

## CO<sub>2</sub> fluxes at leaf and canopy scale in millet, fallow and tiger bush vegetation at the HAPEX-Sahel southern super-site

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### Abstract

Measurements of canopy and leaf scale CO<sub>2</sub> flux from the three sub-sites at the HAPEX-Sahel Southern supersite are presented. These are analysed in relation to biological and environmental variables. At leaf scale, the flux is most strongly influenced by photosynthetic photon flux density (PPFD) and stomatal conductance. Together with measurements of canopy structure at each site, the measurements of leaf photosynthesis, stomatal conductance and stem respiration were used to parameterise sub-models within the canopy model MAESTRO, which predicts canopy net CO<sub>2</sub> flux. Comparison of the independent canopy flux measurements with predictions is informative, as the model represents an integration of our knowledge of the system, and so differences highlight weak points in our understanding as well as measurement artefacts. These differences are largest in tiger bush and smallest in millet, and are attributed to the effect of canopy heterogeneity on measurements rather than biological processes. Generally, good agreement was found at all three sites and the model can be regarded as validated. The model was used to extrapolate measurements in time, and, using a year's weather data, predicted a value for carbon sequestration at the millet site over the growing season very close to harvest measurements.

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### 1. Introduction

Information on CO<sub>2</sub> exchange between terrestrial ecosystems and the atmosphere is necessary for global vegetation and carbon cycle models (Fung et al., 1983; Box, 1988)

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and for coupling these with General Circulation Models (Sellers et al., 1986). Currently, the global data set available is very limited and heavily biased towards leaf scale measurements made in the temperate zones. No previous canopy scale data exist for semi-arid vegetation such as that found in the Sahel, and only one data set exists for West African savanna (Le Roux and Mordelet, 1995). However, the Sahel may be particularly sensitive to environmental change, as it occurs at the marginal end of a steep climatic gradient, and furthermore, feedbacks between the vegetation and the atmospheric environment may be important in the desertification process (Charney, 1975). Here we present results of CO<sub>2</sub> exchange measurements at leaf and canopy scales from the three sub-sites at the HAPEX-Sahel Southern supersite in south west Niger. The main objective of the project was to determine the magnitude of the leaf and canopy scale fluxes and their dependence on controlling variables. A further objective was to provide 'ground truth' measurements of CO<sub>2</sub> flux and canopy properties for comparison with aircraft and satellite measurements.

Most information on CO<sub>2</sub> exchange is obtained from leaf scale measurements as they are logistically simpler and controlled experiments can be done ('leaf scale' is used here as a general term and may include stem and soil chamber measurements). Often, however, results cannot be directly extrapolated to give information concerning the vegetation canopy as a whole without using a scaling-up model. It is therefore essential that the scaling-up process be demonstrably correct if leaf scale measurements are to be used to infer fluxes at larger scales. Plant growth measurements can give information at larger scales but reveal little about the control of processes. Hence micrometeorological techniques such as eddy covariance are important as they permit fluxes to be measured on large spatial scales (e.g. from a few hundred metres upwind) and on short time scales (averaged over half-hour periods). In this way, the short-term dependence of the canopy scale CO<sub>2</sub> flux on environmental and biological variables can be studied. These measurements tend to be restricted to point locations over periods of days or weeks and so a scaling-up model is needed to extrapolate results to the still larger spatial scales and longer periods of time of relevance to global modellers.

The approach of this project was to measure photosynthetic and respiratory properties at the leaf scale together with canopy structure in order to predict canopy scale CO<sub>2</sub> fluxes using the scaling-up model MAESTRO (Wang and Jarvis, 1990a). The fluxes of the components (leaves, woody stems and soil) may be investigated by enclosing the tissue in chambers and measuring the CO<sub>2</sub> and water vapour content of air flowing in and out. These flux measurements can be related to biological and environmental variables such as radiation, temperature and humidity, and parameters for the response functions derived. In MAESTRO, these functions are combined with a model describing the distribution of radiation within the canopy, producing predictions of radiation absorbed, transpiration and net CO<sub>2</sub> flux to the canopy as a whole, given meteorological data as an input.

Most models are not suitable for simulating canopies with a highly heterogeneous distribution of leaf area, such as those commonly found in semi-arid vegetation, as they assume the canopy to be uniform in the horizontal dimensions. However, the MAESTRO model is appropriate as it is highly sophisticated in this respect, and allows structurally complex canopies to be described in three dimensions. The radiative transfer element has undergone sensitivity testing and validation (Grace et al., 1987; Wang and Jarvis, 1990a and Wang and Jarvis, 1990b) which demonstrates its reliability.

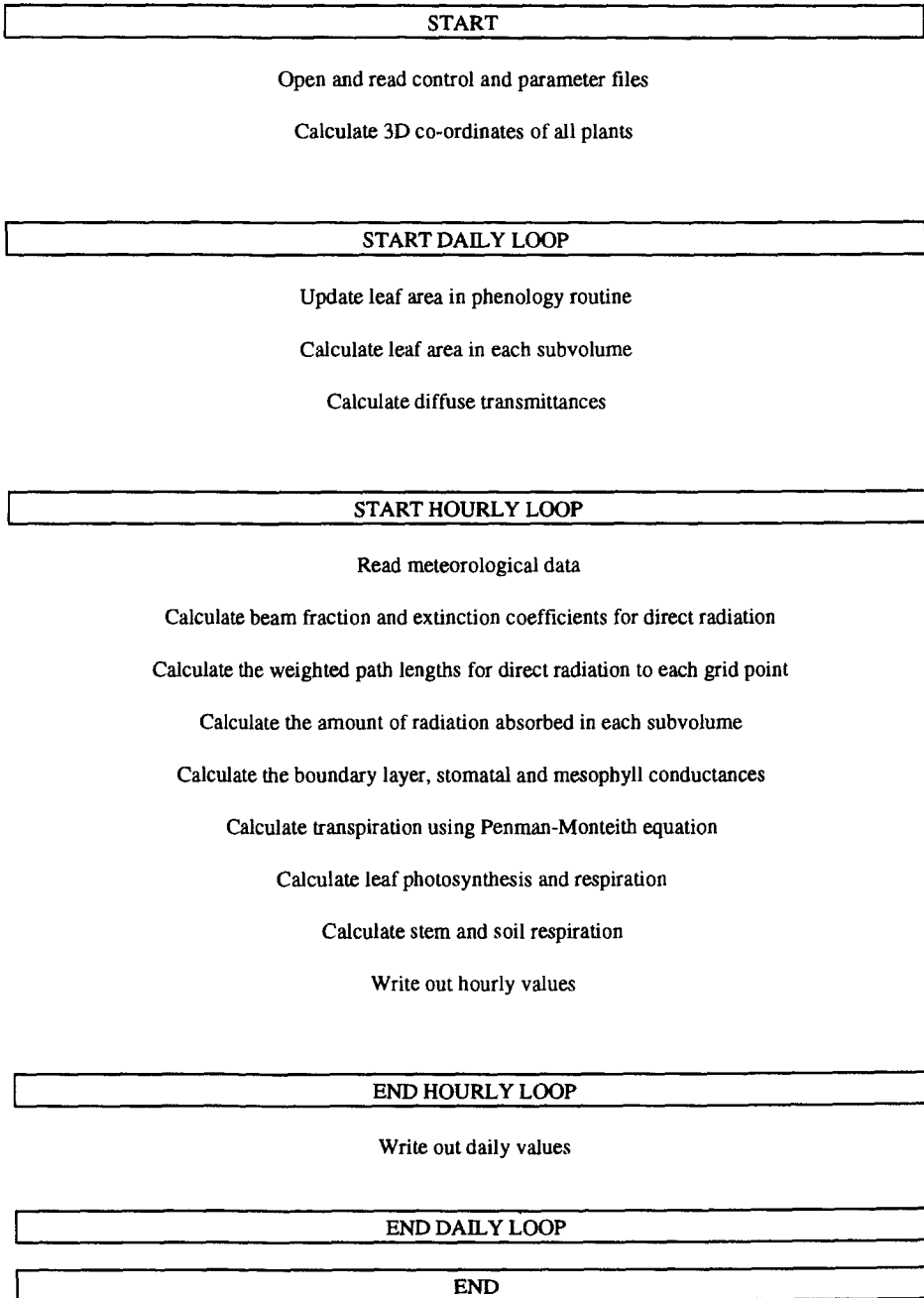


Fig. 1. Flow chart showing MAESTRO program structure.

