Seasonal patterns of soil carbon dioxide efflux from a wet–dry tropical savanna of northern Australia

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Abstract. Soil CO_2 efflux rates were measured in a Eucalypt open forest in a tropical savanna of northern Australia, using a portable closed chamber and CO_2 gas analyser. Both abiotic (soil temperature and water content) and biotic (litterfall and fine root growth) factors that may influence soil CO_2 efflux were examined. Daytime rates of soil CO_2 efflux rate were consistently higher than nocturnal values. Maximal rates occurred during late afternoons when soil temperatures were also maximal and minimum values were recorded during the early morning (0400 to 0800 h). Average soil CO_2 efflux was 5.37 μmol m^{-2} s^{-1} (range 3.5 to 6.7 μmol m^{-2} s^{-1}) during the wet season and declined to 2.20 μmol m^{-2} s^{-1} (range 1.2 to 3.6 μmol m^{-2} s^{-1}) during the dry season. The amount of carbon released from soil was 14.3 t ha^{-1} yr^{-1}, with approximately 70% released during the wet season and 30% during the dry season. The rate of efflux was correlated with soil moisture content and soil temperature only during the wet season, when root growth and respiration were high. During the dry season there was no correlation with soil temperature. These results are discussed in relation to the carbon balance of tropical savannas.

Introduction

Soils are a major terrestrial carbon reservoir. The amount of carbon in soil in the world, estimated between 1000 and 3000 Pg (1 Pg=10^{15}g), constitutes approximately two-thirds of the carbon in

terrestrial ecosystems (Post *et al*. 1982; Houghton *et al*. 1987). This large size has the potential to exert an influence on the concentration of atmospheric CO_2, net ecosystem production and carbon balance at local, regional, and global scales, through human activities. Beside canopy photosynthesis, the efflux of CO_2 from soils is the largest carbon flux in forest ecosystems. Consequently it is essential to quantify daily and seasonal patterns to gain an understanding of ecosystem carbon dynamics and carbon budgets (Keith *et al*. 1997; Janssens *et al*. 1998; Knapp *et al*. 1998).

Soil CO_2 efflux (F_{cs}) is a sensitive indicator of metabolic activity of the soil and the rate of conversion of soil organic matter to free atmospheric CO_2 (Rochette *et al*. 1997). It is the sum of respiration of roots and rhizomes of plants plus the decomposition of soil organic compounds and detritus (Coleman and Crossley 1996; Lavigne *et al*. 1997) and is a major component of the carbon cycle in terrestrial ecosystems. Detritus production, which results from the death of above- and below-ground plant tissues and soil organisms plus inputs from faecal material, dominates carbon input into soil. Ecosystems with high levels of primary and secondary productivity can be expected to have high soil CO_2 efflux rates (Knapp *et al*. 1998). There have been many measurements undertaken to investigate relationships between F_{cs} and biotic and abiotic factors such as soil temperature (Schlentner and van Cleve 1985; Maggs and Hewett 1990; Lloyd and Taylor, 1994), soil moisture (Howard and Howard 1993; Huc *et al*. 1994), litter moisture content (Keith *et al*. 1997), above-ground productivity (Craine *et al*. 1998), fire (Knapp *et al*. 1998) and land management activities (Toland and Zak 1994). However, there have been few such measurements undertaken in the wet–dry savannas of northern Australia. These landscapes are characterised by little seasonal variation in temperature, but large changes in soil water content and above-ground productivity.

Tropical savannas of Australia consist of open forests, woodlands and grasslands. Since tropical savanna occupy approximately one quarter of the land area of continental Australia, Australian savannas have the potential to significantly influence regional, national and global carbon cycling (Eamus *et al*. 2001). Due to low human population density and minimal tree clearing, savannas of northern Australia are relatively intact ecologically (although the impact of grazing and fire management cannot be ignored) when compared with Australia's southern forests and woodlands, and with savanna ecosystems of other countries. Australia is therefore uniquely placed to investigate fluxes of CO_2 from savannas with relatively few anthropogenic impacts or modification (although the impacts of fire management and grazing are acknowledged).

The objective of this study was to quantify the major carbon fluxes determining soil carbon balance for these open-forest savanna, namely inputs from litterfall and root growth, plus losses in the form of soil CO_2 efflux (F_{cs}). In particular, we pose the following questions: what are the diurnal and seasonal patterns of F_{cs} given the large seasonal changes in soil water content? What is the total carbon efflux from the soil on an annual basis and what is its distribution over the wet–dry cycle? What is the seasonal pattern of carbon inputs to the soil from litterfall and root growth, and finally, what are the relationships between F_{cs}, soil temperature and soil water content for this extensive ecosystem?

Methods

Study site

Investigations were conducted at Howard Springs (latitude 12° 30'S, longitude 130° 45'E), approximately 35 km south of Darwin, Northern Territory, Australia. The climate of this region is wet-dry tropical with rainfall in the wet season (November to April) accounting for over 95% of the annual total of *ca* 1700 mm. Soil water content is at or near saturation for much of this period. The rainless dry season persists from May to September with rapid declines in soil moisture (Hutley *et al*. 2000). Air temperature and solar radiation are high throughout the year. Average daily maximum temperatures at the Darwin Airport (35 km from the field site) range from 30.4^oC (July) to 33.1^oC (October and November), and maximum and minimum temperatures have a range of 7^oC (wet season) and 11^oC (dry season) (McDonald and McAlpine 1991).

Vegetation in the study site is Eucalypt open-forest, the most common community type of coastal northern Australia (Wilson *et al*. 1990). The overstorey is dominated by two evergreen species, *Eucalyptus tetrodonta* (F. Muell.) and *Eucalyptus miniata* (Cunn. Ex Schauer) which form a discontinuous canopy of about 50% cover. Sub-dominant tree species include *Erythrophleum chlorostachys* (F. Muell), *Eucalyptus clavigera* (Cunn. Ex Schauer), *Eucalyptus bleeseri* (Blakely), *Eucalyptus porrecta* (S. T. Blake) and *Terminalia ferdinandiana* (F. Muell).

Soils at the site are predominantly sandy to sandy loams and are classified as red and yellow Kandosols (Isbell 1996). They are extensively weathered and laterised, weakly acidic and low in nutrient status (Russell-Smith *et al*. 1995). Rounded ferricrete gravels occur on the sandy soil surface and throughout the profile, and are between 20 and 50% by volume (Hutley *et al*. 2000).

Soil efflux measurement

A portable closed chamber technique was used to measure F_{cs}. A polythene chamber was a simplified version to that described by Rochette *et al*. (1997), with dimensions of 20 x 21.5 x 12 cm, (W x L x H). Preliminary tests conducted under laboratory conditions demonstrated that the plastic material did not absorb CO_2. Inlet and outlet gas lines were connected to a portable infra-red gas analyser (LI-6200, LiCor Inc., Lincoln, Nebraska, USA), calibrated against a gas cylinder of known CO_2 concentration. Within the chamber, a 12 V fan mixed air to be sampled by the CO_2 analyser. Flux (F_{cs}) was calculated using the rate of change of CO_2 concentration in the system $[CO_2]$:

$$F_{cs} = \frac{\partial [CO_2]}{\partial t}\left(\frac{m_w}{m_v}\right)\left(\frac{V}{A}\right) \tag{1}$$

where V is the total volume of the system, A is the area covered by the chamber and m_w and m_v are the molecular weight and volume of CO_2, respectively.

