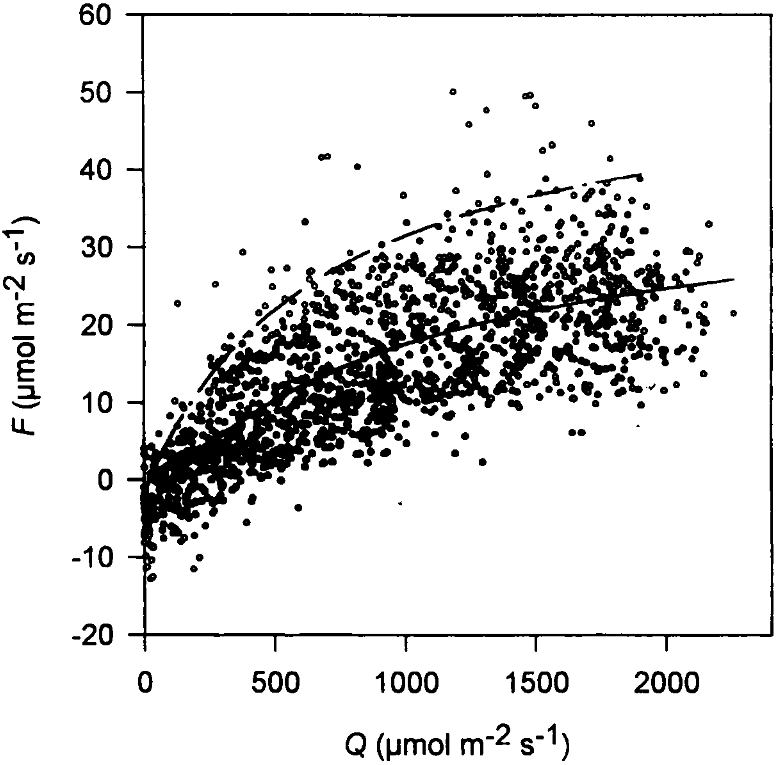

Fig. 10. Relationship between CO_2 flux (F) and quantum flux density (Q) for all data sets on closed canopies. The solid line is the line of best fit through all the data, the dotted line is the line of best fit through the 10% upper boundary values.

(Ceulemans and Saugier, 1991). We analysed the residuals of the rectangular hyperbolic fit through the complete data set. If the variability results from random error around a mean relationship, distribution of residuals would be Gaussian.

Figure 11 shows that the distribution of residuals around the mean relationship is indeed close to a Gaussian distribution. As we have shown above, taking into account factors such as the technique used to measure F or the vegetation class could reduce the variability of this relationship (i.e. increase r^2). Some variables that have not usually been measured, such as nutrient or water availability, could reduce the variability still further.

The upper envelope of the complete data set shown in Figure 10 is:

$$F = \frac{0{\cdot}081Q \times 55.78}{0{\cdot}081Q + 55.78} - 1{\cdot}62 \qquad (r^2 = 0{\cdot}57) \tag{30}$$

The initial slope of this envelope curve ($0{\cdot}08\,\mu\text{mol}\,\mu\text{mol}^{-1}$) is somewhat

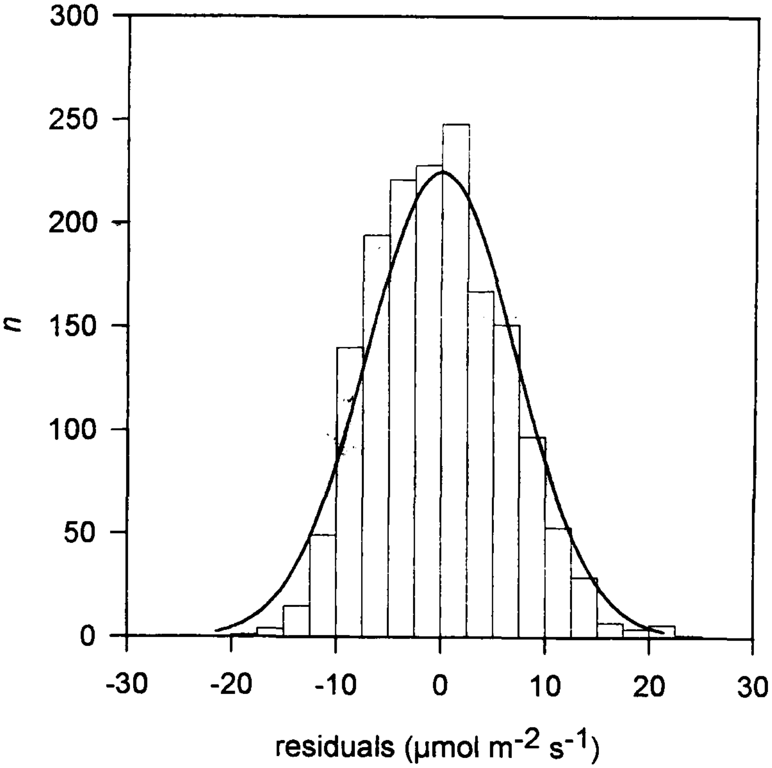

Fig. 11. The frequency of residuals of the rectangular hyperbola fitted through all data sets on closed canopies in figure 10. The line is a Gaussian relationship fitted through the histogram.

higher than typical values for the quantum yield of a C3 leaf (i.e. 0·05) and, therefore, it is not altogether realistic (an apparent quantum requirement of 12). Departure from linearity is high (D = 0·27) which could be the result of mixing data sets derived from micrometeorological and enclosure methods: at low F, the upper envelope is dominated by enclosure measurements, while at high F it is dominated by micrometeorological measurements.

In conclusion, the mean relationship for all data sets is an acceptable predictor of the relationship between CO_2 flux and PPFD, with relatively limited and randomly distributed variation around it. This single relationship could be very useful in modelling of net ecosystem productivity at regional to global scale, where information on vegetation-related parameters and reliable climate data bases are usually lacking. If we suppose that autotrophic and heterotrophic respiration affect only the value of the intercept of this relationship (which would be the case if temperature were not correlated with solar radiation), this relationship could also be adapted to the estimation of gross primary productivity at regional to global scale.

XIV. PERSPECTIVES FOR CO_2 FLUX MEASUREMENTS

A. Scaling up in Space: Plane Mounted Eddy Flux Sensors

The general relationships given above result from data obtained over supposedly homogeneous vegetation, covering areas from a scale of a few metres (enclosures) to a few tens to hundreds of metres (ground-based, eddy-flux measurements). In the context of upscaling tools such as remote sensing, it is preferable to use measurements that integrate several vegetation classes over scales of tens to hundreds of kilometres. Aircraft-mounted eddy covariance instruments, which have these characteristics, are starting to be widely used, particularly in the context of international campaigns such as FIFE, HAPEX-SAHEL and BOREAS. Large scale CO_2 fluxes can be used to do "biology from space". For example, aircraft-based CO_2 fluxes over tallgrass prairie in Kansas, USA, were found to correlate well with satellite-derived vegetation indices over the same sites, at least on a short time scale. No linear relationship was found, however, on a seasonal basis during the FIFE experiment (Cihlar *et al.*, 1992).

We have also included two sets of measurements with aircraft-mounted instruments, which we use to investigate the effects of scaling up in space, even though there were no ground-based measurements on the same sites for comparison. The two examples are wheat fields in Canada (Desjardins, 1991), and mixed forest stands of conifers and broadleaves in Canada (Desjardins *et al.*, 1985). In both cases, the best fit of the F/Q relationship is linear, with $r^2 = 0{\cdot}72$ and 0·56, respectively. Apparent quantum yields are low ($\alpha = 0{\cdot}017$ for the wheat fields, 0·014 for the mixed forest).

In conclusion, CO_2 fluxes measured over large, heterogeneous areas seem to be linearly related to PPFD. With respect to scaling up, we can alternatively regard the differences between F/Q relationships obtained with enclosures, ground-based micrometeorological measurements and aircraft-based flux measurements as a result of increase in spatial scale. We would then conclude that:

(i) The best fit becomes closer to linearity as the scale increases: it is linear for aircraft-based measurements, and closer to linearity for ground-based micrometeorological measurements ($D = 0{\cdot}03$) than for enclosures ($D = 0{\cdot}20$).