The model program structure is shown in Fig. 1. The necessary meteorological variables are windspeed, relative humidity, air and soil temperatures, solar radiation and photosynthetic photon flux density (PPFD), on an hourly basis. The co-ordinates, dimensions and leaf area of all plants in the canopy are specified. Each hour, the radiation regime within the crown of a single 'target tree' is calculated in detail, at up to 120 spatial points for PPFD, near-infrared and thermal wavebands. At each of these points, which represent subvolumes of the canopy, stomatal conductance is calculated using a model based on that of Jarvis (1976). This combines a hyperbolic response to PPFD, a bell-shaped response to temperature and an exponential decline with VPD. Transpiration and photosynthesis are then calculated for leaves at each point. Leaf photosynthesis was based on a semi-empirical model of response to PPFD, temperature and CO<sub>2</sub> (Reed et al., 1976). This was used in preference to the model of Farquhar and von Caemmerer (1982), which is more difficult to parameterise with field data. Values are then integrated to the whole canopy. Woody tissue and soil respiration are calculated as exponential functions of temperature. Stem and soil temperatures are calculated from air temperature using relationships established over the measurement periods by linear regression. Woody tissue and soil respiration are then subtracted from photosynthesis to give the net CO<sub>2</sub> flux to the canopy.

The model was parameterised for each of the three subsites at the Southern Supersite using leaf physiology and canopy structure data, and tested by comparison with canopy fluxes measured during the intensive observation period (IOP) at these sites. Extrapolations to the annual scale were made by incorporating leaf phenology in the model from measurements of the seasonal changes in leaf area. This extrapolation could be tested against measurements of biomass made over the growing season. It may also be possible to make predictions about vegetation functioning under conditions of projected climatic change such as elevated CO<sub>2</sub>, higher temperature and drought.

## 2. Sites

### 2.1. Millet

The millet site was located 1 km to the east of the ICRISAT Sahelian Centre (ISC) (13° 14.48' N, 2° 17.94' E). The site was planted with the local millet land race (*Pennisetum glaucum* (L.) R. Br. var Sadoré local) and cultivated using traditional methods. Several trees were present in the fields, as is typical in the region. These were mainly *Combretum glutinosum* Perrot. ex DC. and *Faidherbia albida* (Del.) A. Chev. with *Annona senegalensis* Pers. also present. The millet was planted between 16 May and early June at a density of 4600 pockets per hectare (i.e. 1.4 m spacing). With sufficient rainfall, the crop grew well, and senescence started in late August. During the period of eddy covariance measurements, the mean height of flowering tillers was 2.6 m, giving an estimated zero plane displacement of around 1.7 m (2/3 h), although some tillers exceeded 3.5 m. Harvesting began in early September, producing a grain yield of 650 kg ha<sup>-1</sup> (a range of 0–2885 kg ha<sup>-1</sup> in 400 5 × 5 m plots, Brouwer et al., in prep.). Cowpea or niebe (*Vigna unguiculata* (L.) Walp.) was sown between the millet plants in early July at a density of

886 plants per hectare and harvested in late October. No measurements were made on cowpea or the trees at the site.

Soil at the site was extremely sandy, approximately 90% sand, 5% silt and 5% clay, and classified as Psammentic Paleustalfs. One hundred samples taken from the 1 hectare millet growth plot gave average values of 0.14% organic carbon, 9.5 meq kg<sup>-1</sup> effective cation exchange capacity and pH 4.07 (Wallace et al., 1994). The water table is at around 25 m with very hard laterite at 2.5–3 m.

## 2.2. Fallow

The fallow site was located 4 km west of the ISC (13° 14.63' N, 2° 14.65' E), measuring approximately 800 × 1000 m, bounded to the north and north-east by tiger bush and by millet fields on other sides. The area of fallow enclosed had not been planted with millet for about seven years and semi-natural vegetation had regrown. This comprised a shrub component, almost exclusively *Guiera senegalensis* L. with an occasional *Combretum micranthum* G. Don, and a herb component dominated by grasses and legumes. Occasional trees, mainly *C. glutinosum*, were also present. There were 327 bushes per hectare of *G. senegalensis*, with an average height of 2 m, giving an estimated zero plane displacement of 1.3 m. The ground flora were dominated by *Eragrostis tremula* Hochst. ex Steud., *Mitracarpus villosus* (Sw.) DC., *Cassia mimosoides* L. and *Cenchrus biflorus* Roxb. There was occasional grazing by sheep and cattle. The soil was similar to that at the millet site. The laterite horizon was slightly higher, often starting at 2 m, whilst the water table was slightly deeper at 32 m.

## 2.3. Tiger bush

The tiger bush site was located 7 km south-west of the ISC (13° 11.89' N, 2° 14.37' E) at the centre of an extensive area of tiger bush, approximately 3 km across. Tiger bush is characterised by stripes or arcs of vegetation tens of metres in width and up to several hundred metres in length. These are separated by areas of completely bare, indurated soil. Measurements were concentrated on seven vegetation strips around the micrometeorological towers. The dominant species were *Combretum nigricans* Lepr. ex Guill. et Perrott (a tree up to 10 m) and the shrubs *C. micranthum* and *G. senegalensis* (typically 2–4 m tall). Other less frequent tree species included *Acacia ataxacantha* DC., *Sclerocarya birrea* (A. Rich.) Hochst. and *Boscia angustifolia* A. Rich. A herb layer was present that included all the major species present at the fallow site plus several more. However, the herb layer did not develop to the same extent as on the fallow site and no measurements were made on it. The mean height of the vegetation was estimated to be around 4 m. The vegetated strips cover approximately 33% of the surface area (estimated from aerial photographs).

Soil at the site was gravelly sandy loam or gravelly loam to a depth of 0.1–0.5 m, above weathered laterite, with solid laterite starting at 0.2–0.9 m. In the open areas, the surface is more or less impermeable to water due to a hard crust. The soils are classified as Xerothents on the bare areas and Ustorthents under the vegetation. Further details of the site are

given by Culf et al. (1993), Wallace et al. (1994) and Wallace and Holwill (1997, this volume).

### 3. Leaf area index and biomass

#### 3.1. Methods

##### 3.1.1. Millet

Estimates of leaf area index (LAI) were made on three occasions between July and September. Around 60 tillers were harvested on each occasion and the following attributes measured: tiller height from the base to the tip of the uppermost leaf when fully extended upwards, green leaf area using a Li-Cor 3100 area meter, and culm length and diameter. The area of the culm was calculated, assuming the shape to be cylindrical, and included in the leaf area estimate, as the tissue was green and photosynthetic. Panicle area was not included. Dry mass was measured on a sub-sample of tillers. Equations to predict surface area and dry biomass from tiller height were derived by linear regression.

The distribution of tiller heights was measured in the field in July and August. Measurements were made at sampling points, located at 10 m intervals on two 100 m transects to the SW of the micrometeorological mast. At each point, the height of every tiller in the four nearest pockets was measured, along with pocket spacing and diameter. LAI was estimated at each point by calculating the mean leaf area of the four pockets from the established relationship between tiller height and area and multiplying by the number of pockets per square metre. Biomass was estimated in a similar way from the relationship between tiller height and dry mass.