Estimates of F_{cs} were made every 4 hours over a 2-3–day period during September 1998, April 1999 and July 1999. After this period, measurement frequency was increased to monthly measurements. In all, F_{cs} was determined over more than a 2 year period, from September 1998 to January 2001. Measurements were made by placing the chamber over marked soil plots and inserting the chamber carefully into the sandy soils to a depth of 2 cm. To reduce heat load during daylight hours, measurement duration was short (< 5 min) and the chamber was also covered with reflective foil. Two replicate plots at three randomly selected locations were established within the study area. Locations were approximately 500 m apart from each other, giving 6 plots per sampling time. Once the chamber was in place, the CO_2 concentration was noted. Air entering the IRGA was then scrubbed of CO_2 to approximately 50 µmol mol^{-1} below ambient concentration. Once this was achieved, logging of CO_2 concentration over time commenced and was continued for 3 min for each plot, with F_{cs} calculated every 60 s of sampling. Changes in concentration of CO_2 within the chamber were strongly linear, suggesting no leaks occurred during measurement. Mean F_{cs} was then calculated for each measurement time, based on 18 rate estimates, being 3 x 1–min estimates from 6 replicate plots.

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For each soil efflux plot, soil temperature was measured by placing a thermocouple (Fluke 51K/J, Everett, Washington, USA) 2-3 cm below the soil surface. Soil moisture content (θ_g) was determined gravimetrically using five replicate soil samples, 0-5 cm depth. Samples were taken adjacent to the plots for each monthly measurement period. To convert gravimetric soil moisture to volumetric soil moisture a bulk density of 1.42 kg m^{-3} was assumed (Calder and Day (1982), a value very close to that used by Cook et al (1998) for soils at the Howard Springs site.

Litterfall and fine root growth measurements

To investigate carbon inputs into the soil, litterfall and fine root abundance were monitored in addition to measurements of soil respirations. Seasonal patterns in litterfall was monitored for two years at another site, a nature reserve (Wildlife Park), located approximately 35 km south–west of the Howard Springs. This site was used because of the previous construction of rhizotrons by the Parks and Wildlife Service of the NT and their availability for the present study. Vegetation, climate and soils are very similar to the Howard Springs site, except that the site has not been burnt for approximately 15 years (Bowman, NTU, pers. comm.). As a result, grass cover is lower than the Howard Springs site and trees are taller (18 m). At the Wildlife Park, 18 litter traps, set 80 cm above the ground, were used to collect litterfall. Trap area was 2463 cm^2 and traps were established in three groups of six, with each group approximately 20 m apart. All litterfall (leaves, bark, trigs and woody fruits) were collected at monthly intervals, and the dry weight determined following drying for 7 days at 70°C.

To measure the seasonal changes in fine root growth, 6 rhizotrons were established at the Wildlife Park site. These rhizotrons were originally established by Janos *et al*. (2001). All rhizotrons were established equidistant from the nearest large tree. Pits were dug to a depth of 1 m and were approximately 1 m x 1 m in area, with 6 mm thick pane of toughened glass placed against one vertical wall of each pit. Concrete blocks were used to hold the glass in place and any air-gaps between glass and soil profile were filled with sieved dry soil that was lightly pressed into place. A 25 mm panel of styrene foam plastic was placed on the ground-surface above each pit to provide a removable weatherproof 'roof'. This sheeting was arranged so that it did not suppress the herbaceous layer directly above or adjacent to the glass sheet.

Measurements of fine roots were made fortnightly from November 1998 to March 1999 and from October to December 1999. During other periods (dry season), measurements were made monthly. At this site, fine root abundance was determined by making tracings of root systems in 33 permanently established sub-samples covering approximately 40% of the glass face of each rhizotron

(Janos *et al*. 2001). This was achieved using a wooden template of 33 holes with a diameter of 11.4 cm was used to relocate sub-samples. The wooden template was placed in the same position over the glass wall each fortnight. The pattern of circular holes was hexagonal in a relatively close arrangement, with the first row of three holes overlapped with the second row of the three holes and so on. A desktop scanner was used to digitise the root tracings and the total length of fine roots calculated within each sub-sample. This value of fine root abundance was expressed as total length of fine roots per unit of area (of vertical cross section of soil).

Results

Soil CO_2 efflux, temperature and water content

A typical diurnal course of soil temperature and F_{cs} during the wet and dry seasons is shown in Fig. 1. Wet season soil temperatures were generally lower than dry season, although differences were not large. Maximum soil temperatures were recorded during the late afternoons and reached 40°C in both seasons. Diurnal patterns of F_{cs} were also similar for both wet and dry seasons, with efflux rates following soil temperature (Fig. 1). Maximum F_{cs} occurred during late afternoon (approximately 1600 hours local time) and declined to a minimum during the early morning (0400–0800 hours). However, the magnitude of F_{cs} differed significantly between wet and dry season and tended to follow rainfall. Average values of F_{cs} during the wet season (November to April) was 5.06 ± 1.40 μmol m^{-2} s^{-1}, with a range of 3.5 to 8.4 μmol m^{-2} s^{-1} (Fig.). Rates declined to 1.53 $\pm$0.29 μmol m^{-2} s^{-1} and 1.51$\pm$0.23 μmol m^{-2} s^{-1} during the mid dry season (June to July) and late dry season (August to September) respectively, with a range from 0.95 to 3.5 μmol m^{-2} s^{-1} during this period (Fig. .

Fig. 3 shows the relationship between F_{cs} and soil temperature (mean of 4-hourly data) for each measurement period. In most cases, there was a positive relationships between F_{cs} and T_{soil} during the wet and dry seasons. However, there were 3 occasions where this relationship was weak, July 1999, November 1999 and December 1999. Data from November 1999 were removed from further analysis as there were problems with the LiCor 6200 relating to condensation of water vapour within the gas lines.

To further investigate the relationship between F_{cs} and T_{soil}, the 4-hourly means from all other measurement runs from the 28 months of observations were pooled. Plots of F_{cs} versus T_{soil} from this data set revealed two relationships (Fig. 3), one significant ($F_{cs} = 0.352T_{soil} - 5.26$, $R^2 = 0.55$) for wet soil conditions, $\theta_v > 0.07$ m^3 m^{-3} (θ_g of 5 %), and another non-significant relationship for dry soil, $\theta_v < 0.07$ m^3 m^{-3} ($R^2 = 0.08$). Wet surface soils ($\theta_v > 0.07$ m^3 m^{-3}) resulted in F_{cs} values ranging

from 2.8 to 8.4 $\mu mol\ m^{-2}\ s^{-1}$. Using the wet season regression equation for F_{cs} v. T_{soil}, a Q_{10} for soil respiration at this site was calculated to be 1.99. Under dry soil conditions ($\theta_v < 0.07\ m^3\ m^{-3}$), the magnitude and range of F_{cs} was smaller, ranging from 0.95 to 2.1 $\mu mol\ m^{-2}\ s^{-1}$.

