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Soil respiration rate and its sensitivity to temperature in pasture systems of dry-tropics

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Abstract

Tree clearing is a topical issue world over. In Queensland, the high rates of clearing in the past were mainly to increase pasture production. The present research evaluates the impact of clearing on some soil biological properties i.e. total soil respiration, root respiration, microbial respiration and microbial biomass (C and N) and the response of soil respiration to change in temperature.

In-field and laboratory (polyhouse) experiments were undertaken. For in-field studies, paired cleared and uncleared (intact) pasture systems were selected to represent three major tree communities of the region i.e. *Eucalyptus populnea*, *E. melanophloia* and *Acacia harpophylla.* The cleared sites were chosen to represent three different time-since-clearing durations (5, 11-13 and 33 years) to determine the temporal impact of clearing on soil biological properties. Experiments were conducted in the polyhouse to study in detail the response of soil respiration to change in soil temperature and soil moisture, and to complement in-field studies for estimating root respiration.

The average rate of CO_2 emissions was 964 g $CO_2/m^2/yr$, with no significant difference ($P<0.05$) among cleared and uncleared sites. Microbial respiration and microbial biomass were greater at uncleared compared to those at cleared sites. The Q_{10} value of 1.42 (measured for different seasons in a year) for in-field measurements suggested a little response of soil respiration to soil temperature possibly due to the limited availability of soil moisture and/or organic matter. However, results from the polyhouse experiment suggested greater sensitivity of root respiration to temperature change than the total soil respiration. Since root biomass (herbaceous roots) was greater at the cleared than uncleared sites and root respiration increased with increase in temperature, we speculate that with rising ambient temperature and consequently soil temperature, total soil respiration in cleared pastures will increase at a faster rate than that in uncleared pastures.

Introduction

Soil respiration is the amount of CO_2 evolved from soil microbes and roots, and to a lesser extent by oxidation of root exudates, plant detritus and humified organic matter (Raich and Schlesinger, 1992), and depends upon quantity and quality of organic matter (Giardiana and Ryan, 2000). Thereby, vegetation plays an important role in soil respiration for determining the quality and quantity of plant detritus, organic matter, microbial composition and biomass (Raich et al., 2006; Kutsch and Dilly, 1999). Any change in vegetation may affect soil biological properties by influencing soil microclimate, the quality and quantity of litter or detritus, soil organisms and availability of their substrate, and the root structure (Raich and Tufekcioglu, 2000).

At the global scale, the net effect of land use change (mostly conversion of forests to agricultural land) contributed about 2.1 Pg C during the year 2000 to the atmosphere which includes estimates for vegetation removal and its decomposition, regrowth and changes in soil carbon (Houghton and Hackler, 2002). The annual flux of carbon from soils to the atmosphere is estimated at 76.5 Pg C per yr (about 10 per cent of total CO_2 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 and subsequent land use that affects soil respiration is of major concern for global climate warming (Raich and Tufekcioglu, 2000).

Soil respiration rate differs with climate, soil and vegetation type (Lal, 2005). On a global scale, each year, forests and savannas alone contribute about 42 Pg of C while temperate grasslands, tundra, desert, cultivated and other ecosystems only the 18 Pg C to the total emissions of about 60

Pg C of respiration (both of vegetation and of microbial decomposition of organic matter) (global estimates vary from 60-75 Pg C) (Grace and Rayment, 2000). Soil respiration is about 20 percent greater in grasslands than forest (Raich and Tufekcioglu, 2000), and about 1.42 times greater in the tropical grasslands (629 g $C/m^2/yr$) than in the temperate grasslands (442 g $C/m^2/yr$) (Raich and Schlesinger, 1992). Therefore, clearing trees in tropical woodlands is of main concern for increase in net CO_2 emissions. Most of the detailed recent studies (Boone et al., 1998; Bowden et al., 1993; Giardiana and Ryan, 2000; Valentini et al., 2000), and the previous studies as Raich and Schlesinger (1992) stated, are conducted in temperate zones while a very few in tropical/subtropical climate such as by Raich et al. (2006) and Falloon et al. (2007). There is little knowledge available on soil respiration rate and its sensitivity to temperature in the semi-arid and tropical ecosystems.

Conversion of woodlands to open/cleared pastures remained a common practice in Queensland until 2004. Changes in soil nutrient status due to land use change (clearing trees to develop open pastures) have been reported (Lawrence et al., 1993; Graham et al., 1981) but the effects of clearing on soil biological properties, such as soil respiration and soil microbial biomass, largely remain unclear. To address this, the present research aims to study:

1. total soil respiration in-field and its response to change in soil temperature and moisture, and soil microbial biomass, root biomass and soil organic carbon

2. Root respiration and other components of total soil respiration, and in-depth response of soil respiration to change in soil temperature and soil moisture under polyhouse conditions

The first part of the present study was to quantify the impacts of change in vegetation structure from woodland (trees, some shrubs with herbaceous understorey) to open grassland. 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. Tree

felling followed by sowing to exotic grasses alters vegetation structure and function, and was predicted to change soil biological properties. The effect of clearing on soil biological properties was studied at different scales of time-since-clearing in cleared grasslands to interpret the long-term effects of clearing.