In early September, little further growth had occurred and large areas of the crop had senesced. Simple relationships between tiller height and area were not present. Consequently, estimates of LAI were based on the proportion of leaf area which had become senescent since the August measurement. Tillers were harvested as before and their height and green leaf area measured. For each tiller, senescence was estimated from the ratio of measured green leaf area to that predicted by the equation derived in August relating tiller height and leaf area. No relationship was present between tiller height and percent senescence, so the mean value was taken and applied to the August LAI estimates.

##### 3.1.2. Fallow — *G. senegalensis*

A survey of the *G. senegalensis* bushes on the fallow site was carried out in February 1992. For each bush, the  $x$ - $y$  co-ordinates with respect to the University of Edinburgh micrometeorological tower were recorded along with bush height, maximum and minimum radii, height of maximum diameter, number of stems less than 10 mm diameter and diameter of all larger stems. All stem diameters were measured at a point 20 cm above the base. The survey covered 220 bushes in an area of approximately 6750 m<sup>2</sup>.

Measurements of leaf area and biomass were made on *G. senegalensis* stems approximately monthly between June and October 1992. Up to 26 stems were harvested on each occasion and the stem diameter, total fresh mass and fresh mass of leaves

recorded. A sub-sample of leaves was taken from each stem for fresh mass, dry mass and surface area measurements using an Li-Cor 3100. Specific leaf area calculated from these measurements was used to estimate the total leaf area for the stem. Regression analysis was used to derive relationships between stem cross-sectional area at 20 cm and both leaf area and fresh biomass. The distribution of stem diameters in the surveyed area was then used to estimate the *G. senegalensis* LAI and biomass per square metre.

Wood surface area was estimated on a small sample of three stems. Each stem was cut into small sections which were then divided into 5 mm diameter classes. The volume of wood in each diameter class was calculated from mass and density measurements. These volumes were converted to surface areas by assuming a surface area to volume ratio of a cylinder with diameter equal to the mid-point of the diameter class. The relationship between the total wood surface area and the basal cross-sectional area of the three stems was used to estimate stem area index for the site as above.

3.1.3. Fallow — ground flora

Estimates of species composition and LAI of the herbs and grasses in the ground layer were made in 24 permanent quadrats (0.5 × 0.5 m) on three occasions over the season. Each quadrat was assessed visually and assigned an arbitrary index of LAI between 0 and 100. This subjective index was calibrated on each occasion by making the same assessment in ten other quadrats which were then measured directly by harvesting and

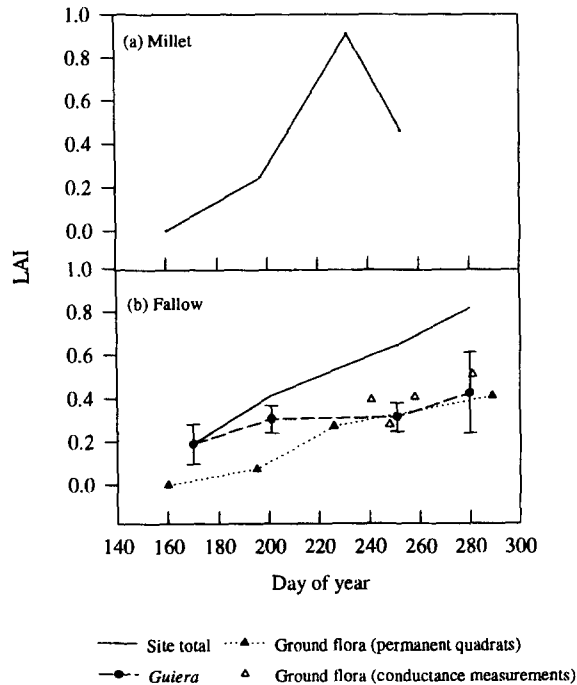


Fig. 2. Changes in the leaf area index (LAI) of the millet and fallow sites over the 1992 growing season. Error bars show 95% confidence intervals for *G. senegalensis*.

determining the surface area with an Li-Cor 3100. Good linear relationships were found between the visual estimates and measured values on each occasion and used to estimate LAI for the permanent quadrats. Direct measurements of LAI were also made in areas enclosed by an evaporation chamber for measurements of herb surface conductance.

#### 3.1.4. Tiger bush

Hemispherical photographs were taken each month at points along transects through the vegetated areas. These transects were placed systematically in the seven vegetated areas nearest the micrometeorological mast, and ran in the direction of the slope, as species composition was different on the up-slope side. The photographs were analysed to give estimates of plant surface area index by gap fraction methods (Norman and Campbell, 1989). Leaf phenology was examined in *C. nigricans*, *C. micranthum* and *G. senegalensis* by marking a number of shoots with coloured tags and counting the number of leaves present each month. A survey of shrub dimensions and stem diameters was carried out in a small area of one vegetated strip. This was used only for canopy structure information.

### 3.2. Results

Fig. 2 shows the increase in LAI of the millet and fallow sites over the wet season. The development of the vegetation begins much earlier at the Southern Super-site than at the central Super-sites, presumably because of the distribution of rainfall. By early September, 50% of the millet surface area present in mid-August had become senescent. At the peak of development, the ground flora at the fallow site comprised around 50% of the leaf area on the site and the stem area index was estimated to be 0.12. The value of LAI for the vegetated areas of tiger bush obtained from hemispherical photographs taken in early October was 2.1. This gives a site average of 0.7 if the vegetation covers only one third of the site. Leaf area was divided approximately evenly between *C. nigricans*, *C. micranthum* and *G. senegalensis*. Peak LAI was similar at all three sites.

## 4. CO<sub>2</sub> flux measurements

### 4.1. Methods

#### 4.1.1. Leaf CO<sub>2</sub> and H<sub>2</sub>O exchange

Simultaneous measurements of leaf CO<sub>2</sub> flux and stomatal conductance were made using a portable open gas exchange system (LCA3, ADC Ltd, Hoddeson, UK) between July 1991 and October 1992. Measurements were made on *P. glaucum*, *G. senegalensis*, *C. mimosoides*, *E. tremula*, *M. villosus*, *C. biflorus*, *A. ataxacantha*, *C. micranthum* and *C. nigricans*. Observations were of two types: those made rapidly (within one minute) so as to be representative of the functioning of the leaf in ambient conditions and those made over several minutes, during which shading was used to investigate the response of CO<sub>2</sub> flux to PPFD.



#### 4.1.2. Wood CO<sub>2</sub> exchange

*In situ* measurements of woody tissue CO<sub>2</sub> flux were made on *G. senegalensis* and *C. micranthum* between February and October 1992. The measurements were made using the same system as for leaves but with purpose-built chambers. Chambers designed to fit on to stems in the field were used, consisting of a perspex tube split longitudinally with rubber seals fitted to the cut edges and ends. Individual stems were monitored continuously for up to ten days. Output voltages from the gas analyser were recorded on a data logger, together with stem temperature and incident PPF. D.

#### 4.1.3. Soil CO<sub>2</sub> exchange

An attempt was made to quantify soil CO<sub>2</sub> flux using an open gas exchange systems with specially designed chambers pressed into the soil. A system using the LCA3 analyser with a small cylindrical chamber was employed at the fallow site. A very limited data set was obtained and is not presented here.