There was a strong and significant relationship between mean daily F_{cs} and θ_v for both wet and dry seasons (

Fig. 4; $F_{cs} = 21.96 \times \theta_v^{0.71}$, $R^2 = 0.91$). Fig. 3 and Fig. 4 suggest that both T_{soil} and θ_v influence F_{cs}. To examine this interaction, a quadratic model was used to describe F_{cs} as a function of both T_{soil} and θ_v (Fig. 5). This relationship is given by

$$Fcs = -3.889 + 0.322T_{soil} + 14.141\theta_v - 0.0057T_{soil}^2 - 0.848\theta_v T_{soil} - 47.448\theta_v^2 \qquad (2)$$

The fit was highly significant ($R^2 = 0.91$, df=28, $P<0.001$) and described 88% of the variation in F_{cs}.

Using 4-hourly F_{cs} values, a 24–hour integral of CO_2 efflux from the soil was calculated for each measurement day. These estimates were then extrapolated to monthly and annual totals. Here we assume that measurements conducted over three days with a 4-hour measurement cycle were representative of other days of the month, and the frequency of measurements was sufficient to represent seasonal variation. This yields a value of 5259 g $CO_2\ m^{-2}\ y^{-1}$ in the Eucalypt open forest (Table 1), which is a total of 14.3 t ha^{-1} of carbon. Of the total annual carbon emitted, over 70% was released during the wet season, while the dry season contributed 30%.

Litterfall and root abundance

The rate of litterfall at the Wildlife Park was strongly seasonal, with a significant increase over the wet season (January to April), followed by a steady rate of litterfall during the dry season (May to September) of 170-200 kg ha^{-1} per month (Fig. 6). By the late dry season/pre-monsoonal period (October-November), litterfall declined to 80 kg ha^{-1} per month. Integrating these monthly values yields an annual litterfall for 1999 of 1.60 t ha^{-1} and 1.90 t ha^{-1} for 2000.

Root abundance rapidly increased from November 1998 to January 1999, the mid-wet season. This was followed by a steady decline in root abundance throughout the dry season to an annual minima of 0.5 m m^{-2} during late-dry season (August 1999). From October to December 1999, this pattern of rapid pre-wet season growth was again repeated during the development of the 1999 wet season (Fig. 6).

Discussion

Daily and seasonal patterns of F_{cs}

Rates of soil CO_2 efflux in these wet-dry open-forest savannas were highly seasonal and reflected seasonal patterns of rainfall and soil water content. The wet season (December to April) is a period of intense biological activity and high soil water contents coupled with high rates of fine root growth resulted in values of F_{cs} of up to 8 μmol m^{-2} s^{-1}, with a wet season daily mean of 5 μmol m^{-2} s^{-1}. Wet season F_{cs} at the Howard Springs site were high and equivalent to rates measured in tropical rainforest (Meir *et al*. 1996). Over the dry season, rates were approximately 30% of equivalent values in the wet season.

The daily course of soil CO_2 efflux was characterised by a late afternoon maximum and pre-dawn minimum and generally followed soil temperature, a common pattern observed in many different ecosystems (Witkamp 1969, Janssens *et al*. 1998; Miranda et al. 1997). However, there were lags of up to several hours and the relationship between F_{cs} and T_{soil} was strong only when the volumetric water content of the surface soils (0-10 cm) was greater than 0.07 m^3 m^{-3}, equivalent to a gravimetric water content of 5%. Below this value of water content, F_{cs} was significantly lower. Miranda et al (1997) have also observed an impact of soil moisture content on soil respiration responses to temperature. At the present site, high soil water contents occur from November to May of each year. Conversely, 170 days of the year had surface soil water contents less than 0.07 m^3 m^{-3} (G. Kelley, NTU, pers. comm.) and this dry period lasted from 2 May 1999 to 15 October 1999. This is likely to be an underestimate of the actual period when soil water limits F_{cs}, as these measurements were made at 20 cm depth, and a more reasonable time period is from mid April to mid October, a period of 6 months.

Total dry season C loss from the soil was 4.3 t ha^{-1}, compared to a wet season C loss of 10 t ha^{-1}, giving an annual total of 14.3 t ha^{-1}. Assuming that root respiration is responsible for 50% of soil carbon efflux gives a total root respiration of 7 t ha^{-1} y^{-1}, approximately 20% of the total root biomass for this ecosystem (38.4 t ha^{-1}, Chen *et al*. 2001).

The annual value of F_{cs}, calculated above, is within the range found in tropical forests (4-21 t ha^{-1} year^{-1}, Schlesinger 1997). Meir *et al*. (1996) reported a value of 19.5 t ha^{-1} year^{-1} for Amazonian equatorial forest while in the seasonally dry tropical rainforest of north Queensland, Maggs and Hewett (1990) reported a value of C efflux of 14 t ha^{-1} year^{-1}, equivalent to that found in this study. The Howard Springs data are larger than other values of soil respiration reported for a

Eucalypt forest type in Australia. Typical values of annual carbon efflux for southern Australian Eucalypt forests (temperate and Mediterranean climate zones) tend to range from 4 to 12 t ha^{-1} year^{-1} (Keith *et al*. 1997). The significantly larger values presumably reflect high annual temperatures, the abundance of water for half of each year and the high C inputs to the soil from litterfall and root turnover.

Using equation (2), we calculated annual F_{cs} using an independently derived data set for mean monthly soil moisture (measured with miniature TDR probes (Theta probes; Delta-T Devices, UK; G Kelley 2001) and Bureau of Meteorology air temperature data. A plot of calculated F_{cs} against measured F_{cs} yielded a slope of close to 1 and an annual flux of 17.2 t ha^{-1} y^{-1} for a year with above average rainfall (1998/9). Such calculations lend support to the applicability of equation 2. The value of 17.2 t ha^{-1} y^{-1} is larger than the 14.3 t ha^{-1} y^{-1} calculated from the monthly measurements made in the present study because measurements in this study could not be made during saturated (flooded) conditions and therefore slightly underestimate the actual annual total flux.

There are few measures of F_{cs} in savanna ecosystems of Australia. Holt *et al*. (1990) reported an annual carbon efflux from soils of 3.7 t ha^{-1} year^{-1} for drier (annual rainfall 850 mm) tropical savanna of north Queensland. Similar to our Howard Springs site, rainfall at the site used by Holt *et al*. (1990) was also highly seasonal and this was reflected in the reported range of F_{cs}, with values ranging from 0.23 to 3.1 μmol m^{-2} s^{-1}. Bridge *et al*. (1983) measured soil respiration in grassland savanna near Katherine, NT, and reported an annual total efflux of 6 t ha^{-1} year^{-1}, closer to that measured at Howard Springs. These two studies (Holt *et al*. 1990 and Bridge *et al*. 1983) are the only two comparable studies of soil respiration in northern Australia and both estimates of annual carbon loss are well below values reported here. Given that F_{cs} is largely determined by soil moisture in the savannas of northern Australia (see below), these results are consistent with mean rainfall of each site, with both annual rainfall and C efflux from the soil at Howard Springs sites approximately twice that of the drier Katherine and north Queensland sites. The Howard Springs measurements were also made during a period of above average rainfall (wet season of 1999–2000). In addition, both the Holt *et al*. (1990) and Bridge *et al*. (1983) studies used the alkali absorption method which tend to underestimate fluxes when compared chamber-based estimates of F_{cs} (Haynes and Gower 1995). Taking these factors into account, our value of 14.3 t C ha^{-1} year^{-1} for total C efflux at this site seems reasonable.