(ii) The apparent quantum yield decreases as the scale increases: $\alpha = 0{\cdot}06$ for enclosures, 0·03 for ground-based micrometeorological measurements and around 0·015 for aircraft-based measurements.

However, scatter in the data increases at larger scales, and this could also explain points (i) and (ii).

B. Scaling up in Time: Instantaneous versus Daily Integrated Measurements

Models of canopy photosynthesis have been used to estimate daily integrated canopy photosynthetic rate and daily integrated absorbed PPFD. The resulting curves are usually closer to linearity than instantaneous curves, but not fully linear (see for example Wang *et al.*, 1992, who used the BIOMASS model to simulate a hypothetical *Pinus radiata* stand with various LAIs over an eight-year period).

Example 7. Winter wheat in Kansas, USA (instantaneous data reported by Wall and Kanemasu, 1990, daily integrals reported by Wall *et al.*, 1990) (Figure 12). The instantaneous measurements resulted in a curvilinear relationship (D = 0·11), while the daily means resulted in a best fit to the linear model (see also Fig. 6). Even though both r^2 are low (0·59 and 0·58), we note that scaling up in time—in this case averaging instantaneous measurements over a day—linearized the PPFD response curve, and decreased the apparent quantum yield (α = 0·027 mol mol^{-1} for the daily data set, 0·065 for the instantaneous data set).

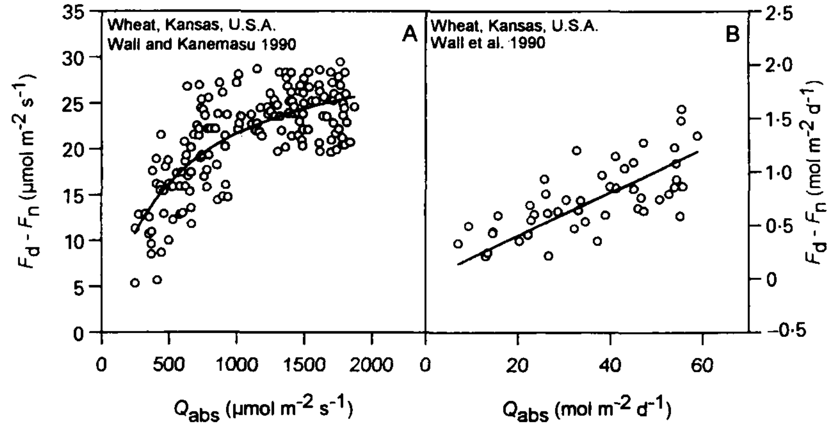

Fig. 12. Effect of scaling up in time: relationship between canopy gross photosynthesis $A = F_d - F_n$ of winter wheat in Kansas, USA measured with enclosures and absorbed quantum flux density (Q_{abs}), (A) instantaneous data, (B) data integrated over daytime hours. The lines shown are the lines of best fit. Replotted from Wall and Kanemasu (1990) and Wall *et al.* (1990).

Statistics on grouped data sets. The instantaneous and daily integrated data sets have been plotted separately. The daily data sets are from CO_2

fluxes measured throughout a growing season with a changing LAI, and plotted against absorbed or intercepted radiation. These data sets are fairly rare and comprise data for herbaceous crops only: winter wheat (Wall *et al.*, 1990) and wheat (Whitfield, 1990). The resulting best fit (Fig. 13) is linear:

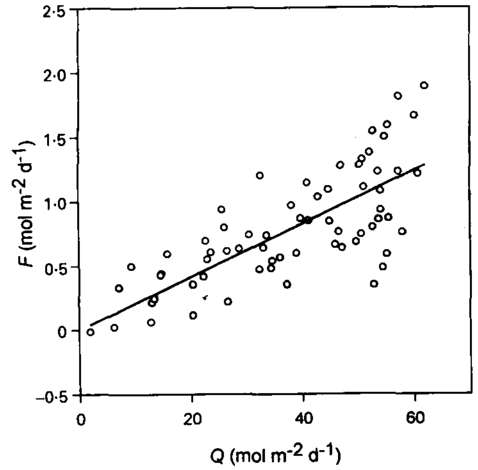

Fig. 13. Effect of scaling up in time: relationship between CO_2 flux integrated over daytime hours (F) and quantum flux density (Q) for all data sets on closed canopies (Wall *et al.*, 1990; Whitfield, 1990). The line shown is the line of best fit with $F = 0{\cdot}020\ Q$ ($n = 66$, $r^2 = 0{\cdot}54$).

The quantum yield for daily data sets is about half the apparent quantum yield for instantaneous data sets ($\alpha = 0{\cdot}020$ versus 0·044 for the complete, instantaneous data set, Figure 10).

In conclusion, scaling up in time tends to linearize the relationship between CO_2 flux and PPFD, and to decrease dramatically the apparent quantum yield. This is supported both by the example presented and by statistics on grouped data sets. A general, linear relationship can be derived between daily integrated F and Q, but it may not be representative, because of the small number of points and great scatter, and because all the vegetation classes are not represented.

C. CO_2 Enrichment

In the context of modelling vegetation responses to global change, it is also essential to assess the response of canopy gas exchange to increase in atmospheric CO_2. Some studies have been done using enclosures to enrich the atmosphere in CO_2 and simultaneously to measure canopy gas exchange (see Appendix 1).

Eucalyptus trees in Australia (Wong and Dunin, 1987) and herbaceous crops, e.g. soybeans in Florida, USA in controlled environment (Jones *et al.*, 1984) have been exposed to elevated CO_2 concentration. In both cases the apparent quantum yield was nearly doubled in doubled atmospheric concentration of CO_2 ($\alpha = 0{\cdot}032$ in normal CO_2, 0·050 in doubled CO_2 for Eucalyptus and $\alpha = 0{\cdot}049$ in normal CO_2, 0·102 in doubled CO_2 for soybean).

These experiments were done, however, on a very small scale with enclosures. It would be preferable, in the context of modelling effects of climate change, to be able to do such experiments on a large spatial scale, and over extended periods of time with fully acclimated trees, grasslands and crops.

XV. CONCLUSIONS

A. Specific Conclusions

1. *Effects of Methodology*

(i) Micrometeorological methods seem better adapted than enclosures to obtain relationships useful for "top down" modelling, because they integrate over a larger scale and do not disturb the environment within the canopy. Micrometeorological methods result in *F/Q* relationships closer to linearity than enclosure methods. Apparent quantum yields obtained with these methods were of the order of 0·02–0·03 mol mol^{-1}, and were significantly lower than the effective quantum yield of leaves of about 0·05 mol mol^{-1}.

(ii) Subtracting respiration rates from net ecosystem CO_2 fluxes to retrieve canopy CO_2 flux does not seem to improve relationships between CO_2 flux and PPFD: this could be a result of the difficulties in measuring accurately soil CO_2 flux or CO_2 flux in the dark. We would recommend that both net ecosystem flux and canopy flux be explicitly published, whenever soil or night-time CO_2 flux were measured.

(iii) The best fit through the daily data sets ($n = 66$) is linear, with an apparent quantum yield of $\alpha = 0{\cdot}020$, and photosynthetic capacity of 1·58 mol m^{-2} d^{-1} at $Q = 80$ mol m^{-2} d^{-1}. The best fits through the few data sets obtained with aircraft-mounted eddy-correlation sensors are also linear. We suspect that scaling up in time and space tends to linearize the *F/Q* relationship, but there are too few data sets, and scatter in the data is too high, to draw a definite conclusion. As statistics on daily integrated curves would be very useful for large-scale modelling, we recommend that more data sets be presented this way, in particular in the case of long-term experiments on forests.

2. *Effects of Vegetation Class*

We have only been able to study the differences between broad vegetation classes (crops, grassland and forests), as there were not enough data sets to segregate them into more detailed classes. When both were measured with micrometeorological methods, crops are found to differ significantly from forests. The *F*/*Q* relationship is linear for crops and curvilinear for forests; the apparent quantum yield is 0·035 for forests and 0·023 for crops; the photosynthetic capacity is lower for forests than for crops (F_m = 20·2 for forest and 37·2 μmol m^{-2} s^{-1} for crops), and there is more scatter in the data for forests.

