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Impact of tree clearing on soil respiration and soil microbial biomass in pasture systems of central Queensland, Australia

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Abstract

Forest clearing, a topical issue the world over, historically occurred at a high rate in Queensland to ostensibly increase pasture production. Our research evaluates the impact of clearing on selected soil biological properties (i.e. total soil respiration, root respiration, microbial respiration and microbial biomass (C and N)). Three major woodland communities of central Queensland region i.e. *Eucalyptus populnea*, *E. melanophloia* and *Acacia harpophylla* were selected for paired comparisons between sites that had, or had not, been cleared of trees to develop land for exotic pastures. The cleared sites representing three different time periods since clearing (5, 11-13 and 33 years) were used to determine the temporal impact of clearing on soil biological properties. Cleared and uncleared sites did not differ in annual or seasonal rates of soil respiration. The average annual rate of CO₂ emission across all treatments was 0.11 g CO₂/m².h. Microbial respiration and microbial biomass (measured in January 2002) were, however, greater at uncleared than at cleared sites, and conversely, root respiration (for roots from herbaceous plants) was greater at cleared than uncleared site. The Q₁₀ value of 1.42 (measured for different seasons over a year) suggested some response of soil respiration to soil temperature, which is less compared to that in temperate climates possibly due to the limited availability of soil moisture or organic matter in the semi-arid climates of central Queensland.

Keywords: soil respiration, root respiration, microbial respiration, microbial biomass, tree clearing, pastures.

Introduction

Soil respiration and microbial biomass are common indicators of soil biological activity. Soil respiration represents the amount of CO₂ evolved from soil microbes and roots, and to a lesser extent by biological oxidation of root exudates, plant detritus and humified organic matter (Raich and Schlesinger 1992). Microbial biomass typically constitutes <5 percent of soil organic matter (Jenkinson and Ladd 1981), however, respiration from microbial activities is an important contributor to total soil respiration.

At the global scale, the net effect of land use change, which includes vegetation removal (mostly conversion of forests to agricultural land) and its decomposition, regrowth and changes in soil C, contributed about 2.1 Pg C during the year 2000 to the atmosphere (Houghton and Hackler 2002). The annual flux of C from soils to the atmosphere is estimated at between 60 (Grace and Rayment 2000) and 76 Pg C/year (about 10 per cent of total CO₂ emissions to atmosphere) (Raich and Potter 1995). Soil contains 1500 Pg of C, about twice the amount that is in the atmosphere (Eswaran *et al.* 1993). Thus any change in vegetation or in land use that affects soil respiration is of major concern for global climate warming (Raich and Tufekcioglu 2000; Batjes and Sombroek 1997).

Vegetation and climate play an important role in determining total soil respiration, directly by their influence on temperature and soil moisture, and indirectly by determining the quantity and quality of organic matter (Giardina and Ryan 2000) and microbial composition and biomass (Kutsch and Dilly 1999). Using the data of Grace and Rayment (2000) forests and savannas contribute about 42 Pg of C while temperate grasslands, tundra, desert, cultivated and other ecosystems contribute only 18 Pg C to the total

emissions of about 60 Pg of C each year. Soil respiration rate is about 20 % greater in natural or long established grasslands than in forests (Raich and Tufekcioglu 2000), and about 1.42 times greater in tropical grasslands (629 g C/m².year) than in temperate grasslands (442 g C/m².year) (Raich and Schlesinger 1992). Clearing tropical woodlands to develop pastures is likely to result in a marked net increase in CO₂ emissions, however there are no data available on the total amount of CO₂ emitted while developing woodland into open grassland, to support this contention. Change in vegetation due to tree clearing may affect soil biological properties by influencing soil microclimate, the quality and quantity of litter or detritus material, soil organisms and availability of their substrate, and root structure (Raich and Tufekcioglu 2000). To date, most of the recent studies (e.g. Boone *et al.* 1998; Bowden *et al.* 1993; Giardiana and Ryan 2000; Valentini *et al.* 2000) were conducted in temperate zones; there is a paucity of information on soil respiration rate, and its sensitivity to temperature, in the semi-arid and tropical ecosystems.

Conversion of woodlands to open/cleared pastures was a common practice in Queensland, Australia from the 1900s until August 2004 when the Queensland Government banned tree clearing (State Policy for Vegetation Management 2004; Vegetation Management Act 1999 revised). During 1999-2001, 577,000 ha of native woodland were cleared annually, primarily to develop open pastures (Department of Natural Resources 2003). The change in vegetation structure from woodland (trees and some shrubs with herbaceous understorey) to open grassland could lead to changes in soil respiration, and in soil microbial activity and biomass. Previous studies by Lawrence *et al.* (1993) and Graham *et al.* (1981) reported the effects of clearing on soil nutrient status, but not on soil respiration and soil microbial

biomass. Our research aimed to study the impacts of tree clearing on soil biological properties in terms of:

- total soil respiration and the contribution of root and microbial respiration to total soil respiration
- soil respiration response to temperature and moisture content
- soil microbial biomass

We hypothesised that tree felling followed by sowing to exotic grasses (mainly *Cenchrus ciliaris* L.), which alters vegetation structure and function, would change soil biological properties.

The paired cleared and uncleared sites for major types of tree woodland communities, i.e. *Eucalyptus populnea*, *E. melanophloia* and *Acacia harpophylla*, were selected in a semi-arid zone in central Queensland. The effect of clearing on soil biological properties was studied at sites with different time periods since clearing to interpret the long-term effects of clearing.

Materials and methods

Research sites and design

The research sites were located in a semi-arid zone within a 5000 ha grazing property “Avocet” in central Queensland (NW 148.13° E, 23.79° S, NE 148.16° E, 23.80° S, SE 148.21° E, 23.85° S and SW 148.12° E, 23.86° S). The property has belonged to the same landholder for the last 55 years, with full records of all land clearance. Average annual rainfall is 600 mm, with sporadic summer storms during October-February. Average (1865-

2001) minimum and maximum temperatures are 6-8 °C and 23-25 °C during winter (June-August), and 22-24 °C and 33-36 °C during summer (December-February) (Commonwealth of Australia Bureau of Meteorology 2003).