F_{cs} as a function of soil temperature and water content

Soil respiration is positively related to soil temperature in numerous ecosystems and changes in soil temperature tend to increase soil respiration rates by changing the rate of utilisation of carbon sources (Lloyd and Taylor 1994; Raich and Potter 1995; Knapp *et al*. 1998). When comparing soil respiration of intact and clear-cut northern hardwood forest, Toland and Zak (1994) found that mean daily rates of soil respiration displayed a significant exponential relationship with soil temperature. Bowden *et al*. (1993) found soil temperature accounted for 80% of the variation in daily soil respiration rates in mixed hardwood forest. Meir *et al*. (1996) reported significant relationships between T_{soil} and F_{cs} for tropical Amazonian forest and Cerrado savanna in Brazil, although the relationship for the savanna ecosystem was weaker. Miranda et al. (1997) inferred a temperature and water interaction for rates of soil respirartion.

In contrast to the above, other studies report no obvious relationship between F_{cs} and T_{soil}. For example, Janssens *et al*. (1998) found that in primary forest, maximum F_{cs} did not occur when soil temperature was highest. Furthermore, there was no obvious correlation between F_{cs} and soil temperature during the night-time. In a more recent study, Giardina and Ryan (2000) examined the decomposition component of soil respiration and using data compiled from 82 sites, found no relationship between decomposition rate and temperature. In fact, decomposition rates from a wide range of soil types and temperatures were remarkably constant.

Soil respiration is likely to be a significant component of the carbon balance of savannas, given high soil moisture levels and root abundance during the wet season and an open tree canopy (LAI <1, O'Grady *et al*. 2000) which permits the high levels of solar radiation reaching the soil surface, resulting in high soil temperatures. However, such conditions are only experienced during the wet season and during the dry season, T_{soil} has no influence on soil respiration (F_{cs}). We therefore conclude that soil moisture content is the most critical factor controlling F_{cs} in tropical savannas of northern Australia. A similar conclusion was reached by Holt *et al*. (1990), who also observed highly seasonal patterns of savanna soil respiration which were largely determined by soil water content. Zepp *et al*. (1996) also demonstrated a significant influence of soil moisture on soil respiration for semi-arid savanna of southern African savanna, with rates increasing 5-fold following light rain (0.6 mm).

For the few Australian studies of soil respiration available, the relative importance of θ_v or T_{soil} on F_{cs} at any given site appears to be a determined by the degree of seasonality of each of the

factors. The wet-dry tropics are characterised by relatively low seasonality in air temperature, which is in contrast to surface soil water contents, which range from saturated ($\theta_v = 0.35$ m^3 m^{-3}) to near air-dried ($\theta_v < 0.015$ m^3 m^{-3}) over a wet-dry cycle. These features determine seasonal patterns of F_{cs}. The dominance of water content is not only observed in savannas. For seasonally dry rainforest of the Atherton Tableland, north Queensland, Maggs and Hewett (1990) reported similar correlations of F_{cs} with temperature and soil water content as found in this study, with low dry season water contents limiting F_{cs} and outweighing any temperature effects.

Where seasonality of soil water content is less extreme, most studies report a stronger relationship with T_{soil} than we found at Howard Springs. Keith *et al*. (1997) examined patterns of soil respiration in temperate Eucalypt forests of southern Australia (*E. pauciflora* stands). In such ecosystems, F_{cs} was limited by low soil temperatures, which were less than 15°C for much of the year and soil water content explained far less of the seasonal variance in soil respiration. Soil water deficits at this site were uncommon. Similarly Ellis (1969) described a strong relationship with soil temperature for cool-temperature Eucalypt forests of southern Victoria, Australia, with soil moisture having a secondary influence on rates of respiration. For Karri forests of south-west Western Australia (*E. diversicolor*), both soil moisture and soil temperature determined respiration (O'Connell 1987), a reflection of the Mediterranean climate with seasonality in both temperature and rainfall.

While the relationship between wet season daily mean F_{cs} and T_{soil} was significant, correlations with 4-hour mean data were more variable (Fig. 1). This is due to the differences in diurnal patterns and response times of T_{soil} and F_{cs}. Interactions of T_{soil} and θ_v are such that the effect of one variable can depend on the range of the other (Keith *et al.* 1997). This was observed in the present study, as during the dry season, changes to T_{soil}, below a threshold soil moisture content, had little or no effect on F_{cs} (Fig. 6). During wet conditions ($\theta_v > 0.07$ m^3 m^{-3}), F_{cs} was related to both T_{soil} and θ_v.

Soil respiration in relation to litterfall and root abundance

The low water contents of the upper soil zones (0-50 cm) of the dry season inhibit soil microbial activity and fine root biomass and growth rates decline rapidly to near zero levels during the dry season (
Fig.). However, litterfall rates are the highest over the dry season and are 6 months out of phase relative to seasonal patterns of root abundance and F_{cs} (Fig. ,7). Maximal rates of fine root growth and F_{cs} peaked together during the wet season (January-February), and since root respiration is

thought to account for approximately 50% of total soil respiration in forests (Ewel *et al*. 1987; Haynes and Gower 1995), we conclude that wet season root respiration dominates seasonal patterns of soil CO_2 efflux at this site.

High rates of litterfall were maintained from the end of the wet season (March) until the late dry season (September), when pre-monsoonal canopy flushing of the Eucalypt overstorey occurs (Williams *et al*. 1997) and litterfall reduces. This is a period of declining rates of soil respiration and litterfall was negatively correlated with F_{cs} (

Fig.). Assuming a carbon content of 50% for litter (Keith *et al*. 1997), for 1999 and 2000, this litterfall represents an input of carbon to the soil of approximately 0.80 and 0.92 t ha^{-1} of carbon. Our estimate of litterfall does not include grass litter, which typically attain levels of 1-2 t ha^{-1} (Williams *et al*. 1997a), giving a total input of carbon to the soil surface of approximately 2.4 t ha^{-1} year^{-1} for these savanna, with the maximum accumulation occurring by the late dry season (September). However, it is during this period that low soil water would limit decomposition and incorporation into soil organic matter and this dry season input of carbon from litterfall did not result in a high or pulses of soil respiration. This build-up of litter is either decomposed and/or respired during the following wet season(s) or is consumed by the regular
dry-season fires of these savanna ecosystems.