3. *Effects of Environment and Season*

The effects of water, nutrient availability and phenology were assessed qualitatively and show that CO_2 fluxes are very sensitive to these variables. Further statistical studies could be done using the methodology described in this paper, e.g. grouping data sets by classes of VPD, soil water content, leaf nitrogen content and phenological stage, provided that relevant information is given by authors. We would recommend that as many data as possible be explicitly published to increase understanding of canopy and stand physiology.

B. General Conclusions

The best fit through all the instantaneous data sets is a rectangular hyperbola. The apparent quantum yield (α = 0·044) is close to the value for leaves of C3 plants of 0·05 mol mol^{-1}. Photosynthetic capacity at 1800 μmol m^{-2} s^{-1} is F_m = 23·7 μmol m^{-2} s^{-1}. The apparent dark respiration rate is 4·3 μmol m^{-2} s^{-1}, i.e. approximately 15% of photosynthetic capacity of the ecosystem, which is higher than what is found at the leaf scale (approximately 10%, e.g. Ceulemans and Saugier, 1991).

The data sets were very heterogeneous, with respect to vegetation class, environmental conditions, and methodology. This caused problems in trying to group them and analyse the grouped data sets: "CO_2 flux", *F*, represents either net ecosystem flux, above-ground flux or calculated canopy photosynthetic rate; "photosynthetic photon flux density", *Q*, is either absorbed, intercepted or incident PPFD, and was derived from PAR, solar radiation or net radiation. Besides, the techniques used to measure CO_2 flux and radiation, and the choice of presentation of data (e.g. instantaneous data, daily means or means per radiation class) vary greatly amongst authors. The general relationships obtained are likely to be biased by the data sets with the largest number of data points; this could be improved by using curve fitting weighted by the number of data points in each data set. Similarly, the comparisons of data sets grouped by factor could be biased because the different groups are formed of data sets that are not similar; this could be improved by careful sampling of data sets, so that in each group there are only strictly comparable data sets.

As a consequence, the variability within the grouped data sets is relatively important. For the complete instantaneous data set, the standard deviation of the residuals is $7{\cdot}2\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$, which leads to error in the estimation of F_m, calculated as the ratio of the standard deviation of the residuals to F_m, of 30%. Analysis of the residuals of the best fit of the complete instantaneous data set suggests that this variability is the result of randomly distributed error around the mean. The variability could be reduced by:

(i) reducing the effects of methodology-related errors by better standardizing data sets;
(ii) identifying data sets in optimal conditions, e.g. without constraints of water or nutrients;
(iii) characterizing the potential of each vegetation class and phenological stage;
(iv) quantifying the effects of water, nutrient and other stresses.

We recommend that CO_2 flux measurements are published whenever possible with the following supplementary information: leaf area index, radiation absorption efficiency, nitrogen content of leaves, and the occurrence of various stresses during measurements (e.g. water stress, high VPD).

The relationships obtained in this study can be used for doing "biology from space", either by applying them to the estimation of net ecosystem productivity, or by adapting them to the estimation of gross primary productivity, by making some assumptions about respiration of the total system.

The relationship through all the instantaneous data sets is far from linear and cannot reasonably be simplified to a linear relationship. Indeed, linear regression through this data set results in $\alpha = 0{\cdot}015\,\mathrm{mol\,mol^{-1}}$ ($r^2 = 0{\cdot}51$), which is unrealistically low. The relationship between daily integrated CO_2 flux and PPFD is linear, but is probably less reliable because it has been obtained from a limited data set and results in a slope of $0{\cdot}020\,\mathrm{mol\,mol^{-1}}$ ($r^2 = 0{\cdot}54$). An alternative way forward is to run the hyperbolic model with actual hourly solar radiation for some sites, and to derive a relationship between CO_2 flux and PPFD at a longer time scale, e.g. daily or monthly.

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APPENDIX 1: DESCRIPTION OF DATA SETS COLLECTED AND DIGITIZED, CLASSIFIED BY VEGETATION KIND, AND IN EACH CLASS BY ALPHABETICAL ORDER OF AUTHORS

column 1: Kind of vegetation, characterized by English name of species (when monospecific) or ecosystem type (when composed of several species: e.g. rainforest).

column 2: Location, characterized by the country, and sometimes the region.

column 3: Indication of phenological stage or season when available: early growth ("↑") / peak growth ("→") / senescence ("↓") (usually characterized by the seasonal course of leaf area index), or "spring/summer/autumn/winter", or day of year, and year of measurement.

column 4: Leaf area index (L) of the period of measurement (in $m^2 m^{-2}$).

column 5: Techniques of measurement of CO_2 flux: micrometeorological methods: energy balance ("en. balance"), aerodynamic ("gradient"), eddy correlation ("eddy corr"); canopy enclosure techniques ("enclosure"). When two sets of eddy correlation instruments have been used, one above and one below the canopy, this is indicated in this column ("above-below"). For enclosure measurements, there is usually no indication in the original article of which portion of the ecosystem was enclosed. Otherwise, the part of the ecosystem enclosed is mentioned in this column ("ecosystem/above-ground").

column 6: Measure of radiation reported in the original paper: photosynthetically active radiation or photosynthetic photon flux density (Q), global radiation ("S_g"), or net radiation ("S_n"). Radiation is either incident (subscript: "0"), intercepted by the canopy (subscript: "int") or absorbed by the canopy (subscript: "abs").

column 7: Respiration measurement mode: whether soil respiration ("F_s") and/or night time respiration ("F_n") were measured, and whether these measurements have already been subtracted from the reported CO_2 flux measurements ("subt.", or "not subt."). When CO_2 storage in the canopy is accounted for, "ΔS_c" is mentioned in this column.

column 8: Time-step of the CO_2 flux measurements, and duration of the experiment. Several cases can occur: instantaneous, raw measurements are reported; instantaneous measurements are averaged over periods varying from 15 minutes to one week; data sets that do not report raw measurements, but report mean CO_2 fluxes in classes of solar radiation ("means/classes").

column 9: Treatment, conditions; this column is used to indicate the different treatment or conditions, between two or more data sets reported in the same article. ppmv $\equiv$ μmol mol^{-1}.

column 10: Identification code of the data sets: names of authors, year, curve number.

Appendix 1—*cont.*

Vegetation class	Location	Phenology date	L	Flux measurements	Radiation measurements	Respiration measurements	Time-step, duration	Treatment, conditions	Reference
broadleaf forests									
Rainforest	Costa Rica	Nov 14 67	?	en. balance	Q_0	?	½ hour 1 day		Allen & Lemon 1976
Mixed oak, hickory	Tennessee, US	summer 92	≈5	eddy corr.	Q_0	F_s (subt.)	½ hour 1 month		Baldocchi & Harley (unpublished data)
Mixed oak, hickory	Tennessee, US	Jul 24–Aug 10 84	4·9	eddy corr. (above-below)	Q_0	F_s (subt.)	½ hour		Baldocchi *et al.* 1987
Deciduous forest	?	Sep 3 86	?	?	$S_{n,0}$	?	½ hour 1 day		den Hartog *et al.* 1987
Eucalyptus	New S. Wales Australia	Nov 16–Mar 16	3·3	gradient	$S_{g,0}$	no	?		Denmead 1991
Rainforest	Manaus, Brazil	Apr 22–May 8 87	≈7	eddy corr.	$S_{g,0}$	F_s (not subt.) ΔS_c	1 hour		Fan *et al.* 1990
Rainforest	Rondonia, Brazil	Sep 92	?	eddy corr.	$S_{g,0}$	F_s (subt.)	?		Grace (unpublished data)
Evergreen beech	New Zealand	Jul (winter) 89	5	eddy corr.	Q_0	F_n (not subt.) ΔS_c	½ hour several days		Hollinger *et al.* 1994–1
Evergreen beech	New Zealand	Sep (early spring) 89	5	eddy corr.	Q_0	F_n (not subt.) ΔS_c	½ hour several days		Hollinger *et al.* 1994–2
Evergreen beech	New Zealand	Dec (late spring) 89	6.8	eddy corr.	Q_0	F_n (not subt.) ΔS_c	½ hour several days		Hollinger *et al.* 1994–3
Evergreen beech	New Zealand	Jan (summer) 90	7.0	eddy corr.	Q_0	F_n (not subt.) ΔS_c	½ hour several days		Hollinger *et al.* 1994–4
Evergreen beech	New Zealand	Mar (late summer) 90	6.3	eddy corr.	Q_0	F_n (not subt.) ΔS_c	½ hour several days		Hollinger *et al.* 1994–5
Evergreen beech	New Zealand	Jul 89–Mar 90	6.3	eddy corr.	Q_0	F_n (not subt.) ΔS_c	several days 1 season		Hollinger *et al.* 1994–6
Evergreen beech	New Zealand	Feb. 18–19 89	≈5	eddy corr.	Q_0	no	1 hour		Kelliher *et al.* 1989
Hevea (young)	Abidjan, Ivory Coast	Apr–May	?	en. balance	$S_{g,0}$	F_s (not subt.)	means/classes, several days	no water stress	Monteny 1989–1
Hevea (young)	Abidjan, Ivory Coast	Apr–May	?	en. balance	$S_{g,0}$	F_s (not subt.)	means/classes, several days	water stress	Monteny 1989–2