Cleared woodland and woodland pasture (control sites) were selected under the guidance of research staff at Department of Natural Resources and Mines, and at Environmental Protection Agency, Emerald, in three major tree communities i.e. *Eucalyptus populnea* F. Muell. (poplar box), *E. melanophloia* F. Muell. (silver-leaved ironbark) and *Acacia harpophylla* F. Muell. ex. Benth. (brigalow) as representative vegetation types of central Queensland region. Paired comparisons of pastures in cleared sites and uncleared (woodland) sites were taken for each tree community in each of three time periods since clearing: i. recent -5 year ii. medium -11-13 year iii. old -33 year.

The study represents a 3 (types of tree communities) x 3 (time since clearing) x 2 (cleared v/s intact) factorial design. There were three uncleared sites and three paired cleared sites (one for each of the time periods since clearing) for each of the selected tree communities. In total, there were 18 sites. As such, the uncleared sites were replicated three times for each tree community but the time periods since clearing were not. None of the uncleared (intact) woodland sites had been cleared in the past 55 years. The paired cleared and uncleared sites were within 50 m of each other. The cleared and uncleared sites had similar original biophysical characteristics (soil type, slope and vegetation) before clearing, according to the information from the landholder, as was the grazing management. The cleared sites were chain pulled and then sown to buffel grass (*C. ciliaris* L.) within a year of clearing. Details on time of clearing and the rate of stocking over the last 20 years are presented in Table 1. All recently cleared plots were burnt in October 1999, those 11-13

years since clearing were blade ploughed in 1994, and those cleared 33 years ago were blade ploughed in 1987.

Vegetation in uncleared pastures represent an upper storey of trees and under storey of grasses, herbs and shrubs. The sown *C. ciliaris* in cleared pastures which largely dominated over other species to create a near mono-culture. The details on plant species at all the studied sites are presented in Sangha *et al.* (2005b); in summary the tree populations did not exceed 2140 per ha and the mean basal area across 9 treatments for all tree communities was 26.3 m² per ha.

Each tree community grows on a particular soil type, *E. populnea* on Sodosol (sandy-loam texture contrast, non-gravelly soils), *E. melanophloia* on Kandosol and Dermosol (sandy or clay loam, moderate, brown, non-gravelly or slightly gravelly soils) and *A. harpophylla* on Sodosol (clay, grey and deep soils) (using the Australian Soil Classification; Isbell 2002). Average soil pH_w (1:5 soil : water) for recent, medium, old cleared and uncleared sites was 6.2, 7.2, 6.8 and 5.7 in *E. populnea* soils; and 7.2, 7.0, 7.9 and 6.9 respectively in *E. melanophloia* soils; and 6.5, 7.6, 8.0 and 6.3 respectively for recent, medium, old cleared and uncleared sites in *A. harpophylla* (Sangha *et al.* 2005a). These soils are relatively poor in nutrient content and organic matter, with maximum depth to 60 cm, at which sandstones and rocks were reached. Detail on the availability of soil nutrients is presented in Sangha *et al.* (2005a).

Measurements

Soil respiration - field measurements

Soil respiration was measured with a soil respiration chamber (10 cm diameter x 24 cm height) connected to an infrared gas analyser (Environmental Gas Monitor (EGM-3), PP Systems, UK). Preliminary trials at one site only were conducted to measure the diurnal rate of soil respiration. As with the data of Mielnick and Douglas (2000) and Blanke (1996), we found that the early morning measurements best reflected the daily average values. Based on this and to maintain data consistency, the field measurements were taken on normal (non-rainy) days during the morning hours (6:00-9:00 am) within a soil temperature range of 5 °C (17-22 °C and 26-30 °C for measurements taken in August and November 2001 respectively; and 20-24 °C and 11-14 °C for measurements taken in March and July 2002 respectively).

At each site, an area 100 m by 100 m was marked as a representative of each site. Soil respiration measurements were taken within this area over the span of a year, in August and November 2001, and March and July 2002. Six readings were taken at random approximately 15 m from each other in each season. At each sampling time, measurements were taken at different locations. The litter layer (if any) was removed before placing the soil respiration chamber on the soil surface (as recommended by Bowden *et al.* 1993; Mielnick and Douglas 2000). The chamber was positioned between plants, and at a distance of >1 m away from standing trees in uncleared sites). Due to an accidental, patchy burn, no measurements were made at the recent cleared site for *E. melanophloia* in March and July 2002. Soil temperature at 5 cm depth was measured during respiration readings with a probe attached to the EGM-3.

To examine the effect of soil moisture and soil temperature on soil respiration, measurements were taken in December 2001 at the 33 year cleared and their paired uncleared sites for each of the three communities before (1-3 days) and after 40 mm of rainfall (from the 2nd until the 6th day after rain). A total of six sites were included in this study. Six random samples were taken at each site as described before. Soil moisture content was measured to 12 cm depth with probes (CS620: Hydrosense water content sensor, Campbell Scientific Australia) on each day.

Soil, root and microbial respiration - pot measurements

To determine the rate of root respiration per unit root biomass (the specific root respiration rate), a polyhouse experiment was conducted with *Cenchrus ciliaris* as it is the most commonly grown grass species in cleared pastures of central Queensland. Seeds were sown (April 2002) in sandy soil to establish three plants in each 34 cm diameter, 35 cm height pot, and were supplied with hydroponic nutrient solution (Manutec Pty Ltd, SA) during the growth phase (on average twice in a week depending upon requirement to maintain soil moisture at 80% of the field capacity). Sandy soil was chosen as an appropriate medium to minimize root loss during extraction, and it was representative of two of the community types in the field. The experiment was set up in a polyhouse (temperature 7-32 °C and relative humidity 14-48 %). Soil respiration, soil temperature and soil moisture were monitored from when the plants were two months (approximate height >30 cm) until their final uprooting (i.e. 9 months) for root respiration measurements. The measurements were taken over 3-5 consecutive days following each irrigation event until the pots reached 60% of field capacity.