#### 4.1.4. Canopy CO<sub>2</sub> exchange

Half-hourly fluxes of the net CO<sub>2</sub> exchange of the three vegetation types were measured

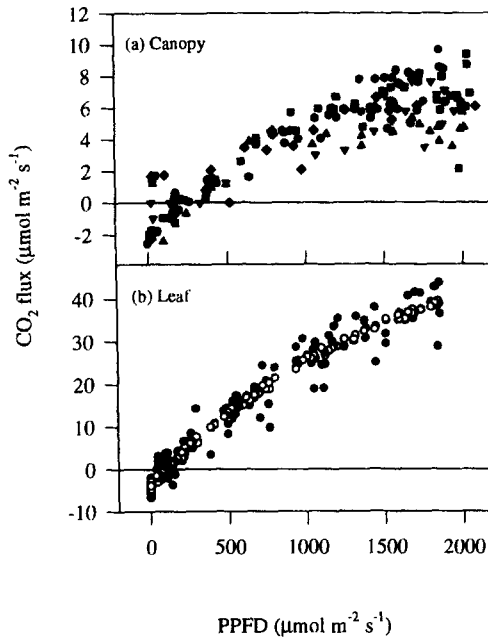


Fig. 3. Relationship between CO<sub>2</sub> flux and PPF at (a) canopy and (b) leaf scale in millet. In all cases, canopy fluxes are expressed per unit ground area, whilst leaf fluxes are expressed per unit leaf area, and so are not expected to be equivalent in magnitude. (a) Points represent half hourly averages of eddy covariance data collected between 5th and 11th September, when the LAI was estimated to be 0.46. Symbols represent data from different days. (b) Points represent data from leaf chamber measurements made on green leaves in July and August, using shading to manipulate PPF. The MAESTRO leaf photosynthesis sub-model incorporating dark respiration was fitted to the data (open circles).

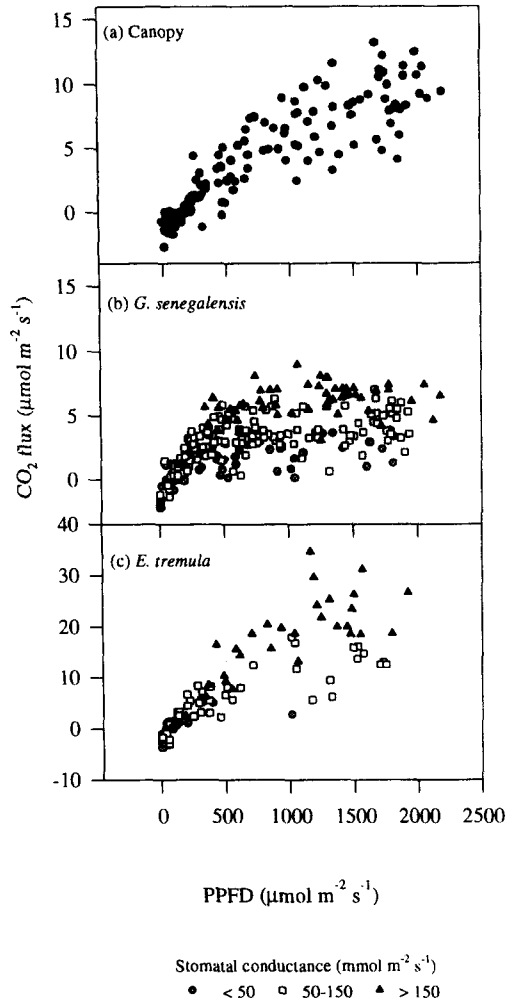


Fig. 4. Relationship between  $\text{CO}_2$  flux and PPFD at the fallow site at (a) canopy scale, (b) leaf scale in *G. senegalensis* and (c) leaf scale in *E. tremula*. Canopy scale data are half hourly averages covering the period 27th August to 5th September, when the total LAI was estimated to be 0.64. Leaf scale data were collected between July and October 1992.

using a closed-path eddy covariance system. The system which had been developed within a consortium of European laboratories is fully described elsewhere (Moncrieff et al., 1997, this volume). EddySol software was used to provide real-time, continuous monitoring of  $\text{CO}_2$  flux and mean atmospheric concentration of carbon dioxide. Surface fluxes were corrected for density fluctuations (Webb et al., 1980) for losses in the closed-path system (Leuning and Moncrieff, 1990) and other system losses (Moore, 1986). At the millet site, an eddy covariance  $\text{CO}_2$  system was mounted on a mast at a height of 9 m above the ground, with a fetch over millet of  $\approx 1.5$  km in all directions, except for a thin strip of

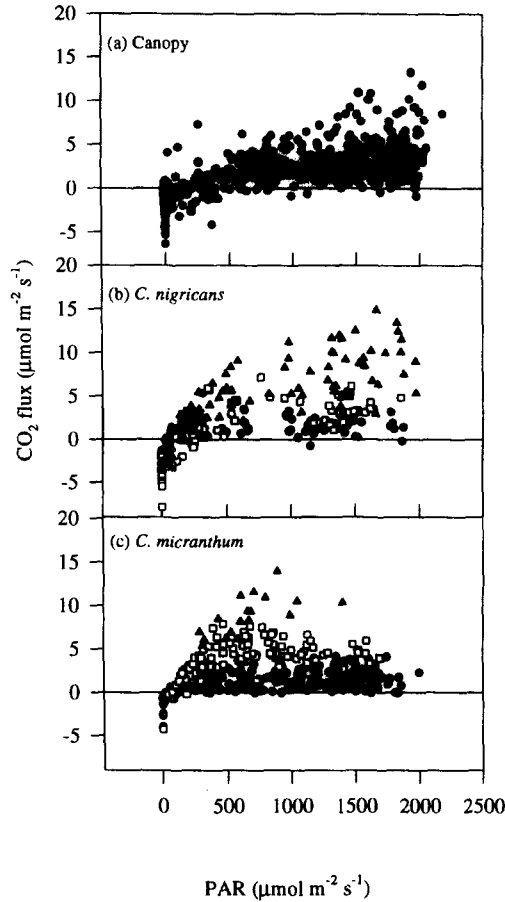


Fig. 5. Relationship between  $\text{CO}_2$  flux and PPFD at the tiger bush site at (a) canopy scale, (b) leaf scale in *C. nigricans* and (c) leaf scale in *C. micranthum*. Canopy scale data are half hourly averages covering the period 14th September to 9th October, when the site average LAI was estimated to be 0.70. Leaf scale data were collected between February and October 1992. Symbols are as in Fig. 4.

fallow land about 400 m away to the south and west. At the fallow site, the eddy covariance  $\text{CO}_2$  system was mounted on a mast at a height of 9 m above the ground, with a fetch of  $\approx 400$  m in most directions. A third eddy covariance  $\text{CO}_2$  system at the tiger bush site was mounted on a tall tower at 18 m, with a fetch of at least 1 km in all directions. The source area model of Schuepp et al. (1990) showed that fetches were adequate at all the sites. Under normal daytime conditions at the millet and fallow sites, around 90% of the signal measured at 9 m came from within 400 m of the masts. Weather stations at each site were left in place over the growing seasons in 1991 and 1992. Solid state data loggers (21X and CR10, Campbell Scientific Ltd, UK) were used to record instrument output every 10 seconds and average over 10 minutes.

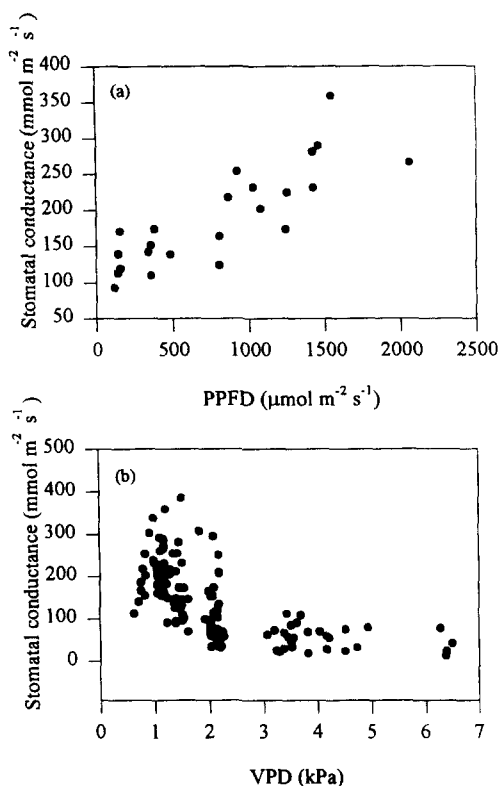


Fig. 6. Relationship between stomatal conductance and (a) PPFD and (b) VPD in *G. senegalensis*. (a) Data shown are measurements made on three shoots from a single stem on 9th September. (b) The data collected between February and September 1992 are shown.