Hevea (old)	Abidjan, Ivory Coast	Dec–Jan	3·5–4·5	en. balance	$S_{g,0}$	F_s (not subt.)	means/classes, several days	no water stress	Monteny 1989–3
Chestnut coppice	Paris, France	Aug 21–Sep 9 84	≈ 4	enclosure	Q_0	F_s (subt.)	4 days		Mordacq *et al.* 1991
Macchia	Italy	Nov 11–14 89	4·5	eddy corr.	Q_0	no	1 hour 3 days		Valentini *et al.* 1991
Mixed oak, hickory	Tennessee, US	Aug 2–Aug 9	4·9	eddy corr.	$S_{g,0}$	no	?	VPD 0–0·6 kPa	Verma *et al.* 1986–1
Mixed oak, hickory	Tennessee, US	Aug 2–Aug 9	4·9	eddy corr.	$S_{g,0}$	no	?	VPD 0·6–1·2 kPa	Verma *et al.* 1986–2
Mixed oak, hickory	Tennessee, US	Aug 2–Aug 9	4·9	eddy corr.	$S_{g,0}$	no	?	VPD 1·2–1·8 kPa	Verma *et al.* 1986–3
Mixed deciduous forest	Massachussets, US	Sep 18–27 81	3·5	eddy corr.	Q_0	F_n, F_s (not subt.) ΔS_c	?	afternoon	Wofsy *et al.* 1993–1
Mixed deciduous forest	Massachussets, US	Sep 18–27 81	3·5	eddy corr.	Q_0	F_n, F_s (not subt.) ΔS_c	?	morning	Wofsy *et al.* 1993–2
Eucalyptus	New S. Wales Australia	Mar 12–Apr 4 84	3·3	enclosure	$S_{g,0}$	?	?	ambient CO_2	Wong & Dunin 1987–1
Eucalyptus	New S. Wales Australia	Mar 12–Apr 4 84	3·3	enclosure	$S_{g,0}$	?	?	double CO_2	Wong & Dunin 1987–2
					conifer forests				
Maritime pine	Les Landes, France	summer 91 or 92	2·5–3·5	eddy corr.	Q_0	F_n (not subt.)	½ hour ? several days ?	no water stress?	Brunet *et al.* 1992
Sitka spruce	Fetteresso, Scotland	summer 70	?	en. balance	Q_0	F_s (enclosure) (not subt.)	means/classes	VPD 0–0·2 kPa	Jarvis 1994–1
Sitka spruce	Fetteresso, Scotland	summer 70	?	en. balance	Q_0	F_s (enclosure) (not subt.)	means/classes	VPD 0.2–0·6 kPa	Jarvis 1994–2
Sitka spruce	Fetteresso, Scotland	summer 70	?	en. balance	Q_0	F_s (enclosure) (not subt.)	means/classes	VPD 0.6–0·8 kPa	Jarvis 1994–3
Sitka spruce	Fetteresso, Scotland	summer 70	?	en. balance	Q_0	F_s (enclosure) (not subt.)	means/classes	VPD 0.8–1 kPa	Jarvis 1994–4
Sitka spruce	Fetteresso, Scotland	summer 70	?	en. balance	Q_0	F_s (enclosure) (not subt.)	means/classes	VPD 1–2 kPa	Jarvis 1994–5
Douglas-fir	British Columbia, Canada	Jul–Aug 84	5·0	en. balance	Q_0	no	½ hour 1 day	July 29	Price & Black 1990–1
Douglas-fir	British Columbia, Canada	Jul–Aug 84	5·0	en. balance	Q_0	no	½ hour 1 day	July 24	Price & Black 1990–2
Douglas-fir	British Columbia, Canada	Jul–Aug 84	5·0	en. balance	Q_0	no	½ hour 1 day	Aug 6 (cloudy)	Price & Black 1990–3

Appendix 1—*cont.*

Vegetation class	Location	Phenology date	L	Flux measurements	Radiation measurements	Respiration measurements	Time-step, duration	Treatment, conditions	Reference
					C3 grasslands				
Fescue	Lusignan, France	day 16 ↑	0.79	enclosure	Q_0	F_n (subt.)	¼ hour 1 day	N = 0 kg/ha	Belanger 1990–1
Fescue	Lusignan, France	day 16 ↑	2.44	enclosure	Q_0	F_n (subt.)	¼ hour 1 day	N = 80 kg/ha	Belanger 1990–2
Fescue	Lusignan, France	day 16 ↑	3.57	enclosure	Q_0	F_n (subt.)	¼ hour 1 day	N = 240 kg/ha	Belanger 1990–3
Tundra	Barrow, Alaska	growing season 71	?	gradient	$S_{g,0}$	no	1 day 3 month		Coyne & Kelley 1975–1
Tundra	Barrow, Alaska	growing season 71	?	gradient	$S_{g,0}$	F_n (subt.)	1 day 3 month		Coyne & Kelley 1975–2
Mixed-grass prairie	Matador, Canada	Jul	0·9	en. balance + gradient	$S_{g,0}$	F_n F_s (not subt.)	mean/classes 5 days		Ripley & Saugier–1 (unpublished data)
Mixed-grass prairie	Matador, Canada	Jun	0·8	en. balance + gradient	$S_{g,0}$	F_n F_s (not subt.)	mean/classes 5 days		Ripley & Saugier–2 (unpublished data)
Mixed-grass prairie	Matador, Canada	May	0·4	en. balance + gradient	$S_{g,0}$	F_n F_s (not subt.)	mean/classes 5 days		Ripley & Saugier–3 (unpublished data)
Dactylis	Montpellier, France	?	6·0	?	Q_0	no	?		Saugier 1986
Ryegrass	Berks., UK	day 36	?	enclosure	$S_{g,0}$ (artificial)	F_n (not subt.)	1 day	reerected after storm	Sheehy 1977–1
Ryegrass	Berks., UK	day 35	?	enclosure	$S_{g,0}$ (artificial)	F_n (not subt.)	1 day	lodged after storm	Sheehy 1977–2
Tall fescue	Berks., UK	day 36	?	enclosure	$S_{g,0}$ (artificial)	F_n (not subt.)	1 day	reerected	Sheehy 1977–3
Tall fescue	Berks., UK	day 35	?	enclosure	$S_{g,0}$ (artificial)	F_n (not subt.)	1 day	lodged	Sheehy 1977–4
Lolium perenne	Berks., UK	day 36	?	enclosure	$S_{g,0}$ (artificial)	F_n (not subt.)	1 day	reerected	Sheehy 1977–5
Lolium perenne	Berks., UK	day 35	?	enclosure	$S_{g,0}$ (artificial)	F_n (not subt.)	1 day	lodged	Sheehy 1977–6
Ryegrass	Berks., UK	day 15	?	enclosure	$S_{g,0}$ (artificial)	F_n (subt.)	1 day	dawn	Sheehy 1977–7
Ryegrass	Berks., UK	day 15	?	enclosure	$S_{g,0}$ (artificial)	F_n (subt.)	1 day	noon	Sheehy 1977–8
Ryegrass	Berks., UK	day 15	?	enclosure	$S_{g,0}$ (artificial)	F_n (subt.)	1 day	dusk	Sheehy 1977–9