Six pots were maintained to estimate root respiration in the absence, and six pots in the presence of defoliation (simulated grazing). For the defoliation, the grass was cut twice to half of the height over the 9 month growth period. Six pots, with soil but no grass, were also maintained to measure root-free soil (microbial) respiration. Treatments were replicated six times in a randomized complete block design.

A soil respiration chamber connected to the EGM-3 was placed on soil in the centre of each pot to measure total soil respiration. Soil moisture and soil temperature were also measured. At the end of the trial, total soil respiration was recorded for all pots just before uprooting. Then the roots were rapidly extracted by emptying a pot onto a plastic sheet to take the plants out of the sand. Sand and shoot parts were then removed before measuring the root respiration. The roots were placed in a 10 cm diameter PVC chamber and the soil respiration chamber was placed vertically and tightly over this to measure respiration. The pots were uprooted one at a time with measurements completed within a minimum time gap and without drying. After respiration measurements, roots were washed to completely remove the sand particles (if any), dried at 60 °C for 48 hours and weighed.

Root biomass and respiration (for herbaceous plants) in the field

The fraction of soil respiration due to root respiration was difficult to measure in the field because digging of cores for recovery of roots was a tough task in hard soils. However, root biomass samples were collected once in the summer season (January 2002), and, with the data on specific root respiration rate, were used to compute in-field root respiration. Eight soil cores to 0.60 m depth (0.04 m diameter) were taken randomly at each site at least 2-3 m away from standing tree trunks and between herbaceous plants during January 2002 using a hydraulic soil corer for measurement of root biomass. Large sized roots from trees were

minimised as samples were taken >2 m away from trees. Moreover, trees were sparsely scattered (Sangha 2003) and there were no visible evidence of lignified tree roots in the samples; the roots were mainly adventitious and from herbaceous plants. Root samples were dried and bulked per site. The visible roots (>1 mm diameter (the very fine roots were excluded)) were extracted by hand following sieving (mesh size 1.5 mm x 1.5 mm), dried at 60 °C and weighed to estimate total root biomass.

Various assumptions and limitations of the method used to compute root respiration in the field were evident:

Assumptions

- The rate of root respiration per unit root biomass of *C. ciliaris* was considered to be the same as for native grass species growing on woodland floors.
- Visible examination of roots from woodland pastures was used to determine that the roots were from herbaceous species.

Limitations

- Root respiration in the field was computed based upon only one measurement of root biomass in January 2002. We acknowledge that root biomass varies throughout the year (McClaugherty *et al.* 1982). Therefore, the separation of soil respiration into rates of root and microbial respiration was also computed for one season only, since measurements of root biomass were not taken in other seasons.
- Soil respiration field measurements were taken only in the morning hours (6:00-9:00 am) for our preliminary experiments and other studies (Mielnick and Douglas

2000; Blanke 1996) suggested that measurement at this time reflects diurnal rates of soil respiration.

Microbial respiration

Soil microbial respiration was computed from average total soil respiration per year minus computed root respiration based upon the estimate of root biomass from herbaceous plants (measured in January 2002), for each site (using the method applied by Kelting *et al.* 1998). Microbial respiration determined in this way includes rhizosphere, but not root, respiration.

Soil microbial biomass

Eight samples of soil from the top 0-5 cm (no organic layer present) were randomly taken in March 2002 from within the marked area at each site. Samples were sieved and bulked for each site. Soil microbial biomass for C (MBC) and N (MBN) were analysed using the chloroform fumigation extraction method (Vance *et al.* 1987) at the Natural Resource Sciences Laboratories (Department of Natural Resources and Mines, Brisbane, Qld). Soil organic C was analysed using the Walkey and Black method (H_2SO_4 and $\text{K}_2\text{Cr}_2\text{O}_7$ in 1:100 dilution, measured colorimetrically).

Soil microbial biomass and soil respiratory quotients were computed as (Sparling 1997):

$$\text{Soil microbial biomass quotient (\%)} = \frac{\text{Soil microbial biomass C}}{\text{Soil organic C}} \times 100$$

$$\text{Soil respiratory quotient} = \frac{\text{Total (in-field) soil respiration (g CO}_2\text{/h)}}{\text{Soil microbial C (g)}}$$

C estimations in the aboveground vegetation

The amount of C stored in aboveground vegetation (trees and shrubs, >1.3 m height) in woodlands was determined as a part of another project on C budget estimation (Rolfe *et al.* 2003). The tree basal area at 30 cm height (as recommended in Queensland) from the ground was measured from 9 transects (each 50 m x 4 m) using the TRAPS method (Back *et al.* 1997). The amount of C was calculated using allometric equations (developed by Burrows *et al.* 2000) for each tree type.

Statistical analysis

Soil respiration

The data were analysed using residual maximum likelihood analysis (REML) in Genstat ver 6.0 (2002). The model estimates the variance from the main effects of tree community*cleared-uncleared and from the random effects of time-since-clearing for recent, medium and old clearing for all the tree communities. For the main effects, if the interaction between a tree community*cleared-uncleared was significant at $P < 0.05$, then l.s.d. (least significant difference of means) were computed for each treatment. In the absence of a significant interaction, the individual effects for a tree community and for cleared-uncleared treatments were computed. The means obtained from REML analysis were used in presenting the results to maintain consistency for both the significant and non-significant levels of interaction.

Soil, microbial and root respiration, root biomass and soil microbial biomass for C and N

REML was applied as for soil respiration. Paired t-tests were also applied to compare means for all the cleared and uncleared treatments.