Climate change, soil temperature and respiration

Many climate change studies have demonstrated the significance of the temperature dependence of respiration to forest carbon cycling (Valentini *et al*. 2000). Predicted temperature increases as a result of climate change for tropical regions are not as large as those anticipated for higher latitudes and changes in water balance resulting from altered precipitation patterns may be more significant (Scholes and van Breemen 1998). This is significant as our data demonstrate the close coupling of soil respiration with soil water content and suggest that for tropical savannas of northern Australia (and elsewhere), shifts in the distribution and amount of rainfall will have a larger impact than temperature increases. Therefore, since soil carbon pools and soil carbon fluxes represent very significant proportions of total forest carbon budgets, it is important to include, for savannas, the dominant driving variable, namely soil water content, in estimates of future changes in forest carbon budgets that result from climate change.

Acknowledgments

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Table 1. Soil CO_2 efflux and soil carbon release from a Eucalypt open forest of northern Australia.

Season	CO_2 efflux (g m^{-2} period^{-1})	Carbon release (t ha^{-1} period^{-1})	% Total
Wet season (Nov–Apr)	3713	10.13	70.6
Dry season (May–Oct)	1546	4.21	29.4
Annual total (t ha^{-1} year^{-1})	52.6	14.3	100
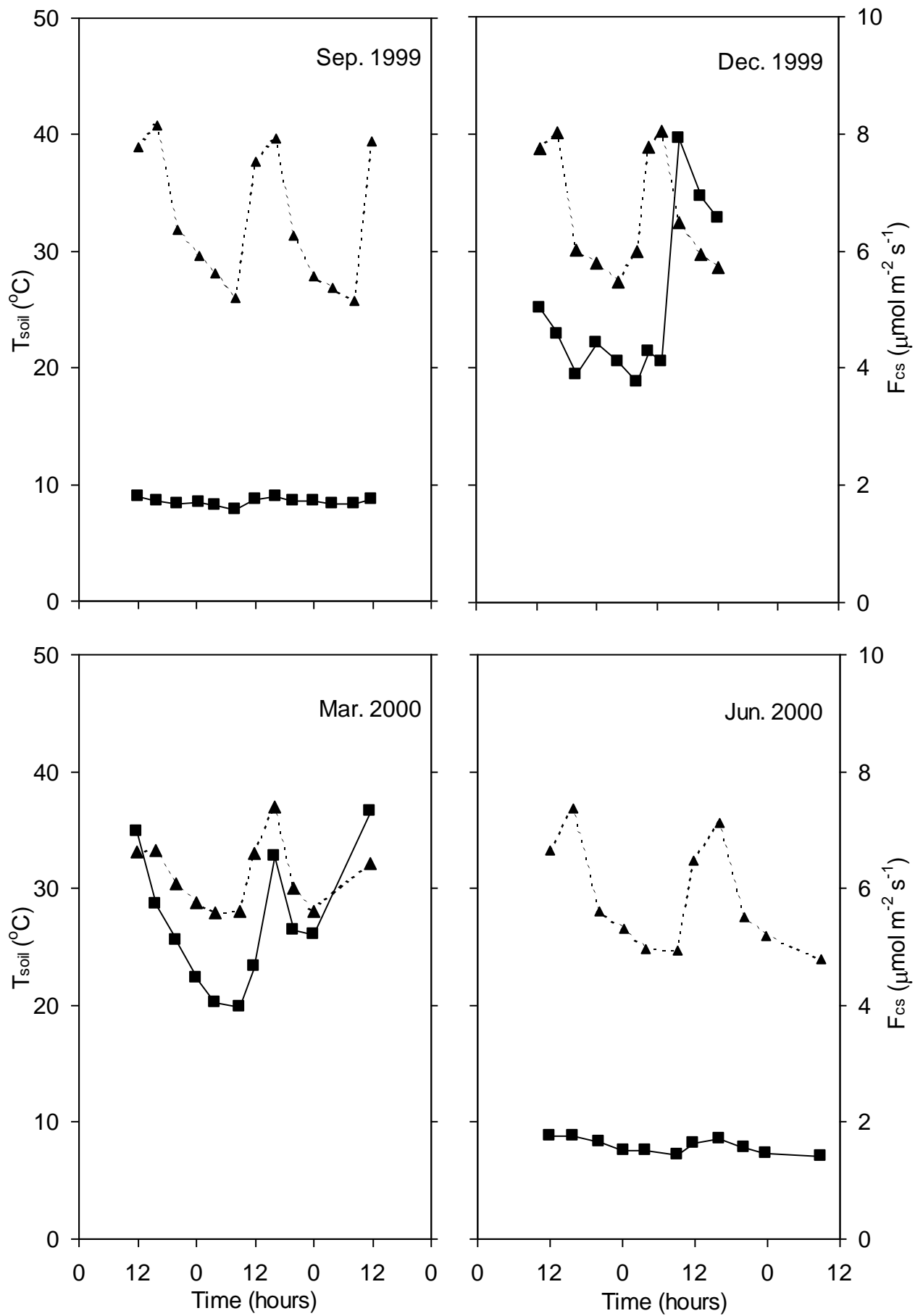