Tundra	W. Alaska, US	Jul 6–Aug 8	?	enclosure	Q_0	no ΔS_c	?	wet site	Whiting *et al.* 1992 - 1
Tundra	W. Alaska, US	Jul 6–Aug 8	?	enclosure	Q_0	no ΔS_c	?	dry site	Whiting *et al.* 1992 - 2
Tundra	W. Alaska, US	?	?	eddy corr.	Q_0	no ΔS_c	?		Whiting *et al.* 1992 - 3
					C4 grasslands				
Salt marsh	Delaware, Virginia, US	May–Oct 87	?	enclosure (ecosystem)	Q_{int}	F_n F_s (not subt.)	3 weeks growing season	3 sites, control & fert.	Bartlett *et al.* 1990
Salt marsh	Maryland, US	Jul 19 77	?	enclosure	Q_0	no	1 hour 1 day		Drake 1984
Salt marsh	New York, US	Jul 7–19	?	gradient	$S_{g,0}$	no	1 hour 2 days		Houghton & Woodwell 1980
Tallgrass prairie	Kansas, US	↑ 87	1·9	eddy corr.	Q_0	F_n (not subt.)	?		Kim & Verma 1990 - 1
Tallgrass prairie	Kansas, US	→ 87	3·0	eddy corr.	Q_0	F_n (not subt.)	?		Kim & Verma 1990 - 2
Tallgrass prairie	Kansas, US	87 ↓	2·7–1·7	eddy corr.	Q_0	F_n (not subt.)	?		Kim & Verma 1990 - 3
Tallgrass prairie	Kansas, US	→ 87	3·0	eddy corr.	Q_0	F_n (not subt.)	?	no water stress VPD 0–1·5 kPa	Kim & Verma 1990 - 4
Tallgrass prairie	Kansas, US	→ 87	3·0	eddy corr.	Q_0	F_n (not subt.)	?	no water stress VPD 1·5–3·0 kPa	Kim & Verma 1990 - 5
Tallgrass prairie	Kansas, US	→ (end) 87	2·7	eddy corr.	Q_0	F_n (not subt.)	?	water stress VPD 0–1·5 kPa	Kim & Verma 1990 - 6
Tallgrass prairie	Kansas, US	→ (end) 87	2·7	eddy corr.	Q_0	F_n (not subt.)	?	water stress VPD 1·5–3·0 kPa	Kim & Verma 1990 - 7
Tallgrass prairie	Kansas, US	→ (end) 87	2·7	eddy corr.	Q_0	F_n (not subt.)	?	water stress VPD 3·0–4·5 kPa	Kim & Verma 1990 - 8
Savanna	Lamto, Ivory Coast	early growing season (Feb)	0·80	enclosure	Q_0	F_s (subt.)	instant several days		Leroux & Mordelet - 1 1995

Appendix 1—*cont.*

Vegetation class	Location	Phenology date	L	Flux measurements	Radiation measurements	Respiration measurements	Time-step, duration	Treatment, conditions	Reference
Savanna	Lamto, Ivory Coast	early growing season (Mar)	1·48	enclosure	Q_0	F_s (subt.)	instant several days		Leroux & Mordelet – 2 1995
Savanna	Lamto, Ivory Coast	early growing season (Apr)	1·87	enclosure	Q_0	F_s (subt.)	instant several days		Leroux & Mordelet – 3 1995
Bermudagrass	Georgia, US	Jun–Oct	?	enclosure	Q_{int} (calcul.)	no	mean/class weekly	mowed monthly	Morgan & Brown 1983 – 1
Bermudagrass	Georgia, US	Jun–Oct	?	enclosure	Q_{int} (calcul.)	no	mean/class weekly	mowed weekly	Morgan & Brown 1983 – 2
Tallgrass prairie	Kansas, US	Aug 5–6 86	2·0	eddy corr.	Q_0	no	1 hour several days	no water stress VPD 0–1 kPa	Verma *et al.* 1989 – 1
Tallgrass prairie	Kansas, US	Aug 5–6 86	2·0	eddy corr.	Q_0	no	1 hour several days	no water stress VPD 1–2 kPa	Verma *et al.* 1989 – 2
Tallgrass prairie	Kansas, US	Jul 30–Aug 4 86	2·0	eddy corr.	Q_0	no	1 hour several days	water stress VPD 0–1 kPa	Verma *et al.* 1989 – 3
Tallgrass prairie	Kansas, US	Jul 30–Aug 4 86	2·0	eddy corr.	Q_0	no	1 hour several days	water stress VPD 1–2 kPa	Verma *et al.* 1989 – 4
Tallgrass prairie	Kansas, US	Jul 30–Aug 4 86	2·0	eddy corr.	Q_0	no	1 hour several days	water stress VPD 2–3 kPa	Verma *et al.* 1989 – 5
Tallgrass prairie	Kansas, US	Jul 30–Aug 4 86	2·0	eddy corr.	Q_0	no	1 hour several days	water stress VPD 3–4 kPa	Verma *et al.* 1989 – 6
C3 crops									
Soybean	Nebraska, US	Aug 22–Sep 3	≥4	eddy corr.	Q_0	no	several days	no water stress	Anderson *et al.* 1984
Rice	Florida, US control chamber	↑	?	enclosure	$S_{g,0}$	F_n (subt.)	1 day	early planted day 41	Baker *et al.* 1990 – 1

Rice	Florida, US control chamber	→	11·8–14·3	enclosure	$S_{g,0}$	F_n (subt.)	1 day	early planted day 74	Baker *et al.* 1990–2
Wheat	Oregon, US	↑	3·0	eddy corr.	Q_0	F_n (not subt.)	1 day		Baldocchi *et al.* 1994–1
Alfalfa	Nebraska, US	Sep 1	?	gradient	$S_{n,0}$	F_n F_s (not subt.)	1 day		Baldocchi *et al.* 1981–a
Soybean	Nebraska, US	summer	4·1	gradient	Q_0	no	1 day several days	T 20–30°C irrigated	Baldocchi *et al.* 1981–b
Barley	Leics., UK	Jun 17–18 →	5·45	en. balance + gradient	$S_{g,0}$	F_s (enclosure) (subt.)	1 hour 2 days		Biscoe *et al.* 1975–1
Barley	Leics., UK	Jun 28 ↓	5·9	en. balance + gradient	$S_{g,0}$	F_s (enclosure) (subt.)	1 hour 1 day		Biscoe *et al.* 1975–2
Barley	Leics., UK	Jul 5 ↓	5·1	en. balance + gradient	$S_{g,0}$	F_s (enclosure) (subt.)	1 hour 1 day		Biscoe *et al.* 1975–3
Barley	Leics., UK	Jul 12 ↓	4·7	en. balance + gradient	$S_{g,0}$	F_s (enclosure) (subt.)	1 hour 1 day		Biscoe *et al.* 1975–4
Barley	Leics., UK	Jul 19 ↓	3·4	en. balance + gradient	$S_{g,0}$	F_s (enclosure) (subt.)	1 hour 1 day		Biscoe *et al.* 1975–5
Barley	Leics., UK	Jul 26 ↓	2·0	en. balance + gradient	$S_{g,0}$	F_s (enclosure) (subt.)	1 hour 1 day		Biscoe *et al.* 1975–6
Barley	Leics., UK	Jul 14	4·05	en. balance + gradient	$S_{g,0}$	F_s (enclosure) (subt.)	1 hour 1 day	leaf water pot. normal	Biscoe *et al.* 1975–7
Barley	Leics., UK	Jul 17	?	en. balance + gradient	$S_{g,0}$	F_s (enclosure) (subt.)	1 hour 1 day	leaf water pot. low	Biscoe *et al.* 1975–8
Wheat	Australia	?	1·6	gradient	$S_{g,0}$	F_s (not subt.) (subt.)	1 hour 5 weeks	dryland	Denmead 1976–1
Wheat	Australia	?	3·2	gradient	$S_{g,0}$	F_s (not subt.) (subt.)	1 hour 5 weeks	irrigated	Denmead 1976–2
Soybean	Florida, US control chamber	Oct 6	9·0	enclosure	Q_0	no	1 hour 1 day	double CO_2	Jones *et al.* 1984–2
Soybean	Florida, US control chamber	Oct 6	6·9	enclosure	Q_0	no	1 hour 1 day	ambient CO_2	Jones *et al.* 1984–1
Rice	Japan	Sep 2–3 (ear emergence)	?	eddy corr.	$S_{n,0}$	no	2 days		Ohtaki 1980
Soybean	Illinois, US	?	?	enclosure	Q_0	no	½ hour 1 day	fertilized, irrigated	Pettigrew *et al.* 1990
Wheat	Australia	Sep → 67	≈4	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	dry season fertilized	Puckridge 1971–1