Soil respiration response to soil temperature, and soil moisture (changes induced by rain)

The relationship between soil respiration and soil temperature was analysed using regression analysis. All data (for six samples per site for each of four sampling times per year) for soil respiration were combined irrespective of tree type or time-since-clearing since there were no significant interactions between these treatments. Soil respiration response to temperature was computed from the temperature quotient $Q_{10} = e^{\beta_1 T}$ obtained from the exponential regression $y = \beta_0 e^{\beta_1 T}$ (where y = soil respiration, β_0 and β_1 = fitted constants and T = temperature (°C)) fitted to the data. To quantify the effect of rain on soil moisture, soil temperature and soil respiration, an ANOVA was applied for the data collected before and after rain at all cleared and uncleared treatments.

Results

Soil respiration

There was no significant difference in the rate of soil respiration between cleared and uncleared sites, nor with time-since-clearing for any of the tree communities (Fig 1a) with the exception that the recent clearing had a greater rate than that of uncleared, medium and old cleared sites for *E. populnea* in August 2001 (Fig 1a).

Soil respiration rate showed seasonal variation, and was notably greater during the warmer wet season (November 2001 and March 2002) compared to the cooler dry season (August 2001 and July 2002) (Fig 1a and 1b). The respiration rates differed between the warmer wet (130 ± 4.01 mg CO₂/ m².h (mean \pm se)) and dry (90.1 ± 3.03 mg CO₂/ m².h) seasons for all treatments irrespective of whether cleared or uncleared, or of tree type.

The differences in the rate of soil respiration between the wet and dry seasons were greater at the uncleared (100 ± 4.02 mg CO₂/m².h) and medium age of clearing (100.2 ± 1.05 mg CO₂/m².h increase) than at the recent (60.2 ± 5.04) and the oldest (50.3 ± 1.04) clearing, regardless of tree community.

In general, cleared grasslands and native woodlands had similar average rates of soil respiration (110 mg CO₂/m².h, equivalent to 263 g C/m².year) based upon measurements taken in the morning hours over 4 sampling events in a year.

Root biomass

Root biomass of fibrous roots (roots > 1 mm from herbaceous plants) for 0-60 cm depth was greater at all cleared than uncleared treatments for *E. populnea* and *A. harpophylla*, and at recent clearing than at uncleared sites for *E. melanophloia* (Table 2).

Microbial and root respiration

The specific root respiration rate defined earlier was estimated from the regression of root respiration on root biomass from the polyhouse experiment with *C. ciliaris*. The rate was 0.08 g CO₂/g of root biomass ($r^2 = 0.88$ at $P < 0.001$, Fig 2). The rate was the same for treatments with or without simulated grazing. The rate was then used to compute in-field root respiration based on in-field root biomass measurements. Although the average rate of total soil respiration over a year (sum of root and microbial respiration, Fig 3) showed no significant difference between cleared and uncleared sites, computed root respiration was greater, by virtue of its greater root biomass, at recent and medium age of clearing compared to uncleared sites in all the tree types other than for the medium cleared *E. melanophloia* site (Fig 3). Microbial respiration was greater at uncleared compared to (1) the oldest clearing for *E. populnea* (Fig 3i), and (2) all cleared sites for *A. harpophylla* (Fig

3iii). There was no significant difference between cleared and uncleared sites for *E. melanophloia* (Fig 3ii).

Soil microbial respiration was positively but weakly related to MBC ($r = 0.20$, $P=0.05$) and MBN ($r = 0.27$) across all the sites. Recently cleared *E. populnea* had greater MBC compared to the oldest cleared sites, but there was no significant difference in terms of MBN (Table 2). In *E. melanophloia*, MBC content did not differ between any of the cleared and uncleared sites, but MBN was greater at uncleared than recently cleared sites. MBC and MBN were greater at uncleared *A. harpophylla* than the cleared treatments except for the oldest clearing. Soil organic C did not differ significantly among the cleared and uncleared treatments for any tree type except that for *E. populnea* where it was greater in the recent clearing than in the uncleared site (Table 2).

Microbial quotient (the ratio of MBC to soil organic C) did not show any notable difference between cleared and uncleared treatments. Respiratory quotient (ratio of soil respiration to MBC) was greater at the recently cleared *E. melanophloia* site, and at all cleared sites for *A. harpophylla* compared to their uncleared sites, but did not differ between cleared and uncleared treatments for *E. populnea* (Table 2).

Comparison between cleared and uncleared treatments averaged across time-since-clearing and tree type showed that uncleared sites had significantly greater microbial respiration compared to cleared sites (Table 3). The rate of root respiration was greater at cleared ($60.3 \text{ mg CO}_2/\text{m}^2\cdot\text{h}$) than uncleared ($40.4 \text{ mg CO}_2/\text{m}^2\cdot\text{h}$) sites. Microbial respiration contributed 45% at cleared and 62% at uncleared sites to total soil respiration. Root respiration was 38% of total soil respiration at uncleared sites. At cleared sites, root

biomass was significantly higher compared to uncleared sites (Table 3), and, therefore, the root respiration contributed more to total soil respiration than did microbial respiration.

Environmental factors affecting soil respiration

Soil respiration responded positively to rise in soil temperature (Fig 4) although there was background variation within the data set. The Q_{10} value of 1.42 was calculated for exponential change in soil respiration (for all the data collected over the 12 month period) with each 10 °C rise in temperature over the range 10-32 °C.

A significant increase in soil respiration occurred after rainfall (Table 4). The data were collected in December 2001 in the middle of a rainy season (40 mm rainfall in December, after 85 mm in November and 37 mm October). Soil moisture accounted for 18% of the variation in soil respiration for measurements taken daily before a rainfall event (13-15th of December 2001) and over the next six days after the rainfall event (18th- 23rd of December 2001) (the rainfall event was on 16-17th of December 2001) (Fig 5).