#### 4.2. Results

Figs. 3, 4 and 5 show the relationship between CO<sub>2</sub> flux and incident PPFD for the three sites at canopy and leaf scales. In all cases, canopy fluxes are expressed per unit ground area, whilst leaf fluxes are expressed per unit leaf area, and so are not expected to be equivalent in magnitude. Fig. 3 shows data for millet. The shape of the curves is similar, neither showing saturation in full PPFD as is typical of C4 photosynthesis. There is rather more variability in the canopy measurements (relative to the maximum value) which is largely unexplained. The relationship tends to be more constant within individual days, and may reflect day-to-day variation in wind direction, so that the CO<sub>2</sub> flux signal comes from areas differing in crop growth on different days. The magnitude of the flux was much less at canopy scale than at leaf scale (a maximum of around 10 compared with 44 μmol m<sup>-2</sup> s<sup>-1</sup>) for several reasons. The leaf area index (LAI) of the millet site at the time of measurements was 0.46. In the leaf scale measurements, the leaf blade was always held normal to the measured radiation, whilst at canopy scale, the leaves are distributed over a range of angles relative to the horizontal PPFD sensor. Although the LAI was low, leaves were clumped together on plants and in pockets and shaded each other. The magnitude of

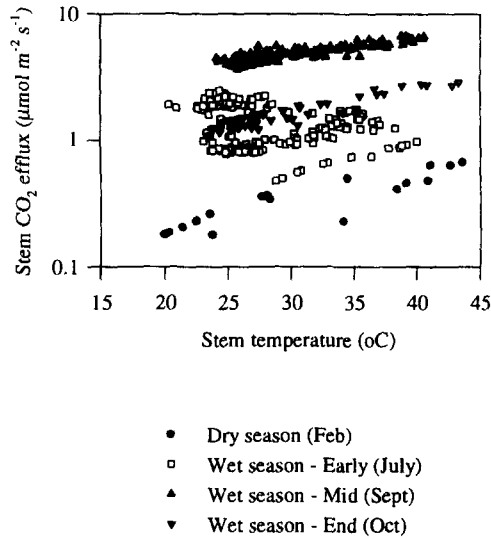


Fig. 7. Relationship between stem CO<sub>2</sub> efflux in *C. micranthum* and stem temperature during 1992. Measurements were made over several days on two to three stems in each period. Data shown are hourly averages, expressed on a stem surface area basis (note logarithmic scale).

the canopy flux was also low in relation to other C4 crops: in their review, Ruimy et al. (1995) found a mean value of  $33 \mu\text{mol m}^{-2} \text{s}^{-1}$  for the canopy flux at  $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD in C4 crops, compared with  $10 \mu\text{mol m}^{-2} \text{s}^{-1}$  here. This is largely explained by the low LAI, as leaf fluxes are relatively high.

Fig. 4 shows the relationship between CO<sub>2</sub> flux and PPFD at the fallow site for the canopy, leaves of *G. senegalensis* and leaves of the C4 grass *E. tremula*, the most common species in the ground flora. Saturation is not apparent in the canopy relationship or that of *E. tremula* but *G. senegalensis* was clearly PPFD-saturated at around  $700 \mu\text{mol m}^{-2} \text{s}^{-1}$ . This is characteristic of the difference between C3 and C4 photosynthesis. The shape of the canopy relationship is intermediate between the two leaf-level relationships shown, as a lower slope is apparent beyond the point of PPFD saturation in *G. senegalensis*. The magnitude of the canopy flux was also intermediate. As in millet, the canopy flux was lower than the mean value for C4 grasslands at  $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$  PPFD found by Ruimy et al. (1995) ( $23 \mu\text{mol m}^{-2} \text{s}^{-1}$ , compared with our value of  $12 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). A clear effect of stomatal conductance on leaf photosynthesis can be seen in both species. The relationships between stomatal conductance and PPFD and saturation water vapour pressure deficit (VPD) in *G. senegalensis* are shown in Fig. 6.

The relationships between PPFD and CO<sub>2</sub> flux for the tiger bush site are shown in Fig. 5. At stomatal conductances below  $150 \text{mmol m}^{-2} \text{s}^{-1}$ , leaf photosynthesis in both *Combretum* species was clearly PPFD-saturated at around  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The influence of stomatal conductance on leaf photosynthesis is again apparent in both species. The shape of the canopy relationship was similar to that at leaf scale, and there is no clear relationship with PPFD beyond around  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Although not shown here, there was a notable decrease in the canopy flux over the three week measurement period, which

coincided with the transition from wet to dry season. This accounts for some of the considerable variability seen in Fig. 5(a). The magnitude of the canopy flux was similar to that of the leaf fluxes.

The results of stem CO<sub>2</sub> efflux measurements on *C. micranthum* are shown in Fig. 7 and results were similar for *G. senegalensis*. Other measurements indicate that the flux is proportional to stem surface area (Levy, 1995) and data are expressed on this basis. The results show an exponential increase with temperature. At 40°C, dry season rates were generally less than 1  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in both species and between 2 and 6  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in the growing season. Within the growing season, rates were highest in August and early September, the peak of the season, and were lower in July and October in both species.

#### 4.3. Discussion

The relationships with PPFD indicate the extent to which CO<sub>2</sub> flux can be predicted from one or two primary variables. Under ambient conditions, leaf photosynthesis in millet never became PPFD-saturated for two reasons. Leaf conductance was generally high, rarely below 300  $\text{mmol m}^{-2} \text{s}^{-1}$  in sunny conditions. Even at low leaf conductances, the supply of CO<sub>2</sub> to the site of carboxylation was always maintained by the C4 mechanism of phosphoenolpyruvate carboxylase. Consequently, PPFD was the only significant controlling variable, with leaf temperature having an effect on respiration, but no evident effect on photosynthesis over the range 28 to 42°C.

The situation is less simple in C3 plants such as the fallow and tiger bush shrubs, where PPFD saturation occurred at around 500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and stomatal conductance was the

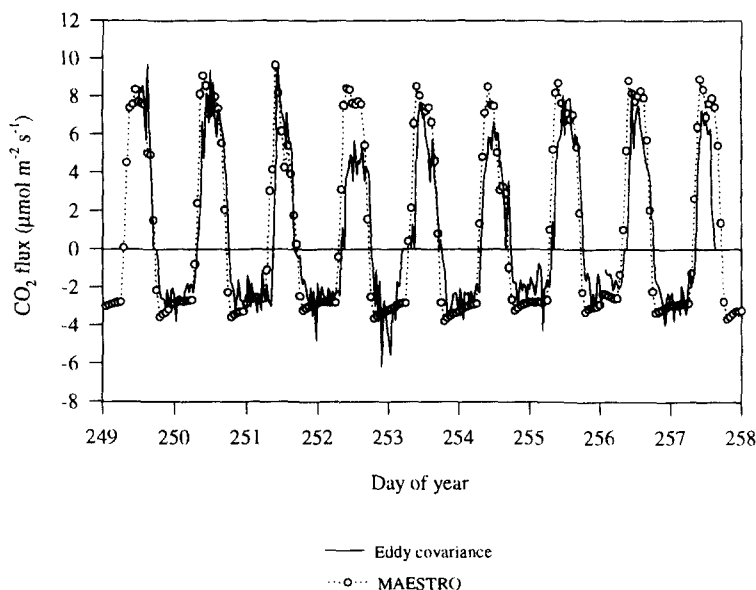


Fig. 8. Comparison between eddy covariance measurements and MAESTRO predictions of CO<sub>2</sub> flux at the millet site for the period 5th to 12th September, 1992.