Appendix 1—*cont.*

Vegetation class	Location	Phenology date	L	Flux measurements	Radiation measurements	Respiration measurements	Time-step, duration	Treatment, conditions	Reference
Wheat	Australia	Sep → 68	≈3	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	wet season fertilized	Puckridge 1971 - 2
Wheat (Australian var)	Australia	Sep 6	0·8	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	low N	Puckridge & Ratkowski 1971 - 1
Wheat (Australian var)	Australia	Sep 13	4·6	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	high N	Puckridge & Ratkowski 1971 - 2
Wheat (Australian var)	Australia	Sep 12	0·9	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	low N	Puckridge & Ratkowski 1971 - 3
Wheat (Australian var)	Australia	Sep 19	4·9	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	high N	Puckridge & Ratkowski 1971 - 4
Wheat (Australian var)	Australia	Sep 18	1·2	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	low N	Puckridge & Ratkowski 1971 - 5
Wheat (Australian var)	Australia	Sep 28	4·1	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	high N	Puckridge & Ratkowski 1971 - 6
Wheat (Australian var)	Australia	Sep 24	1·4	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	low N	Puckridge & Ratkowski 1971 - 7
Wheat (Australian var)	Australia	Oct 4	4·6	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	high N	Puckridge & Ratkowski 1971 - 8
Wheat (Australian var)	Australia	Oct 12	4·3	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	high N	Puckridge & Ratkowski 1971 - 9
Wheat (Australian var)	Australia	Oct 8	1·7	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	low N	Puckridge & Ratkowski 1971 - 10
Wheat (Mexican var)	Australia	Sep 5	0·8	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	low N	Puckridge & Ratkowski 1971 - 11
Wheat (Mexican var)	Australia	Sep 14	4·9	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	high N	Puckridge & Ratkowski 1971 - 12
Wheat (Mexican var)	Australia	Sep 11	1·2	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	low N	Puckridge & Ratkowski 1971 - 13

Wheat (Mexican var)	Australia	Sep 20	5·0	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	high N	Puckridge & Ratkowski 1971–14
Wheat (Mexican var)	Australia	Sep 17	2·2	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	low N	Puckridge & Ratkowski 1971–15
Wheat (Mexican var)	Australia	Sep 27	2·0	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	low N	Puckridge & Ratkowski 1971–16
Wheat (Mexican var)	Australia	Oct 16	4·2	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	high N	Puckridge & Ratkowski 1971–17
Wheat (Mexican var)	Australia	Oct 22	1·4	enclosure	$S_{g,0}$	F_s (separate enclosure)	¼ hour 1 day	low N	Puckridge & Ratkowski 1971–18
Winter wheat	Kansas, US	May 16–25 ↑	peak 4·5	enclosure	Q_{abs}	F_n (subt.)	9 days	N–S orientated	Wall & Kanemasu 1990
Winter wheat	Kansas, US	April 20–June 19	?	enclosure	Q_{abs} (calcul.)	F_n (subt.)	1 day 2 months		Wall *et al.* 1990
Cucumber	Australia control chamber	June 14–16 88	3·4	enclosure	Q_0	no	10 min 3 days	glasshouse	Warren Wilson *et al.* 1992
Wheat	Australia	?	5·3–7·7	enclosure	$S_{g,int}$	no	1 day	irrigated, fertilized	Whitfield 1990
					C4 crops				
Sorghum	Nebraska, US	→	3·7	eddy corr.	Q_0	no	several days		Anderson & Verma 1986–1
Sorghum	Nebraska, US	↑	2·7–3·6	eddy corr.	Q_0	no	several days		Anderson & Verma 1986–2
Sorghum	Nebraska, US	↓	3·5	eddy corr.	Q_0	no	several days		Anderson & Verma 1986–3
Corn	Oregon, US	↑	1·8	eddy corr.	Q_0	F_n (not subt.)	1 day		Baldocchi 1994–2
Corn	?	Jul 17	?	eddy corr.	Q_{int}	no	1 hour 1 day	water stress	Desjardins *et al.* 1984–1
Corn	?	Aug 15	?	eddy corr.	Q_{int}	no	several days	no water stress	Desjardins *et al.* 1984–2
Corn	Florida, US	May 10 ↑	3·26	enclosure	Q_0	no	several days	low N, irrigated	Jones *et al.* 1986–1

Appendix 1—*cont.*

Vegetation class	Location	Phenology date	L	Flux measurements	Radiation measurements	Respiration measurements	Time-step, duration	Treatment, conditions	Reference
Corn	Florida, US	May 10 ↑	4·02	enclosure	Q_0	no	several days	high N, irrigated	Jones *et al.* 1986–2
Corn	Florida, US	May 10 ↑	2·76	enclosure	Q_0	no	several days	low N, water stress	Jones *et al.* 1986–3
Corn	Florida, US	May 10 ↑	3·70	enclosure	Q_0	no	several days	high N, water stress	Jones *et al.* 1986–4
Corn	New York, US	Jul 29–Aug 8	?	enclosure	$S_{g,0}$	F_s (enclosure,) F_n	1 hour 1 day	CO$_2$ 510 ppmv	Moss *et al.* 1961–1
Corn	New York, US	Jul 29–Aug 8	?	enclosure	$S_{g,0}$	F_s (enclosure,) F_n	1 hour 1 day	CO$_2$ 270 ppmv	Moss *et al.* 1961–2
Corn	New York, US	Jul 29–Aug 8	?	enclosure	$S_{g,0}$	F_s (enclosure,) F_n	1 hour 1 day	CO$_2$ 155 ppmv	Moss *et al.* 1961–3
Corn	New York, US	Jul 29–Aug 8	?	enclosure	$S_{g,0}$	F_s (enclosure,) F_n	1 hour 1 day	CO$_2$ 30 ppmv	Moss *et al.* 1961–4
				mixed vegetation types					
Mixed conifer, deciduous	Ottawa, Canada	summer	?	plane mounted eddy corr.	$S_{g,0}$	no	different passes several days		Desjardins *et al.* 1985–1
White pine	Ottawa, Canada	summer	?	plane mounted eddy corr.	$S_{g,0}$	no	different passes several days		Desjardins *et al.* 1985–2
Wheat fields	Manitoba, US	July 14 84	?	plane mounted eddy corr.	$S_{g,0}$	no	1·5 hour 1 day		Desjardins 1991
Various crops	Nebraska, US	June–Oct 72	?	flux gradient	$S_{g,0}$	F_n (not subt.)	daily means, growing season		Verma & Rosenberg 1976

APPENDIX 2: STATISTICS ON THE RELATIONSHIP BETWEEN CO_2 FLUX (*F*) AND PPFD (*Q*), ON INDIVIDUAL DATA SETS

In some cases two or more data sets have been aggregated to form bigger data sets, when original data sets are too small or present the same relationship. This is indicated in the reference column: for example the data set Desjardins *et al.* 1985–3 (1 + 2) results from the aggregation of dáta sets Desjardins *et al.* 1985–1 and Desjardins *et al.* 1985–2 of Appendix 1. *n* is number of data points; "means" indicates that reported data sets are averaged per radiation class. A rectangular hyperbolic (H) and a linear model (L) are tested; best fit is defined by the relationship having the highest coefficient of determination (r^2). Statistical parameters are not given when there is no statistical relationship, i.e. $r^2 < 0{\cdot}4$ ("N" in column best fit). The parameters of the statistical models are initial slope (α), intercept on the y axis (R), and, for the hyperbolic model, value of F at saturating Q (F_∞). Derived parameters are departure from linearity (D) defined as r^2(H)–r^2(L), and photosynthetic capacity (F_m), defined as F at maximum Q (1800 μmol m^{-2} s^{-1} for instantaneous data sets, 80 mol m^{-2} d^{-1} for daily data sets). $R = 0{\cdot}00$ indicates that the intercept would be positive (therefore the value of R negative), but is constrained by the model.