The second part of the study investigated the contribution of each of root, microbial and rhizosphere respiration to total soil respiration and the impact of simulated grazing on soil respiration under polyhouse conditions. During this experiment, soil respiration response to change in soil temperature and moisture, and plant growth were studied in detail.

Materials and methods

a) In-field study

i. Research sites and design

Paired sites of cleared and intact/uncleared woodlands for *Eucalyptus populnea* F. Muell. (poplar box), *E. melanophloia* F. Muell. (silver-leaved ironbark) and *Acacia harpophylla* F. Muell. ex. Benth. (brigalow) communities were selected across three age groups of clearing i.e. recent (5 yr), medium (11-13 yr) and old (33 yr). The study represents a 3 (types of tree communities) x 3 (time since clearing) x 2 (cleared v/s intact) factorial design (Table 1). The paired cleared and uncleared sites were selected in close proximity to have similar original biophysical characteristics (soil type, slope and vegetation) before clearing, and to some extent to minimize variation in grazing management for the same cattle grazed the cleared and their paired uncleared sites.

The research sites were located in a semi-arid zone. All the sites were selected at a grazing property "Avocet" of a total area about 5000 ha (NW Long 148.13^o Lat 23.79^o, NE Long 148.16^o Lat 23.80^o, SE Long 148.21^o Lat 23.85^o and SW Long 148.12^o Lat 23.86 ^{o}) in central Queensland. The average annual rainfall is 600 mm, with sporadic summer storms during November-February. Average (over the 165 years from 1865-2001) minimum and maximum temperatures during winter (June- Aug) are 6-8 ^{o}C and 23-25 ^{o}C, and during summer (Dec-Feb) are 22-24 ^{o}C and 33-36 ^{o}C respectively.

ii. Measurements

Soil respiration

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 were conducted to measure rate of soil respiration with change in soil temperature (during different times of a day) and moisture. Based on these observations and to keep consistency

in data, the field measurements were taken on normal (non-rainy) days for the morning hours (6:00-9:00 am) within a soil temperature range of 5 $^\circ$C.

The data were collected during different seasons in a year, in August and November 2001, and March and July 2002. Six readings were taken randomly at an approximate 15 m distance from each other within a 100 m x 100 m of total area at each site in each season, at the inter-canopy areas at a distance of about 1 m away from a tree trunk and at the inter-grass areas. Due to accidental patchy burning, no readings were taken 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.

The litter layer (if any) was removed before placing the soil respiration chamber on the soil surface. The chamber was placed onto bare soil, avoiding grass stumps and exposed roots. Soil temperature probes were inserted into the soil near to the chamber. The measurements were taken on clear mornings firstly in the cleared (because of its open exposure to sun) and subsequently at the paired uncleared sites to minimize the effect of soil warming. Only one paired site was monitored on any one day.

To study the in-field response of soil respiration to soil moisture and soil temperature, measurements were taken in Dec 2001 at the oldest set of all the cleared and uncleared sites before (1-3 days) and after rain (starting from 2nd till 6th day after rain). Soil moisture content was measured at six sampling places at a site on each day to 12 cm depth with probes (Hydrosense Soil Moisture Measurement System, Campbell Scientific Australia).

Root respiration (for herbaceous plants)
Eight soil cores to 60 cm depth (4 cm diameter) were taken at each site during January 2002 using a hydraulic soil corer. The cores were taken from space between plants. Soil samples were dried and

bulked per site. The visible roots (>1 mm diameter) were removed by hand following sieving, dried at 60 $^{\circ}$C and weighed. This method would not have removed the very fine roots, hence total root biomass values may have been underestimated.

The rate of root respiration per unit root biomass was determined in the polyhouse experiment with the most commonly grown grass species *Cenchrus ciliaris*. The average rate of root respiration per unit root biomass (g) obtained from polyhouse experiment was used to calculate in-field root respiration based on in-field root biomass determination.

Microbial respiration

Soil microbial respiration was computed from average soil respiration per year minus computed root respiration based upon the estimate of root biomass, for each site.