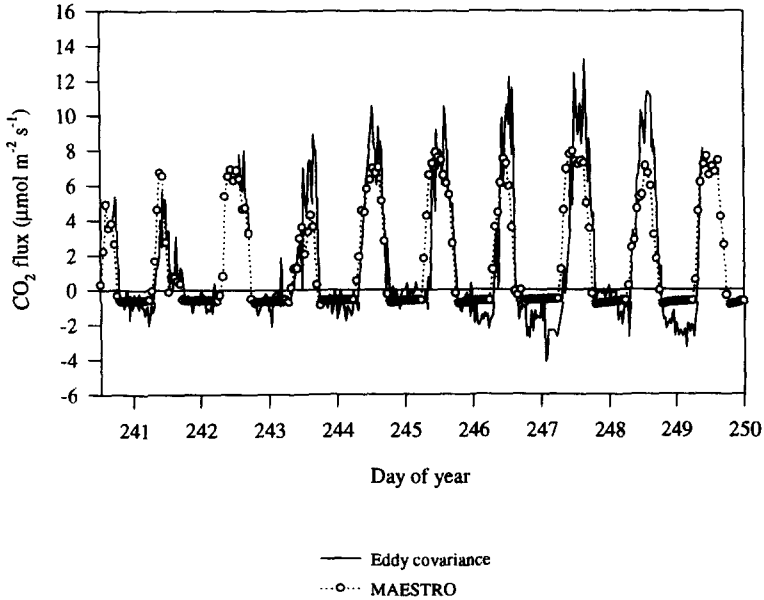


Fig. 9. Comparison between eddy covariance measurements and MAESTRO predictions of  $\text{CO}_2$  flux at the fallow site for the period 27th August to 4th September, 1992.

dominant factor beyond this point. In *E. tremula*, although saturation was not found, the slope of the PPF<sub>D</sub> relationship was reduced at lower leaf conductances. As a result, the relation between conductance and other environmental variables (Fig. 6) was used to predict photosynthetic rate. However, stomatal behaviour was not always easy to predict on this basis, and the influence of PPF<sub>D</sub>, temperature and VPD accounted for only around 50% of the variability in the data. This relatively poor fit may be explained by several factors. Stomatal action is an inherently more complex phenomenon than photosynthesis, and responds to variables such as leaf or soil water status which were not measured. The response time is longer (minutes rather than nanoseconds) so a steady state may not be measured.

The seasonal pattern in stem  $\text{CO}_2$  flux is attributable to changes in growth respiration. The dry season values represent the basal maintenance rate. As growth begins in the wet season, respiration rates are increased by the costs of producing new tissue (Sprugel and Benecke, 1991). The values found fell within the range of 1.3 to 5.3  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at 20°C quoted by Jarvis and Leverenz (1983) for a wide range of species during times of high meristematic activity. A maximum value of 2.8  $\mu\text{mol m}^{-2} \text{s}^{-1}$  was obtained for *C. micranthum* by extrapolation to this temperature.

## 5. Canopy modelling

### 5.1. Parameterisation

The leaf scale measurements of photosynthesis, stomatal conductance and respiration

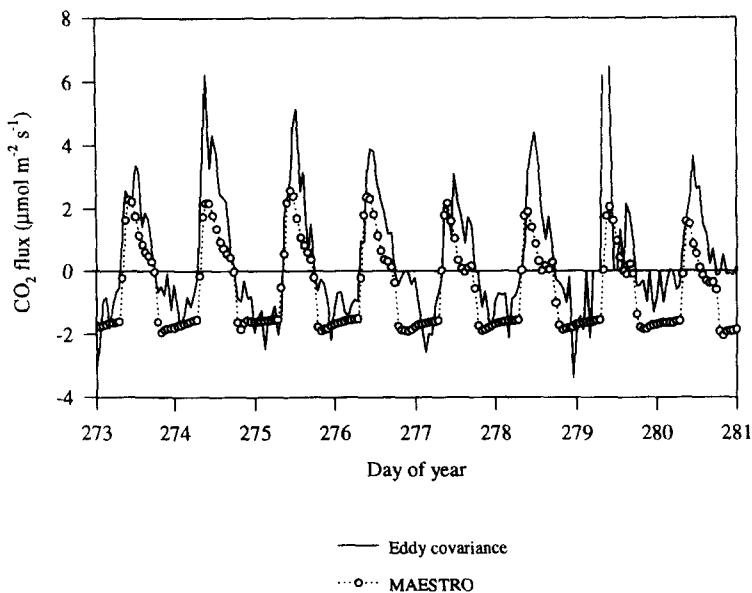


Fig. 10. Comparison between eddy covariance measurements and MAESTRO predictions of  $\text{CO}_2$  flux at the tiger bush site for the period 1st to 8th October, 1992.

were used to derive the physiological parameters for MAESTRO. The sub-models were fitted to the data using least squares nonlinear regression (SPSS statistical software). The key parameters required were: for photosynthesis, quantum efficiency, convexity of the PPFD response, maximum mesophyll conductance; for respiration, the basal rate and temperature response parameters for leaf, wood and soil; for stomatal conductance, maximum and minimum values, the initial slope of the response to PPFD, and an empirical parameter determining the decrease with VPD. Close fits to the physiological sub-models were achieved, accounting for 79–97% of the variation in the leaf  $\text{CO}_2$  flux data (depending on the species).

The canopy structure parameters were derived from the direct measurements of leaf area and its 3-D distribution. The millet clumps were represented as an array of cones at 1.4 m spacing. In the more heterogeneous canopies of the fallow and tiger bush site, the measurements of shrub dimensions and co-ordinates were used to represent the canopy structure of the measured areas in the model, with each individual represented as a half-ellipsoid. The fallow site ground flora were represented as a homogeneous layer beneath the bushes.

Measurements of leaf optical properties were made with a portable custom-built instrument. Other parameters, such as soil reflectance, were taken from the literature as no measurements were available. The driving meteorological variables were obtained from weather stations at each site, located on the micrometeorological masts.

## 5.2. Results

Fig. 8 shows very close agreement between the measured  $\text{CO}_2$  fluxes and MAESTRO



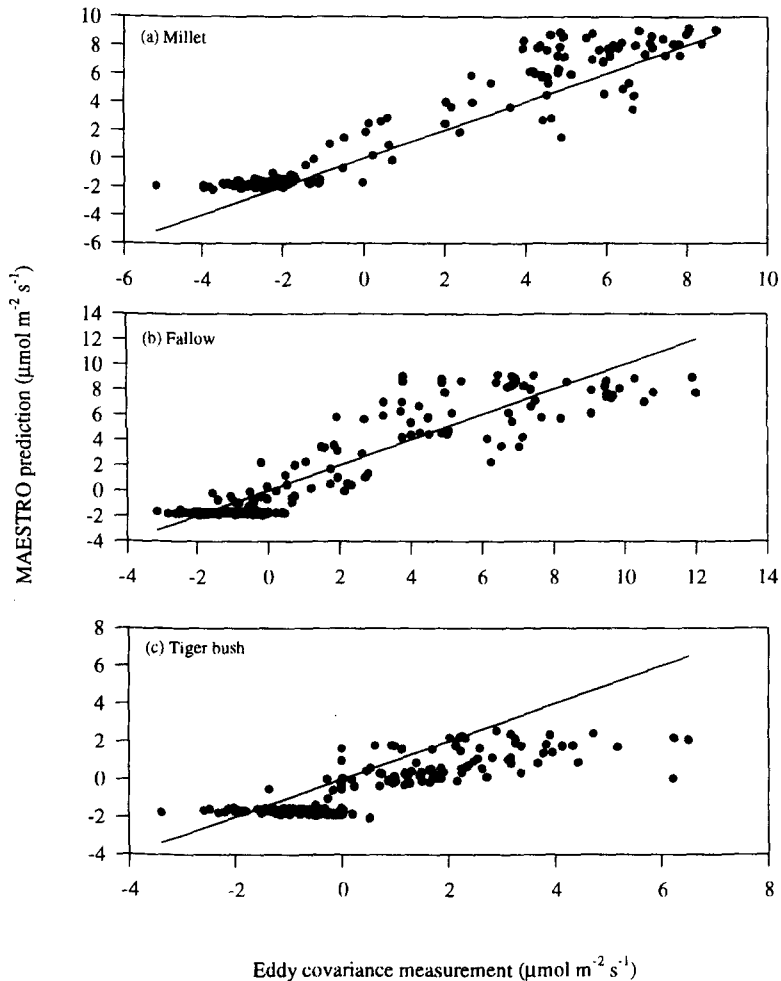


Fig. 11. Plots of MAESTRO predictions of CO<sub>2</sub> flux against eddy covariance measurements for the three sites. Data are the same as shown in Figs 8–10. 1:1 lines are shown.