C stored in aboveground vegetation

The total C stored in the aboveground woodland vegetation (trees and shrubs) was amounted to 52.18 t/ha in *E. populnea*, 24.08 t/ha in *E. melanophloia*, and 42.04 t/ha in *A. harpophylla* woodlands.

Discussion

The mean rate of soil respiration reported herein for the semi-arid zone (263 ± 18 g C/m².year) was less than that reported for semi-arid woodlands of north Queensland (380 g C/m².year) (Holt *et al.* 1990), tropical savannas and grassland (629 g C/m².year), temperate grassland (442 g C/m².year) (Raich and Schlesinger 1992), and much less than the 1.71 kg

CO₂-C/m².year reported for temperate tall grass prairie (Mielnick and Dugas 2000). The reasons may be the differences in climate, chiefly rainfall and temperature, and may in part be due to the vegetation communities.

Based upon the present study at one property in the semi-arid climates of central Queensland, the conversion of woodlands to open pastures (grasslands) did not affect the rate of soil respiration when compared to their paired uncleared pastures. These results could play an important role in decision-making on tree clearing policies in Queensland where it is a topical issue. Our results contrasted with the lower soil respiration reported in juniper woodland compared to paired grassland in eastern Kansas (USA) by Smith and Johnson (2004). However climatic conditions and vegetation type could impact significantly on determining soil respiration, and there is paucity of data for both woodland and cleared pasture systems in Queensland.

Nonetheless, clearing certainly affected the total ecosystem C stock of cleared compared to woodland pastures. Although the rate of total soil respiration did not differ following clearing, changes occurred in soil and vegetation C stocks over time (Guo and Gifford 2002). In the present study, the content of soil organic carbon at 0-0.60 m depth (at the same sites; Sangha 2003) did not differ between cleared and uncleared sites. However, the amount of aboveground C stored in the vegetation was certainly greater in the woodlands (24.08 to 52.18 t ha⁻¹) compared to that in cleared pastures where the maximum amount of C stored was 2.4 ha⁻¹ (for a range of 1-2.4 t ha⁻¹; Sangha 2003). The total ecosystem C stock, therefore, was certainly greater in woodlands than the cleared pastures (details mentioned in Rolfe *et al.* 2003).

Soil respiration varies with temperature and moisture. The Q_{10} value of 1.42 suggested a positive response of soil respiration to temperature for in field conditions of central Queensland. The reported median Q_{10} value for various ecosystems is 2.4 with a range of 1.3-3.3 (Raich and Schlesinger 1992). The temperate zones are more sensitive to increase in soil respiration with increase in temperature (Valentini *et al.* 2000); Kicklighter *et al.* (1994) calculated $Q_{10} = 3.1$ based upon data from various temperate studies.

In the present study, soil moisture was not measured in the field in the dry season due to difficulty in inserting the delicate soil moisture probes in dry hard soils. However, measurements taken during different seasons over a year suggested that the rate of soil respiration increased during the wet compared to the dry season. Similarly, during a single rainfall event (40 mm), soil respiration increased in response to soil moisture ($r^2 = 0.18$, $P < 0.05$). Soils at uncleared sites probably retain moisture over a longer time compared to cleared sites, where lesser vegetation cover will let the soils dry quickly. Davidson *et al.* (2000) conducted a detailed study on the response of soil respiration to soil moisture for four different land use systems (active pastures, degraded pastures, secondary forest and primary forest) of eastern Amazonia and reported higher rates of soil respiration during the wet compared to dry season. Soil moisture, a primary factor that limits plant growth in semi-arid woodlands (Scholes 1993), and soil moisture and soil temperature or their interaction with other limiting factors such as soil C that regulate root and microbial activity, may affect the rates of soil respiration in semi-arid climates. A detailed study on soil respiration response to major environmental factors (moisture, temperature and soil C) in semi-arid climates is important to clarify the impact of land-use practices (that affect soil moisture or soil C) on net soil CO₂ emissions.

The rate of root respiration per unit root biomass was determined in a polyhouse experiment and was used to compute in-field root respiration according to in-field root biomass measurements. The calculated contribution of root respiration (herbaceous plants) to total soil respiration was 55 % in cleared pastures and 36% in woodlands. Raich and Tufekcioglu (2000) similarly reported that 17-40 per cent of total soil respiration in grasslands was due to root respiration. We acknowledge that respiration from tree roots in deeper soil in woodland, if incorporated, may increase the contribution of root respiration to total soil respiration. The contribution of root respiration in total soil respiration can vary from 10-90 percent depending on vegetation type and season of the year (Hanson *et al.* 2000). The amount of root biomass can significantly affect the rates of root and hence total soil respiration. The root biomass was expected to be greater in woodlands than in open grasslands, if all the roots from herbaceous plants and trees were considered, and this may contribute to higher respiration rates in the former than in the latter (the amount of total roots respiring may vary according to the species). However, a large amount of C is released upon clearing aboveground vegetation, so it is important to consider the total C stored in aboveground vegetation and in soils when comparing the cleared and uncleared pasture systems. Moreover, with clearing, ecosystem functions i.e. soil processes that affect C storage in soils are disturbed.

Conversion of woodlands to cleared pastures presents a different scenario for microbial activities and for microbial C and N biomass to that for total soil respiration. The cleared pastures had lesser rate of microbial activity and lesser microbial biomass for C and N than did the uncleared pastures (Table 3). Similar results were also seen by Sparling *et al.* (1994). For established woodland systems, the lesser microbial activity in relation to their

biomass (low respiratory quotient) in uncleared *E. melanophloia* than the recent cleared pastures, and in uncleared *A. harpophylla* than that at all the cleared pastures indicated the potential of these woodlands to efficiently use the soil resources whereas higher respiratory quotient values in cleared pastures indicate stress response and ‘poor soil health’ (Sparling 1997). Soil respiration was reported to be poorly correlated with MBC (Wang *et al.* 2003) or MBN (as also evident from the present study), suggesting that other factors (climate and substrate quality) could play a significant role in soil CO₂ emissions.