Soil microbial biomass

Samples of soil from the top 0-5 cm were collected in March 2002 at each site. Soil microbial biomass carbon (MBC) and nitrogen (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 microbial biomass and soil respiratory quotients were determined as Sparling (1997):

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

$$\text{Soil respiratory quotient} = \frac{\text{Total soil respiration (g } CO_2/\text{hr)}}{\text{Soil microbial carbon (g)}}$$

iii. Statistical analyses

The data were analysed using residual maximum likelihood analysis (REML) (Genstat ver 6.0 (Genstat Committee, 2002). All the uncleared sites for a tree type at each group of clearing were taken as replicates, whereas the paired cleared sites for each age group were considered as such with no replication within a community but replicated across the communities. The data are therefore presented for uncleared, recent, medium and old age since clearing treatments in each tree community.

Soil respiration

The main effects (fixed term) of tree community*cleared-uncleared and random effects of time-since-clearing for recent, medium and old clearing of paired cleared and uncleared treatments for all the tree communities were analysed using REML.

For the main effects, if the interaction between a tree community*cleared-uncleared was significant at *P < 0.05,* then LSDs (least significant difference of means) were computed for each treatment. In the absence of any significant interaction, the individual effects for a tree community and cleared-uncleared treatments were computed.

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

Relationships between soil respiration- temperature and -moisture were analysed using regression analysis. Soil respiration response to temperature over a year was computed from the temperature quotient $Q_{10} = e^{\beta_1 T}$ (represents the sensitivity of respiration for every 10 ^{o}C change in temperature)

obtained from an exponential regression $y = \beta_0 e^{\beta_1 T}$ (where y = soil respiration, β_0 and β_1 = fitted constants and T = temperature (^{o}C)) fitted to the data. An ANOVA was applied for the data collected before and after rain at all cleared and uncleared treatments.

b) Experiments in the polyhouse

i Experimental design and measurements

Root respiration was difficult to measure in the field at each site in different seasons because of hard soils. However, soil samples were taken once using a hydraulic soil corer at each site to quantify soil chemical properties and to determine root biomass. To complement the in-field studies on total soil respiration, an experiment was conducted to estimate the contribution of root respiration to total soil respiration. The estimated specific root respiration rate (i.e. in relation to root biomass) was used to determine in-field root respiration based on root biomass (in-field). This experiment was also aimed to determine soil respiration response for change in soil temperature and soil moisture, and the impact of simulated grazing (defoliation).

The most common pasture grass *C. ciliaris* was grown in pots (34 cm diameter, 35 cm height) in two sets to estimate root respiration in the absence (set I) and presence of defoliation (simulated grazing - set II) (Table 2). For defoliation, plants were successively defoliated once, twice and thrice in defoliation treatments D1, D2 and D3 respectively (Table 2). Two types of controls were maintained: C1 with soil but no grass to measure root-free soil (microbial) respiration, and C2 with grass but without defoliation (Table 2).

Seeds were sown on 4th April 2002 to sandy soil in each pot, and supplied with nutrient solution (Manutec Pty Ltd, SA) during growth. Sandy soil was chosen as an appropriate medium to minimize root loss during extraction.

The experiment was set up in the polyhouse (temperature range 7-32 ^{o}C and relative humidity range 14-48 per cent), in a randomised block design with four blocks for all the grass and control pots. Soil respiration, soil temperature and soil moisture were monitored in the centre of each pot since the plants were two months old (approximate height >30 cm) until their uprooting for root respiration measurements. The measurements were taken over consecutive days following each irrigation event that occurred once a week.

To determine the contribution of root respiration to total soil respiration, total soil respiration was recorded for all pots just before uprooting. The roots were extracted by emptying a pot onto a plastic sheet, and sand and shoot parts were then removed before measuring the root respiration. The roots were kept in a PVC chamber (specially constructed of the size of the soil respiration chamber) and the soil respiration chamber was placed vertically on this to measure respiration (R_{root}). 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 remove sand particles (if any), dried at 60 ^{o}C for 48 hours and weighed.

The pots were refilled with the same soil from which the plants were removed, and monitored at 3-4 day intervals until respiration stabilised (normally about one month). The stabilised rate of respiration was taken as root-free soil respiration/microbial respiration (R_{rfs}) as per the basal respiration method (Kelting et al., 1998). R_{rfs} was then used to estimate rhizosphere respiration (R_{rhizo}) as follows (Kelting et al., 1998):

Total soil respiration $R_s = R_{root} + R_{rfs} + R_{rhizo}$ (i)

Where each component is measured as:

R_s - using soil respiration chamber

R_{root} - by extraction + soil respiration chamber

R_{rfs} - using basal method

Rearranging equation (i) solving for R_{rhizo}:

$$R_{rhizo} = R_s - (R_{rfs} + R_{root}) \tag{ii}$$

The above-mentioned procedure, a combination of two methods i.e. the root extraction and the basal, was followed to determine root, microbial and rhizosphere respiration and to avoid overestimation of any of these three components of soil respiration. Use of one method either extraction method or basal method overestimates the root and microbial components of total respiration (Kelting et al., 1998).

ii Statistical analyses

The soil, root, microbial/root-free soil, and rhizosphere respiration, and root biomass data were analysed using ANOVA for comparisons between treatments. Simple regression analysis was used for R_{root} relationship to root biomass. R_s response to temperature and moisture was analysed using multiple regression for the interactive, and simple regression for individual effects of temperature and moisture for each treatment (C1, C2, D0, D1, D2 and D3).