2.1. Instantaneous data sets, F_∞, R and F_m are in μmol m^{-2} s^{-1}

References	n	Constraint	F_∞	α	R	r^2 (best fit)	D	F_m	Best fit
broadleaf forests									
Allen & Lemon 1976	5		/	/	/	−0·58	/	/	N
Baldocchi & Harley	277		43·80	0·040	4·74	0·60	0·05	22·49	H
Baldocchi *et al.* 1987	28		43·43	0·033	0·55	0·72	0·22	24·54	H
den Hartog *et al.* 1987	16		/	0·010	0·00	0·51	0·00	18·00	L
Denmead 1991 (Fig. 4A)	17		/	0·014	1·13	0·96	0·00	24·07	L
Fan *et al.* 1990	13		44·14	0·049	11·11	0·92	0·06	18·31	H
Hollinger *et al.* 1994 – 1	19	R = 2·4	7·64	0·009	2·40	0·78	0·00	3·62	H
Hollinger *et al.* 1994 – 2	47	R = 4·5	15·62	0·043	4·50	0·72	0·16	8·50	H
Hollinger *et al.* 1994 – 3	75	R = 6·7	16·05	0·042	6·70	0·50	0·09	6·54	H
Hollinger *et al.* 1994 – 4	57	R = 5·2	/	/	/	0·38	/	/	N
Hollinger *et al.* 1994 – 5	51	R = 0·50	24·37	0·031	0·50	0·51	0·01	16·46	H
Kelliher *et al.* 1989	19		40·33	0·048	4·48	0·93	0·01	23·02	H
Monteny 1989 – 1	7		30·58	0·076	12·20	0·98	0·25	12·79	H
Monteny 1989 – 2	7		52·26	0·089	11·75	0·99	0·16	27·66	H
Monteny 1989 – 3	7		81·70	0·076	11·16	0·99	0·09	39·99	H
Mordacq *et al.* 1991	45		41·10	0·073	0·39	0·90	0·30	30·92	H
Valentini *et al.* 1991	122		/	0·015	0·93	0·61	0·00	26·07	L
Verma *et al.* 1986–4 (1 + 2 + 3)	51		28·51	0·033	3·94	0·72	0·14	15·32	H
Wofsy *et al.* 1993 – 3 (1 + 2)	20		28·92	0·044	4·88	0·95	0·06	16·30	H
Wong & Dunin 1987 – 1 (Fig. 4B)	68		34·60	0·049	2·49	0·94	0·09	22·36	H
Wong & Dunin 1987 – 2	35		66·55	0·102	0·00	0·89	0·45	48·49	H
conifer forests									
Brunet *et al.* 1992	103		49·22	0·018	1·06	0·45	0·03	18·48	H
Jarvis 1994 – 1	4 (means)		59·95	0·174	12·73	0·99	0·07	37·59	H
Jarvis 1994 – 2	5 (means)		54·35	0·135	12·48	0·97	0·10	31·94	H
Jarvis 1994 – 3	4 (means)		42·98	0·049	7·53	0·99	0·04	21·37	H
Jarvis 1994 – 4	4 (means)		24·27	0·051	4·74	0·83	0·38	14·40	H
Jarvis 1994 – 5	5 (means)		26·91	0·023	5·04	0·99	0·02	11·27	H
Price & Black 1990 – 1	48		/	/	/	0·10	/	/	N

Price & Black 1990–2	48		/	/	/	0·00	/	/	N
Price & Black 1990–3	48		40·86	0·020	3·58	0·72	0·02	14·87	H
			C3 grasslands						
Belanger 1990–1	24	$R = 0$	44·60	0·112	0·00	0·94	0·57	36·52	H
Belanger 1990–2	27	$R = 0$	41·91	0·100	0·00	0·97	0·33	33·99	H
Belanger 1990–3	55	$R = 0$	17·52	0·029	0·00	0·90	0·77	13·12	H
Ripley & Saugier–1	12 (means)	$R = 3{\cdot}22$	13·65	0·039	3·63	0·94	0·21	7·80	H
Ripley & Saugier–2	12 (means)	$R = 2{\cdot}54$	15·79	0·012	2·54	0·88	0·17	6·58	H
Ripley & Saugier–3	12 (means)	$R = 1{\cdot}45$	4·13	0·010	1·45	0·98	0·18	1·91	H
Saugier 1986	13		62·42	0·061	0·86	0·98	0·21	38·94	H
Sheehy 1977–1	6 (means)	$R = 5{\cdot}05$	33·85	0·126	5·05	0·97	0·19	24·40	H
Sheehy 1977–2	5 (means)	$R = 5{\cdot}62$	40·08	0·224	5·62	0·99	0·21	30·78	H
Sheehy 1977–3	6 (means)	$R = 3{\cdot}78$	40·38	0·099	3·78	0·99	0·12	29·14	H
Sheehy 1977–4	5 (means)	$R = 6{\cdot}94$	41·84	0·190	6·94	0·98	0·12	30·34	H
Sheehy 1977–5	6 (means)	$R = 3{\cdot}78$	39·53	0·119	3·78	0·99	0·12	29·59	H
Sheehy 1977–6	5 (means)	$R = 6{\cdot}94$	43·65	0·220	0·94	0·98	0·12	38·36	H
Sheehy 1977–7	5 (means)	$R = 0$	71·74	0·206	0·00	0·99	0·49	60·11	H
Sheehy 1977–8	5 (means)	$R = 0$	61·87	0·186	0·00	0·99	0·53	52·22	H
Sheehy 1977–9	5 (means)	$R = 0$	69·82	0·177	0·00	0·99	0·41	57·27	H
Whiting *et al.* 1992–1	103		5·36	0·031	2·12	0·80	0·30	2·77	H
Whiting *et al.* 1992–2	73		2·48	0·033	1·14	0·80	0·37	0·89	H
Whiting *et al.* 1992–3	20		2·36	0·008	0·61	0·92	0·22	1·42	H
			C4 grasslands						
Bartlett *et al.* 1990	31		/	0·031	3·45	0·69	0·00	52·35	L
Drake 1984	12		37·79	0·043	6·50	0·99	0·06	18·89	H
Houghton & Woodwell 1980	55		32·56	0·032	4·41	0·62	0·06	16·39	H
Kim & Verma 1990–1	77		53·61	0·035	7·99	0·89	0·07	20·97	H
Kim & Verma 1990–2	87		82·20	0·032	8·77	0·91	0·02	25·10	H
Kim & Verma 1990–3	36		76·24	0·017	7·60	0·91	0·01	14·24	H
Kim & Verma 1990–4	91		82·31	0·032	8·42	0·91	0·02	24·47	H
Kim & Verma 1990–5	71		73·61	0·030	10·25	0·81	0·02	20·90	H
Kim & Verma 1990–6	23		/	0·014	4·06	0·94	0·00	21·14	L
Kim & Verma 1990–7	50		18·56	0·020	4·85	0·68	0·06	7·40	H
Kim & Verma 1990–8	46		/	/	/	0·03	/	/	N