The soil microbial biomass results did not concur with those of earlier studies conducted in Queensland by Graham *et al.* (1981) and Lawrence *et al.* (1988). They suggested that with age, the cleared pastures decline in soil fertility due to an increase in soil microbial biomass as nutrients tie up in microbial biomass. According to their argument, the oldest cleared pastures in the present study should have had the maximum amount of microbial biomass. However, microbial biomass and activity was either not affected or lesser at the oldest and medium clearing than at the uncleared sites (except the oldest cleared site for *A. harpophylla*) (Fig 3 and Table 2). Soil microbial biomass supports ecosystem functions i.e. microbial mineralisation (Bardgett *et al.* 1999; Sparling *et al.* 1994), this suggests that woodland communities with greater amounts of soil microbial biomass maintain ecosystem function better to support soil processes compared to cleared pastures. These changes in soil biological properties are likely due to change in vegetation structure from woodlands to open grasslands. Changed pasture composition from a multi-species system in native woodlands to monocultures of predominantly *C. ciliaris* (Sangha *et al.* 2005b) seems responsible for altered soil biological properties. The reduced species diversity may affect the use of resources in cleared systems as the diverse systems possess better potential for

use of resources due to greater functional diversity, compared to the less diverse systems in grasslands (Tilman *et al.* 1996).

The plant-soil relationship is disturbed in cleared pastures with introduction of exotic grass species, for different plant species harbour different microbial communities that affect ecosystem functions (Bardgett *et al.* 1999). Tree clearing led to changes at the macroscopic (vegetation communities: tree, shrubs and pasture plant species) and at the microscopic level (microbial biomass and microbial respiration), which could further affect the functioning processes of an ecosystem. A detailed study needs to be conducted to understand the impact of tree clearing in tropical pasture systems on soil functional processes that, as a consequence, affect C storage in soils and the total amount of C stored in a system. This would help plan land use policies that reduce soil CO₂ emissions, and maintain the ecosystem functions for future production gains.

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Tables:

Table 1. Details of time since clearing (years), post-clearing treatments and annual stocking rate (hectare per cattle, over the last 20 years) for cleared and uncleared sites of *E. populnea*, *E. melanophloia* and *A. harpophylla*.

Tree community	Cleared treatments		Uncleared treatments
	Time since clearing	Stocking rate	Stocking rate
<i>E. populnea</i>			
Recent clearing	5	5	5
Medium clearing	13	3	4.8
Old clearing	33	6	4.8
<i>E. melanophloia</i>			
Recent clearing	5	5	5
Medium clearing	11	3	3
Old clearing	33	6	6
<i>A. harpophylla</i>			
Recent clearing	5	5	11
Medium clearing	13	3	4.8
Old clearing	33	6	4.8

Table 2. Root biomass (for roots from herbaceous plants, measured in January 2002) for 0-60 cm depth, microbial biomass C (MBC) and N (MBN), and soil organic C, microbial quotient (%), and respiratory quotient for 0-5 cm depth for cleared (recent, medium and old) and uncleared treatments at *E. populnea* (EP), *E. melanophloia* (EM) and *A. harpophylla* (AH) sites.

Parameter	Tree type	Uncleared*	Recent	Medium	Old	l.s.d.#
Root biomass (g 0.005 m ⁻³)	EP	3.56 ^d	5.71 ^b	6.59 ^a	4.41 ^c	0.52
	EM	2.64 ^b	3.67 ^a	2.96 ^b	2.61 ^b	
	AH	3.74 ^d	5.74 ^b	7.18 ^a	4.95 ^c	
MBC (mg kg ⁻¹)	EP	349.2 ^{ab}	447.7 ^a	339.1 ^{ab}	178.4 ^b	240.45
	EM	315.5 ^a	181.0 ^a	250.0 ^a	147.1 ^a	
	AH	492.9 ^a	148.1 ^b	204.9 ^b	386.5 ^{ab}	
MBN (mg kg ⁻¹)	EP	32.1 ^a	45.4 ^a	28.4 ^a	30.2 ^a	23.48
	EM	40.6 ^a	21.1 ^b	28.7 ^{ab}	28.0 ^{ab}	
	AH	47.8 ^a	20.1 ^b	19.2 ^b	47.8 ^a	
Soil organic C (g kg ⁻¹)	EP	11 ^b	18 ^a	14 ^{ab}	11 ^b	4.97
	EM	13 ^a	12 ^a	11 ^a	10 ^a	
	AH	18 ^a	18 ^a	14 ^a	15 ^a	
Microbial quotient (%)	EP	3.26 ^a	2.49 ^a	2.42 ^a	1.62 ^a	2.716
	EM	2.38 ^a	1.51 ^a	2.27 ^a	1.47 ^a	
	AH	2.93 ^a	0.82 ^a	1.46 ^a	2.58 ^a	
Respiratory quotient (g CO ₂ /h per g MBC)	EP	0.10 ^a	0.08 ^a	0.14 ^a	0.14 ^a	0.061
	EM	0.12 ^b	0.23 ^a	0.16 ^b	0.22 ^{ab}	
	AH	0.09 ^b	0.24 ^a	0.21 ^a	0.28 ^a	

*different superscripts in a row represent significant difference at $P < 0.05$

#Average values for least significant difference (l.s.d.) of means at $P < 0.05$

Table 3. The mean values (\pm standard error of mean) for total soil respiration (measured over 4 sampling events in a year), microbial and root respiration, root biomass (roots from herbaceous plants) (in January 2002), and soil microbial biomass for C and N (in March 2002) for all the cleared and the uncleared treatments.