Fig. 1 Typical diurnal patterns of F_{cs} and T_{soil} for the late dry (Sep. 1999), early-wet season (Dec. 2000), late wet season (Mar. 2000) and mid-dry (Jul. 2000) for the Howard Springs site.
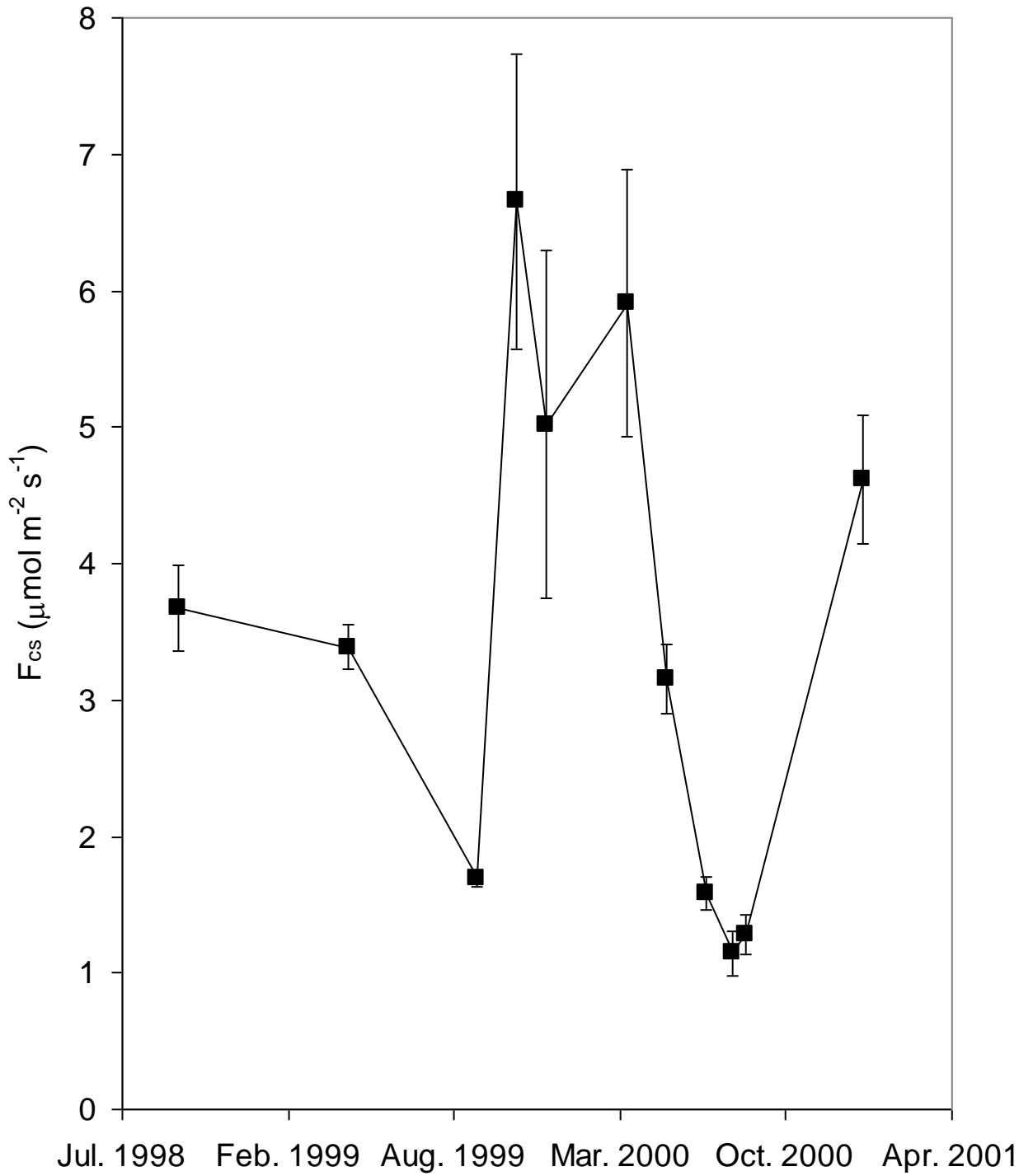
Fig. 2 Seasonal variation in F_{cs} over a 2 year period, October 1998 to January 2001, measured at the Howard Springs open-forest savanna site.
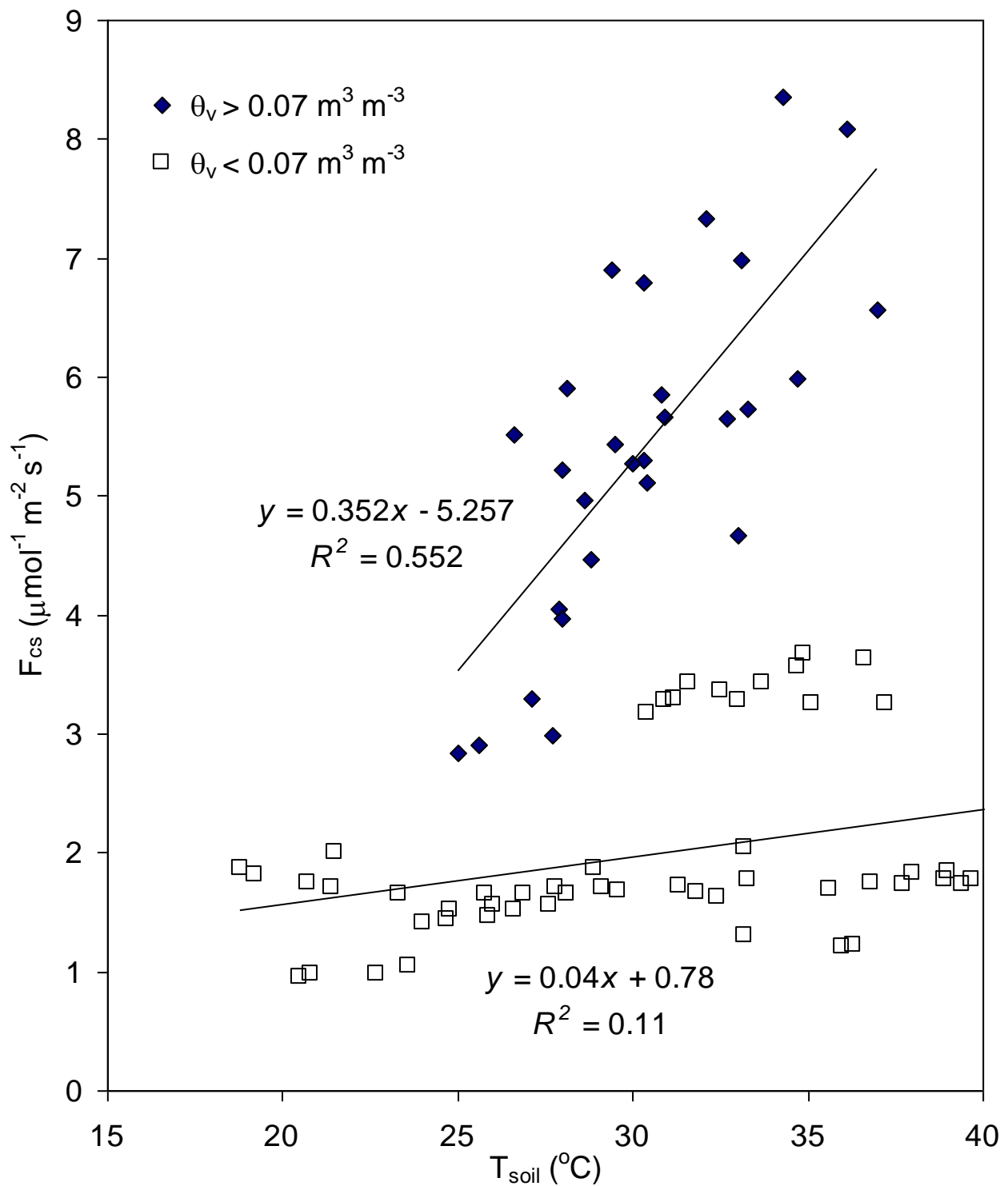
Fig. 3 Relationships between F_{cs} and T_{soil} using pooled 4-hour mean data drawn from observations from September 1998 to January 2001. The relationship describes two 2 discrete groups. The upper line describes wet season fluxes and soil moisture > 0.07 m^3 m^{-3}. The lower line describes the dry season data and soil moisture is < 0.07 m^3 m^{-3}.
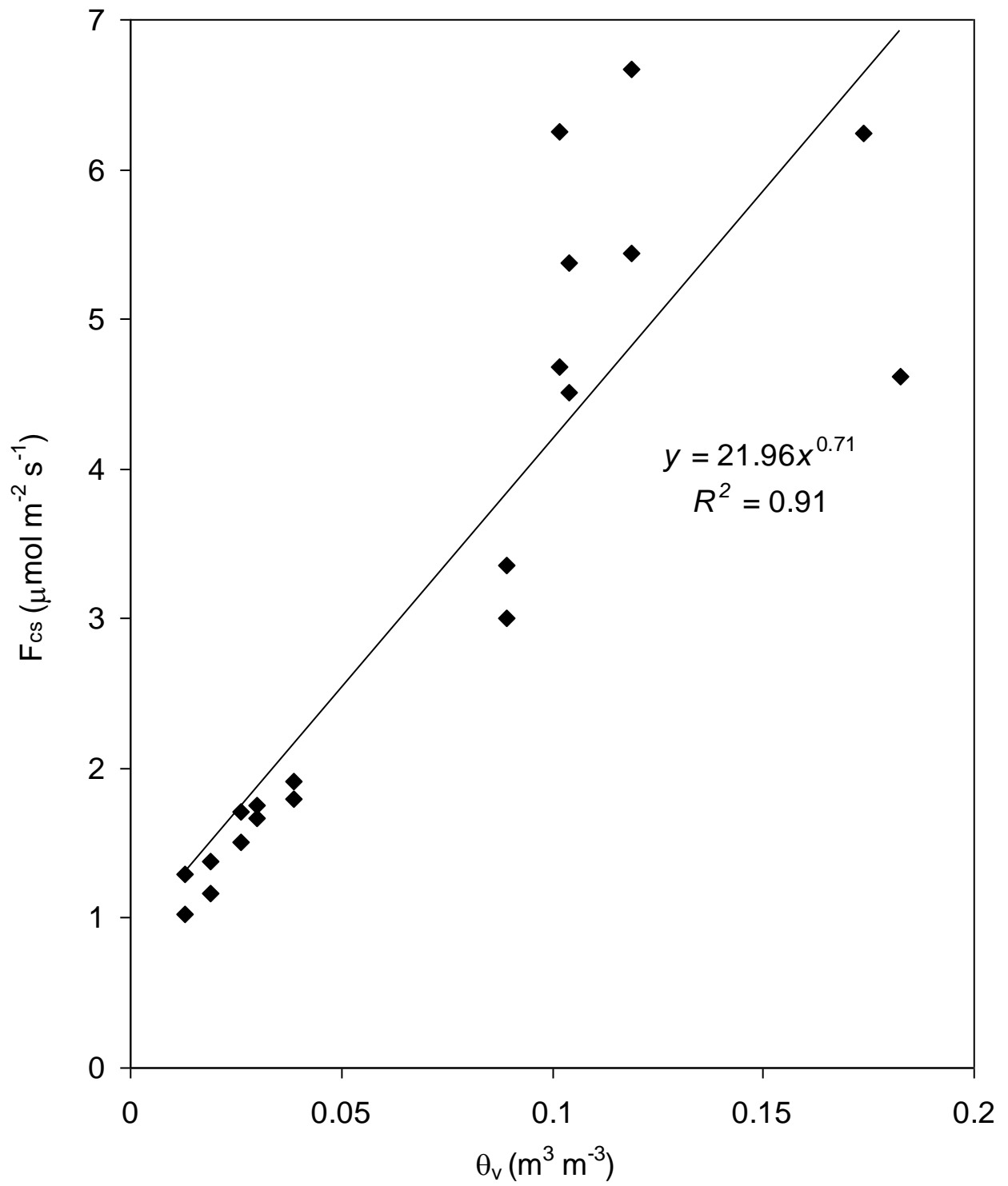