predictions for millet. The model tended to overestimate slightly after day 251, but this was only substantial on day 252. Figs. 9 and 10 show that agreement was poorer but still acceptable for the fallow site, although the model underestimated fluxes at the tiger bush site. The measurements at these sites show rather more variability than the model predicted, and hourly averages are plotted in Fig. 10 to reduce some of the scatter seen in Fig. 5(a). After day 242, the model tended to underestimate the fluxes at the fallow site. This may possibly be the result of sampling error in the LAI estimate for this period: Fig. 2(b) shows little increase in LAI of *G. senegalensis* between the July and September measurements, although this was the main part of the growing season. It seems likely that the September LAI estimate is erroneously low, as the slope of the regression line relating

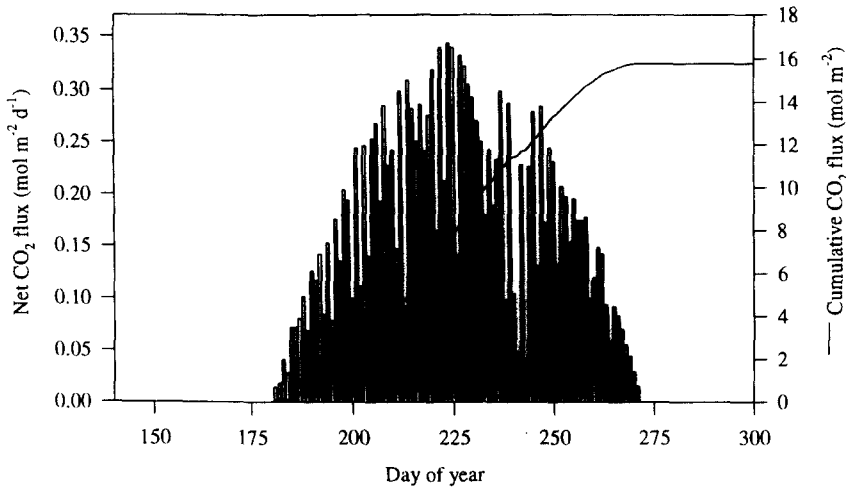


Fig. 12. Predictions of net daily CO<sub>2</sub> flux at the millet site over the 1992 growing season made using MAESTRO.

stem diameter and leaf area is lowered by a single large stem. Closer agreement was found if the model was run with the upper confidence limit of LAI.

A more rigorous comparison is obtained by plotting MAESTRO predictions of CO<sub>2</sub> flux against eddy covariance measurements. The errors in MAESTRO predictions in millet do not deviate systematically from the measurements (Fig. 11(a)). The model tended to overestimate in fallow below about  $7 \mu\text{mol m}^{-2} \text{s}^{-1}$ , but consistently underestimated beyond this point (Fig. 11(b)). At the tiger bush site, the model generally underestimated by a roughly constant proportion over the whole range (Fig. 11(c)). Linear regression between MAESTRO predictions and eddy covariance measurements showed close linear relationships, giving  $r^2$  values of 0.91, 0.84 and 0.71 for the millet, fallow and tiger bush sites, respectively, indicating that the model accounted for most of the variation in the measurement data when systematic error was removed.

### 5.3. Discussion

In order to predict canopy CO<sub>2</sub> flux, the processes controlling the flux at leaf scale and the factors involved in scaling up from leaf to canopy need to be understood. The comparison of measured canopy fluxes with the predictions made independently by MAESTRO represents a test of our understanding of both of these. At all sites, the agreement is generally good, as the model simulated the magnitude and broad features of the diurnal curve with reasonable accuracy. We conclude that our understanding of leaf scale CO<sub>2</sub> flux in terms of PPFD, temperature and conductance is satisfactory and that the simulation of canopy microclimate within MAESTRO is adequate. The model does appear to have weaknesses, however. A photosynthetic response of the fallow vegetation to water supply is visible in the data (Fig. 9), as the vegetation became more active after rain on 28 and 30 August (days 241 and 243). This is not simulated well by the model, possibly as the rain had a longer term influence via leaf water status, which was not measured, as well as the

effect on atmospheric VPD. A similar result was found by Kim and Verma (1991) in temperate grassland.

The larger variability in measurements relative to model predictions at the fallow and particularly the tiger bush site may be because the model simulates a single patch, whilst the area measured by eddy covariance changes as the 'flux footprint' changes with wind speed and direction. This may explain why this variability is greatest at the tiger bush site and least in millet, as it corresponds with the range of canopy heterogeneity, and so the differences amongst the areas being sampled are largest in tiger bush. This would appear to be an unavoidable problem in using eddy covariance to validate the model where the canopy is not homogeneous. Night-time data are considerably more variable than daytime data, relative to model predictions, although the model generally estimates the mean nocturnal flux correctly. This is largely unexplained, but may be related to the difference between the turbulence regimes during the day and night.

The model predicts the magnitude of fluxes at the millet site more accurately than at the fallow or tiger bush sites, irrespective of the difference in variability in the measurements. This is likely to be for two reasons. Firstly, the control of CO<sub>2</sub> flux at the leaf scale is simpler in millet, as discussed in Section 4.3. Secondly, measurement of canopy properties was considerably simpler at the millet site than at the other sites. The millet canopy was relatively uniform at a large scale and had a regular structure, allowing the LAI and spatial distribution parameters to be measured accurately. The measurement of the amount and distribution of leaf area in the irregular canopy structures found in natural ecosystems is one of the most difficult tasks involved in this approach.

Analysis of model predictions for the fallow site illustrates the importance of representing the canopy in three dimensions. The bush and ground flora components behaved very differently because of both their different physiology and spatial distribution. Despite the similar leaf area in the two components, the CO<sub>2</sub> flux to the ground flora was much larger than to the bushes, and this phenomenon may not be captured properly in a simple one-dimensional model.

The validated parameterisation of MAESTRO for the millet site was used to predict fluxes for the whole growing season from hourly meteorological data. The phenology measurements shown in Fig. 2(a) were used to update the leaf area parameters in the model on a daily time step. The predicted daily net CO<sub>2</sub> fluxes closely follow the course of LAI over the growing season (Fig. 12). The sum of these daily fluxes up to the harvest on day 232 gives a value of 9.8 mol C m<sup>-2</sup> or 250 g biomass m<sup>-2</sup>, assuming that biomass consisted of 47% carbon (Penning de Vries et al., 1989, p. 64). This agrees well with the value of 258 g biomass m<sup>-2</sup> from the above-ground biomass estimate described in Section 3.1. It should be noted that the discrepancy will be larger in reality, as roots are not included in the biomass measurements, and will add approximately 20% to the biomass estimate (Brouwer et al., 1997).