	Uncleared	Cleared
Total soil respiration (mg CO ₂ /m ² .h)	110 (\pm 3.02)	110 (\pm 5.01)
Microbial respiration (mg CO ₂ /m ² .h)	70.1(\pm 4.1)*	50.5 (\pm 6.04)
Root respiration (mg CO ₂ /m ² .h)	40.4 (\pm 3.3)*	60.3 (\pm 7.2)
Root biomass (g 0.005 m ⁻³)	3.31 (\pm 0.21)*	4.87 (\pm 0.53)
Microbial biomass - C (mg kg ⁻¹)	385.9 (\pm 37.0)*	253.6 (\pm 37.0)
Microbial biomass - N (mg kg ⁻¹)	40.17 (\pm 3.29)*	29.87 (\pm 3.45)

*represents significant difference at $P=0.05$ (8 df) in a row after applying t-test

Table 4. Soil respiration ($\text{g CO}_2/\text{m}^2\cdot\text{h}$), soil moisture (SM - % volumetric water content (to 12 cm soil depth)) and temperature (ST- $^{\circ}\text{C}$) before (-3 to -1 day) and after (2-6 days) 40 mm of rainfall in December 2001.

Days after rain	-3 to -1 (before)	2	3	4	5	6	F value
Soil respiration*	0.1508 ^c	0.3081 ^a	0.2888 ^a	0.2847 ^a	0.2911 ^a	0.245 ^b	0.001
ST*	27.52 ^a	26.05 ^a	25.51 ^a	26.38 ^a	26.19 ^a	28.07 ^a	0.065
SM*	4.0 ^b	8.6 ^a	8.7 ^a	7.1 ^a	5.1 ^{ab}	4.0 ^b	0.001
ST x SM							0.276

df = 191, number of replicates=6

*different superscripts in a row represent significant difference at $P < 0.05$

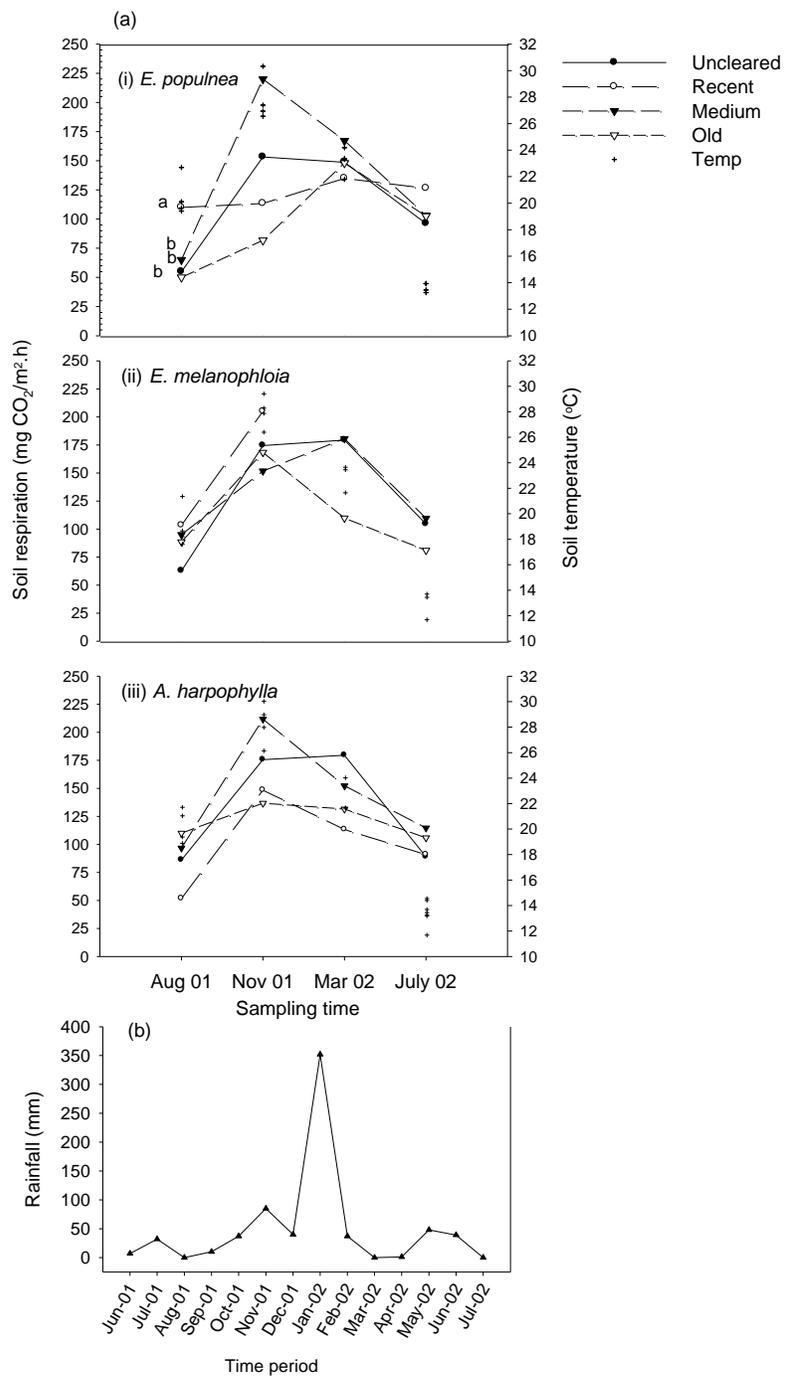


Fig. 1. (a) Soil respiration (joined by lines) and soil temperature (not joined by lines) for cleared (recent, medium and old) and uncleared treatments for (i) *E. populnea*, (ii) *E. melanophloia*, and (iii) *A. harpophylla* communities. (b) Monthly rainfall at all the sites during soil respiration measurements.

Treatment differences existed on any date where treatments are denoted by different letters i.e. August 2001 measurements for *E. populnea* only.