Appendix 2—*cont.*

References	n	Constraint	F_∞	α	R	r^2 (best fit)	D	F_m	Best fit
Leroux & Mordelet 1994–1	19		28·91	0·043	2·14	0·96	0·19	18·98	H
Leroux & Mordelet 1994–2	25		33·46	0·045	1·12	0·98	0·11	22·59	H
Leroux & Mordelet 1994–3	31		31·02	0·052	1·38	0·95	0·10	21·87	H
Morgan & Brown 1983–1	7 (means)		/	0·031	7·09	0·99	0·00	48·71	L
Morgan & Brown 1983–2	8 (means)		/	0·019	2·17	0·83	0·00	32·03	L
Verma *et al.* 1989–1	10		/	0·011	3·77	0·87	0·00	16·03	L
Verma *et al.* 1989–2	8		51·98	0·009	0·00	0·77	0·00	12·35	H
Verma *et al.* 1989–7 (3 + 4 + 5 + 6)	17		/	/	/	0·33	/	/	N
			C3 crops						
Anderson *et al.* 1984	16		/	0·018	1·01	0·77	0·00	31·39	L
Baker *et al.* 1990–1	110	$R = 0$	67·18	0·055	0·00	0·96	0·11	39·01	H
Baker *et al.* 1990–2	8·5	$R = 0$	/	0·048	0·00	0·98	0·00	86·40	L
Baldocchi 1994–1	47		/	0·021	3·94	0·98	0·00	33·86	L
Baldocchi *et al.* 1981–a	8		62·68	0·055	5·54	0·68	0·09	32·84	H
Baldocchi *et al.* 1981–b	36		/	0·017	2·59	0·81	0·00	28·01	L
Biscoe *et al.* 1975–1	28		/	0·020	0·00	0·81	0·00	36·00	L
Biscoe *et al.* 1975–2	8		34·62	0·098	4·72	0·98	0·17	24·22	H
Biscoe *et al.* 1975–3	7		31·42	0·047	2·79	0·98	0·07	20·12	H
Biscoe *et al.* 1975–4	6		33·33	0·031	4·06	0·98	0·06	16·81	H
Biscoe *et al.* 1975–5	8		25·57	0·031	3·60	0·98	0·09	13·93	H
Biscoe *et al.* 1975–6	7		10·07	0·055	3·17	0·96	0·26	5·97	H
Biscoe *et al.* 1975–7	14		/	0·014	4·90	0·96	0·00	20·30	L
Biscoe *et al.* 1975–8	17		/	0·010	4·23	0·80	0·00	13·77	L
Denmead 1976–1	63		62·76	0·030	3·72	0·66	0·03	25·35	H
Denmead 1976–2	29		/	0·021	2·75	0·87	0·00	35·05	L
Jones *et al.* 1984–1	64		/	0·032	0·00	0·98	0·01	57·60	L
Jones *et al.* 1984–2	62		/	0·050	0·00	0·95	0·04	90·00	L
Ohtaki 1980	28		/	0·020	3·12	0·94	0·00	32·88	L
Pettigrew *et al.* 1990	22		57·54	0·021	0·00	0·58	0·12	22·81	H

Puckridge & Ratkowski 1971 – 1	15	19·06	0·163	8·32	0·84	0·09	9·58	H
Puckridge & Ratkowski 1971 – 2	15	53·31	0·094	5·52	0·97	0·21	35·02	H
Puckridge & Ratkowski 1971 – 3	15	22·21	0·048	1·70	0·97	0·40	15·97	H
Puckridge & Ratkowski 1971 – 4	17	/	0·033	0·00	0·94	0·02	59·40	L
Puckridge & Ratkowski 1971 – 5	19	17·64	0·068	2·03	0·80	0·10	13·39	H
Puckridge & Ratkowski 1971 – 6	11	32·00	0·120	4·37	0·87	0·19	23·50	H
Puckridge & Ratkowski 1971 – 7	19	20·27	0·037	1·17	0·97	0·22	14·37	H
Puckridge & Ratkowski 1971 – 8	14	26·77	0·042	1·09	0·94	0·36	15·00	H
Puckridge & Ratkowski 1971 – 9	16	51·68	0·046	0·82	0·94	0·19	30·40	H
Puckridge & Ratkowski 1971 – 10	18	30·69	0·038	0·00	0·89	0·48	21·18	H
Puckridge & Ratkowski 1971 – 11	14	17·57	0·090	5·07	0·94	0·57	10·78	H
Puckridge & Ratkowski 1971 – 12	10	64·24	0·311	28·25	0·98	0·11	29·38	H
Puckridge & Ratkowski 1971 – 13	18	19·98	0·081	0·00	0·84	0·12	17·57	H
Puckridge & Ratkowski 1971 – 14	14	52·78	0·051	0·14	0·96	0·22	33·37	H
Puckridge & Ratkowski 1971 – 15	17	34·55	0·097	7·84	0·95	0·51	21·00	H
Puckridge & Ratkowski 1971 – 16	15	52·73	0·098	4·88	0·97	0·27	35·19	H
Puckridge & Ratkowski 1971 – 17	10	57·61	0·040	4·24	0·98	0·07	27·76	H
Puckridge & Ratkowski 1971 – 18	17	17·57	0·090	5·07	0·94	0·57	10·78	H
Puckridge 1970 – 1	17	71·08	0·109	0·00	0·78	0·06	52·18	H
Puckridge 1970 – 2	18	55·47	0·076	6·09	0·98	0·07	33·38	H
Wall & Kanemasu 1990 (Fig. 8a)	157	62·30	0·465	32·89	0·59	0·11	25·09	H
Warren Wilson *et al.* 1992	24	/	0·018	0·00	0·87	0·02	30·91	L
		C4 crops						
Anderson & Verma 1986 – 1	24	/	0·018	1·49	0·87	0·01	30·91	L
Anderson & Verma 1986 – 2	14	48·76	0·106	6·89	0·85	0·37	31·94	H
Anderson & Verma 1986 – 3	10	43·48	0·059	5·84	0·98	0·17	25·16	H
Baldocchi 1994 – 2	48	/	0·015	2·82	0·97	0·01	24·18	L
Desjardins *et al.* 1984 – 1	10	98·14	0·058	7·21	0·61	0·01	43·38	H
Desjardins *et al.* 1984 – 2	13	/	0·039	0·00	0·88	0·05	70·20	L

Appendix 2—*cont.*

Appendix 2—*cont.*

References	n	Constraint	F_∞	α	R	r^2 (best fit)	D	F_m	Best fit
Jones *et al.* 1984–1	14		75·62	0·057	7·82	0·99	0·04	35·71	H
Jones *et al.* 1984–2	11		/	0·028	2·32	0·95	0·03	48·08	L
Jones *et al.* 1984–3	13		/	/	/	0·23	/	/	N
Jones *et al.* 1984–4	14		40·24	0·091	7·55	0·68	0·23	24·75	H
Moss *et al.* 1961–1	10		43·56	0·029	2·39	0·98	0·02	22·36	H
Moss *et al.* 1961–2	10		38·82	0·026	2·54	0·99	0·01	18·68	H
Moss *et al.* 1961–3	6		39·85	0·020	1·60	0·99	0·01	17·31	H
Moss *et al.* 1961–4	6		3·46	0·018	1·93	0·99	0·59	1·19	H
mixed vegetation types									
Desjardins *et al.* 1985–3 (1 + 2)	8		/	0·014	2·90	0·56	0·00	22·30	L
Desjardins 1991	16		/	0·017	10·63	0·71	0·00	19·99	L

2.2. Daily data sets, F_∞, R and F_m are in μmol m^{-2} d^{-1}

References	n	Constraint	F_∞	α	R	r^2 (best fit)	D	F_m	Best fit
various vegetation types									
Coyne & Kelley 1975–1 (Fig. 6a)	20		/	/	/	0·34	/	/	N
Coyne & Kelley 1975–1 (Fig. 6b)	61		0·94	0·052	0·32	0·60	0·03	0·44	H
Hollinger *et al.* 1994–6	8		/	/	/	0·21	/	/	N
Verma & Rosenberg 1976	28		/	/	/	0·12	/	/	N
Wall *et al.* 1990 (Fig. 8b)	45		/	0·027	0·34	0·67	0·00	1·82	L
Whitfield 1990	21		/	0·013	0·33	0·67	0·00	0·71	L