Fig.4 Relationship between F_{cs} and θ_v using pooled daily means.
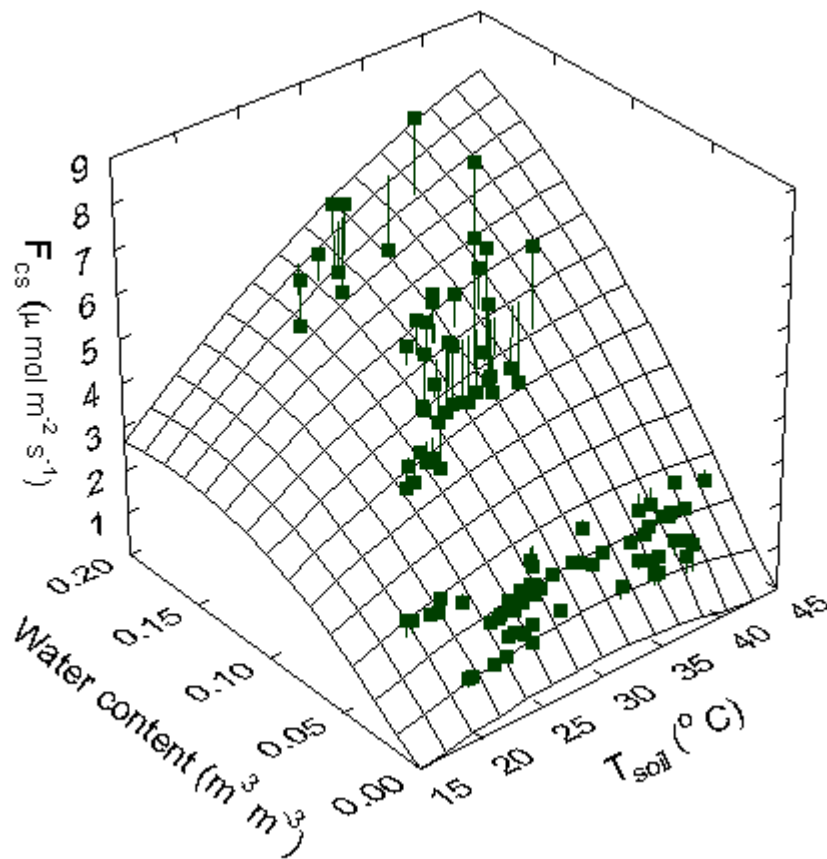
Figure 5 Surface plot (smoothed quadratic) describing the efflux of CO_2 from the soil (F_{cs}) as a function of soil temperature and soil water content.
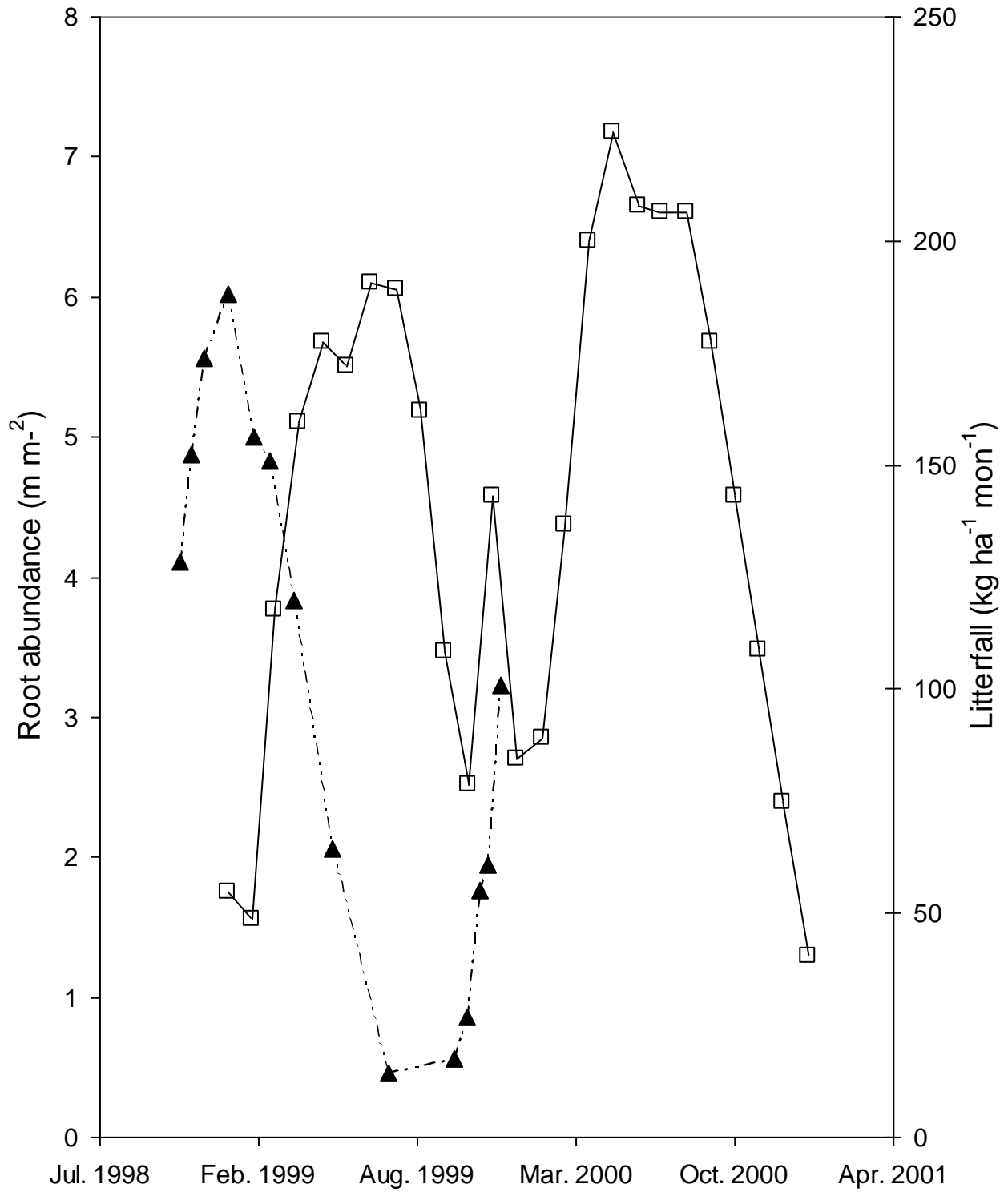
Fig. 6 Seasonal patterns of fine root abundance and litterfall. Root abundance was calculated from the measurements made using the 6 rhizotrons at the Wildlife Park site and is expressed as the total root length per m^2 of sampled pit wall.
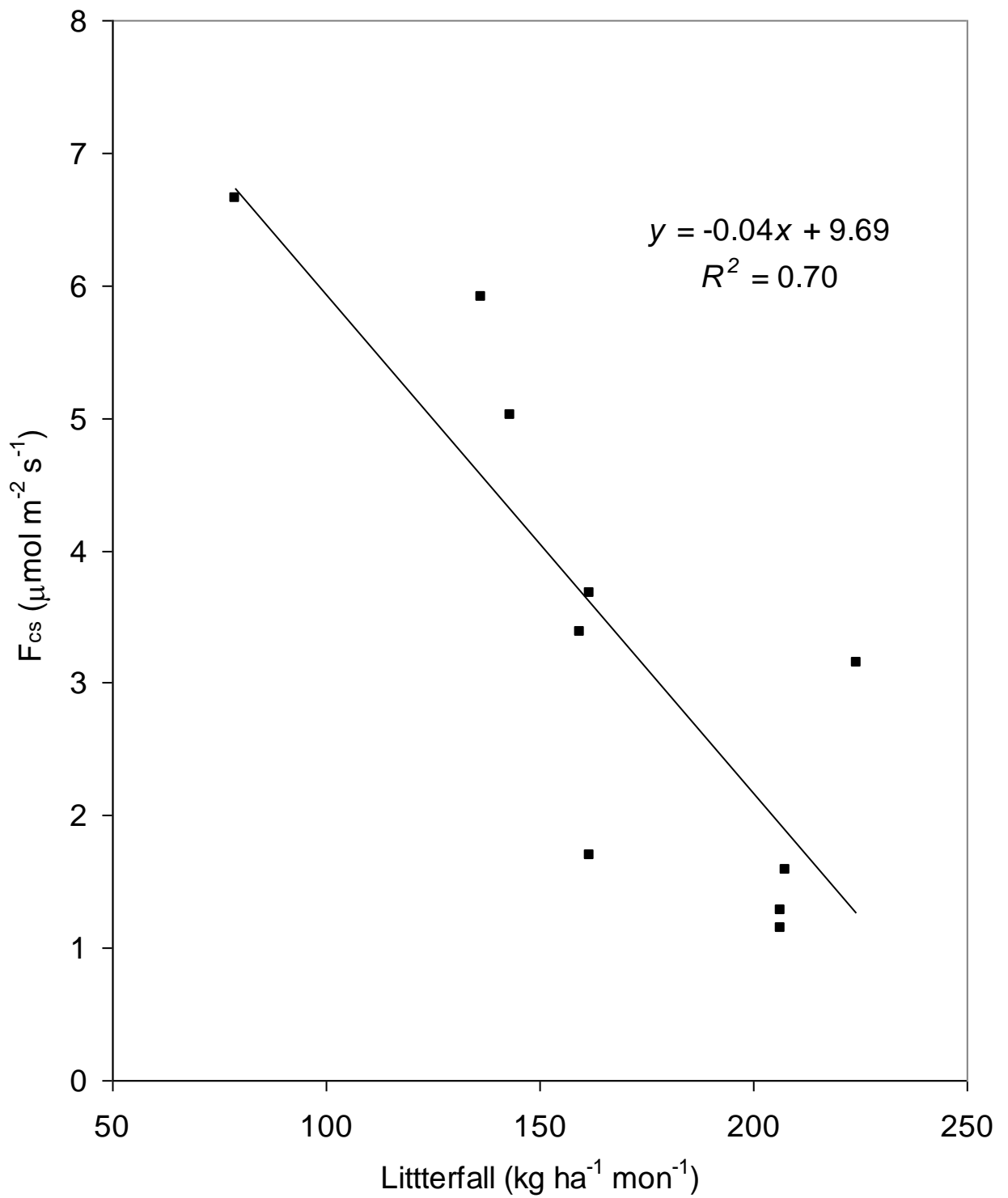
Fig.7 Relationship between mean monthly values of soil respiration (F_{cs}) and rate of litterfall for the period 1999-2000 inclusive.

$y = 0.21x + 383.52$

$R^2 = 1.00$

X-axis: Time (sec)

Y-axis: CO_2 (mol mol^{-1})