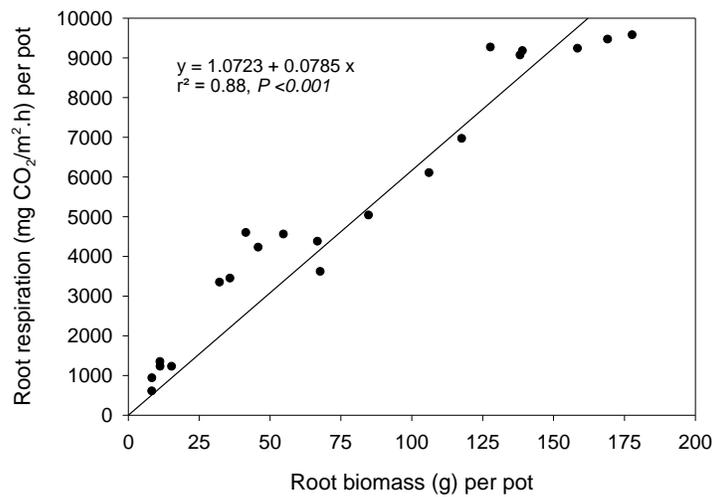


Fig. 2. Relationship between root respiration and root biomass for *C. ciliaris* in the pot experiment.

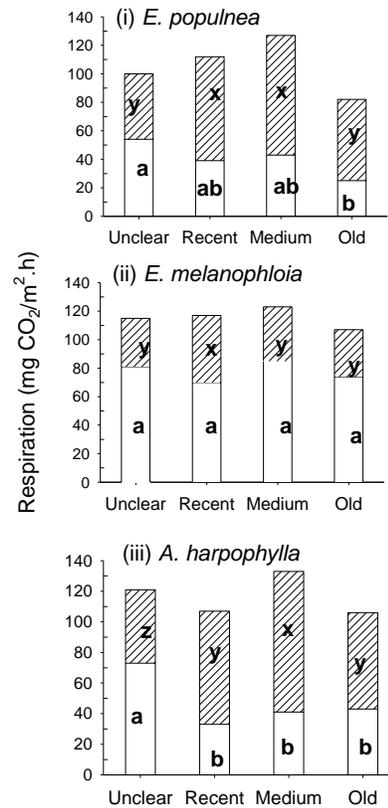


Fig. 3. Soil microbial (empty bars)- and root (stippled bars)-respiration at cleared and uncleared treatments for (i) *E. populnea*, (ii) *E. melanophloia* and (iii) *A. harpophylla* communities (where root respiration was calculated according to root biomass measured in January 2002).

Different letters on stippled (root respiration) and empty (microbial respiration) bars represent significant difference at $P < 0.05$ between treatments within a tree community.

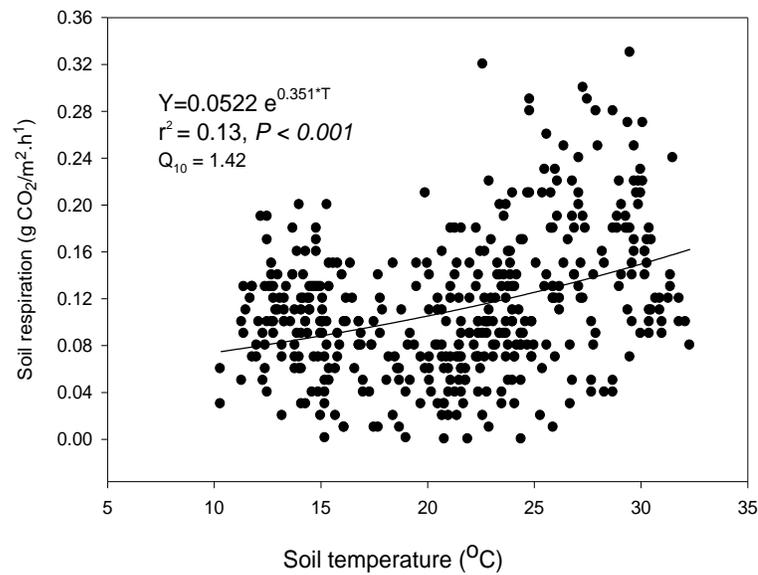


Fig 4. Soil respiration as a function of soil temperature. Data were collected at four sampling times from August 2001-July 2002 at cleared and uncleared sites for *E. populnea*, *E. melanophloia* and *A. harpophylla* communities.

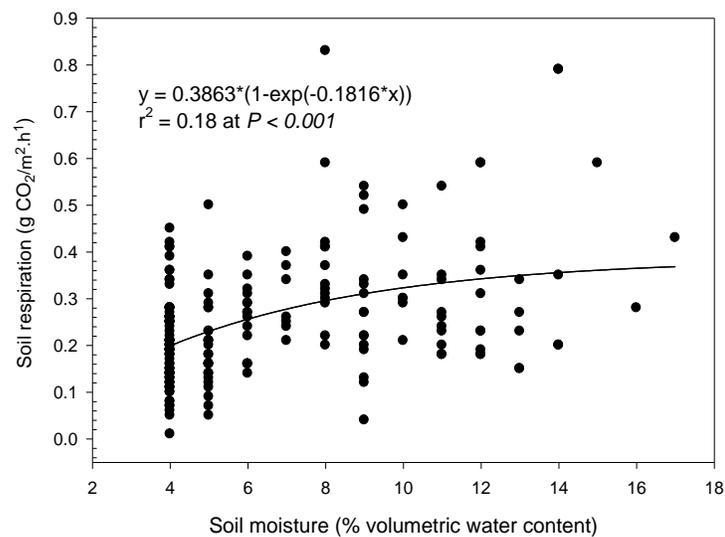


Fig. 5. Soil respiration as a function of soil moisture (before and after rainfall event (40 mm of rainfall)) at the oldest cleared and uncleared sites for *E. populnea*, *E. melanophloia* and *A. harpophylla* communities.