## 6. Conclusions

The leaf scale CO<sub>2</sub> fluxes were well accounted for by the physiological sub-models, with PPFD and stomatal conductance strongly determining the photosynthetic rate.

MAESTRO predictions were relatively accurate at the millet and fallow sites. At the tiger bush site, MAESTRO consistently underestimated the canopy CO<sub>2</sub> flux and this was attributed to error in the LAI measurements, as the effect of canopy heterogeneity on eddy covariance measurements would produce random rather than systematic errors. The error in the LAI estimates may be related to the indirect measurement technique or simply sampling error. Comparison of the independent canopy flux measurements with predictions is informative, as the model represents an integration of our knowledge of the system, and so differences highlight weak points in our understanding as well as measurement artefacts. The model predicted a value for carbon sequestration at the millet site over the growing season close to harvest measurements, given the uncertainty introduced by the comparison with biomass production rather than with measured CO<sub>2</sub> fluxes. This suggests that the theory on which the model is based is sound, as it apparently copes well with the range of LAI and environmental variables encountered over the year.

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### References

- Box, E.O., 1988. Estimating the seasonal carbon source-sink geography of a natural, steady-state biosphere. *J. Appl. Meteorol.*, 27: 1109–1124.
- Brouwer, J., Simmonds, L.P., Gaze, S.R. and Levy, P.E., 1997. Spatial variability and upscaling of millet root, shoot, and leaf growth at the HAPEX- Sahel Southern Supersite, in preparation.
- Charney, J., 1975. Dynamics of deserts and droughts in the Sahel. *Quart. J. Royal. Met. Soc.*, 101: 193–202.
- Culf, A.D., Allen, S.J., Gash, J.H.C., Lloyd, C.R. and Wallace, J.S., 1993. The energy and water budgets of an area of patterned woodland in the Sahel. *Agric. Forest Meteorol.* 66: 65–80.
- Farquhar, G.D. and von Caemmerer, S., 1982. Modelling of photosynthetic response to environmental conditions. In: O.L. Lange, P.S. Nobel, C.B. Osmond and H. Zeigler (Editors), *Encyclopedia of Plant Physiology*. Vol. 12D. Springer-Verlag, Berlin, pp. 549–588.
- Fung, I., Prentice, K., Mathews, E., Lerner, J. and Russell, G., 1983. Three dimensional tracer model study of atmospheric CO<sub>2</sub>: response to seasonal exchanges with the terrestrial biosphere. *J. Geophys. Res.*, 88: 1281–1294.
- Grace, J.C., Jarvis, P.G. and Norman, J.M., 1987. Modelling the interception of solar radiant energy in intensively managed stands. *New Zealand J. Forest Sci.*, 17: 193–209.
- Jarvis, P.G., 1976. The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. *Phil. Trans. R. Soc. London Ser. B*, 273: 593–610.
- Jarvis, P.G. and Leverenz, J.W., 1983. Productivity of temperate deciduous and evergreen forests. In: O.L. Lange, P.S. Nobel, C.B. Osmond and H. Zeigler (Editors), *Physiological Plant Ecology IV*. Springer-Verlag, Berlin, pp. 233–280.
- Kim, J. and Verma, S.B., 1991. Modelling canopy photosynthesis: scaling up from a leaf to canopy in a temperate grassland ecosystem. *Agric. Forest Meteorol.*, 57: 187–208.
- Le Roux, X. and Mordelet, P., 1995. Leaf and canopy CO<sub>2</sub> assimilation in a west African humid savanna during the early growing-season. *J. Trop. Ecology.*, 11: 529–545.
- Leuning, R. and Moncrieff, J.B., 1990. Eddy covariance CO<sub>2</sub> flux measurements using open- and closed-path CO<sub>2</sub> analysers: corrections for analyser water vapour sensitivity and damping of fluctuations in air sampling tubes. *Boundary Layer Meteorology*, 53: 63–76.

- Levy, P.E., 1995. CO<sub>2</sub> exchange of Sahelian vegetation in HAPEX-Sahel. Unpublished Ph.D. thesis, University of Edinburgh.
- Moncrieff, J.B., Massheder, J.M., De Bruin, H., Elbers, J., Friborg, T., Huesinkveld, B., Kabat, P., Scott, S., Soegaard, H. and Verhoef, A., 1997. A system to measure surface fluxes of momentum, sensible heat, water vapour and carbon dioxide. *J. Hydrology*, this volume.
- Moore, C.J., 1986. Frequency corrections for eddy correlation systems. *Boundary Layer Meteorology*, 37: 17–35.
- Norman, J.M. and Campbell, G.S., 1989. Canopy structure. In: R.W. Pearcy, J. Ehleringer, H.A. Mooney and P.W. Rundel (Editors), *Plant Physiological Ecology: Field Methods and Instrumentation*. Chapman and Hall, London, pp. 301–325.
- Penning de Vries, F.W.T., Jansen, D.M., ten Berge, H.F.M. and Bakema, A., 1989. Simulation of ecophysiological processes of growth in several annual crops. Pudoc, Wageningen. 271 pp.
- Reed, K.L., Hamerly, E.R., Dinger, B.E. and Jarvis, P.G., 1976. An analytical model for field measurements of photosynthesis. *J. Appl. Ecology*, 13: 925–932.
- Ruimy, A., Jarvis, P.G., Baldocchi, D.D. and Saugier, B., 1995. CO<sub>2</sub> fluxes over plant canopies and solar radiation: a review. *Adv. Ecol. Res.*, 26: 1–68.
- Sellers, P.J., Mintz, Y., Sud, Y.C. and Dalcher, A., 1986. A simple biosphere model (SiB) for use within General Circulation Models. *J. Atmos. Sci.*, 43: 505–531.
- Sprugel, D.G. and Benecke, U., 1991. Measuring woody-tissue respiration and photosynthesis. In: J.P. Lassoie and T.M. Hinckley (Editors), *Techniques and Approaches in Forest Tree Ecophysiology*. CRC Press, Berlin, pp. 329–355.
- Schuepp, P.H., Leclerc, M.Y., Macpherson, J.I. and Desjardins, R.I., 1990. Footprint prediction of scalar fluxes from analytical solutions of the diffusion equation. *Boundary Layer Meteorol.*, 9: 355–373.
- Wallace, J.S. and Holwill, C.J., 1997. Soil evaporation from tiger-bush in south-west Niger. *J. Hydrology*, this volume.
- Wallace, J.S., Brouwer, J., Allen, S.J., Banthorpe, D., Blyth, E.M., Blyth, K., Bromley, J., Buerkert, A.C., Cantwell, M., Cooper, J.D., Cropley, F.D., Culf, A.D., Dolman, A.J., Dugdale, G., Gash, J.H.C., Gaze, S.R., Harding, R.H., Harrison, R.G., Holwill, C.J., Jarvis, P.G., Levy, P.E., Lloyd, C.R., Malhi, Y.S., Massheder, J.M., Moncrieff, J.B., Pearson, D., Settle, J.J., Sewell, I.J., Sivakumar, M.V.K., Sudlow, J.D., Taylor, C.M. and Wilson, A.K., 1994. HAPEX-Sahel Southern Supersite Report: an overview of the site and the experimental programme during the intensive observation period in 1992. Institute of Hydrology, Wallingford, UK. 55 pp.
- Wang, Y.P. and Jarvis, P.G., 1990a. Description and validation of an array model — MAESTRO. *Agric. Forest Meteorol.*, 51: 257–280.
- Wang, Y.P. and Jarvis, P.G., 1990b. Influence of crown structural properties on PAR absorption, photosynthesis and transpiration in Sitka spruce: application of a model (MAESTRO). *Tree Physiology*, 7: 297–316.
- Webb, E.K., Pearman, G.I. and Leuning, R., 1980. Correction of flux measurements for density effects due to heat and water vapour transfer. *Quart. J. Roy. Meteorol. Soc.*, 106: 85–100.