Results

a) Field study

i. Soil respiration (R_s)

There was no significant difference in the rate of R_s between cleared (0.12 ± 0.023 g $CO_2/m^2/hr$ (mean $\pm$ standard error of means)) and uncleared (0.11 ± 0.015 g $CO_2/m^2/hr$) sites, nor with time-since-clearing for any of the tree communities (data not presented).

ii. Microbial (R_{micro}) and root respiration (R_{root})

R_{micro} was greater at uncleared compared to the oldest clearing for *E. populnea,* and to all cleared sites for *A. harpophylla* (Fig 1 a and c), while it showed no significant difference at cleared and uncleared sites for *E. melanophloia* (Fig 1 b).

Biomass of fibrous roots for 0-60 cm depth was greater at all cleared than uncleared treatments for *E. populnea* and *A. harpophylla,* and at recent clearing than uncleared site at *E. melanophloia* (Table 3).

R_{micro} was positively but weakly related to MBC (r = 0.20 at *P=0.05*) and MBN (r = 0.27) across all the sites. In *E. populnea,* uncleared, medium and recent clearing had greater MBC compared to the oldest clearing, but did not significantly differ in terms of MBN (Table 3). In *E. melanophloia,* MBC did not show difference between any of the cleared and uncleared sites, but MBN was greater at uncleared than recent clearing. MBC and MBN were greater at uncleared *A. harpophylla* than the cleared treatments except for the oldest clearing. The cleared and uncleared treatments for all the tree types did not differ significantly in soil organic carbon with the exception that the recent clearing had greater amount than the uncleared site in *E. populnea* (Table 3).

Microbial quotient, the ratio of MBC to soil organic carbon, did not differ between cleared and uncleared treatments. Respiratory quotient, ratio of soil respiration to MBC, was greater at recent

and the oldest clearing for *E. melanophloia,* and at all cleared sites for *A. harpophylla* compared to their uncleared sites, but did not differ between cleared and uncleared treatments at *E. populnea* (Table 3).

Overall, uncleared sites had significantly greater microbial respiration compared to cleared sites (Table 4). But the root respiration was greater at cleared (0.06 g CO_2/m^2/hr) than uncleared (0.04 g CO_2/m^2/hr) sites. The microbial respiration contributed 45 per cent at cleared and 62 per cent at uncleared sites to total soil respiration. Root respiration contributed 55 per cent at cleared and 38 per cent of total soil respiration at uncleared sites (Table 4).

Factors affecting in-field soil respiration

R_s increased with soil temperature (Fig 2). The Q_{10} value of 1.42 was determined over the range 10-32 ^{o}C.

A significant increase in R_s occurred after rainfall (Table 5). The data were collected in Dec 2001 in the middle of the rainy season (40 mm rainfall in Dec, after 85 mm in Nov and 37 mm Oct). Soil moisture accounted for 18 per cent of the variation in R_s (Fig 3) when measured daily before (13-15th of Dec 2001) and over 6 days (18th- 23rd of Dec 2001) after a rainfall event on 16-17th of Dec 2001.

b) Polyhouse experiments

To simulate grazing of *C. ciliaris,* defoliation was conducted to quantify the different components of root, microbial and rhizosphere respiration in soil respiration (R_s), and to determine R_s response to change in temperature.

R_s and R_{root} (per unit chamber volume and pot) increased during growth, particularly from four to nine months. The R_s of defoliation treatments D2 and D3 did not differ from the un-defoliated control C2; defoliation *per se,* therefore, had no effect on R_s (Table 6).

Root-free soil R_{rfs} (microbial (or R_{micro} as in-field) respiration and R_{root} per unit root biomass showed no difference between any of the treatments (Table 6). Rhizosphere respiration (R_{rhizo}) was at a maximum in D2, was less in D3 and was least in D0 (Table 6).

R_{root} per unit root biomass was similar across all the treatments. But R_{root} per pot or per unit volume of soil respiration chamber increased with plant growth (Table 6). R_{root} was clearly related to root biomass (Fig 4). The increase in root biomass contributed to increased rate of R_{root} with the growth of plant, and consequently increase of R_s.

Factors affecting R_s (polyhouse experiment)

Soil temperature accounted for significant variation in R_s ($r^2 = 0.64$ at *P<0.05*) in all defoliation treatments. The R_s response to change in temperature was very small in C1 ($r^2 = 0.07$ at *P<0.05*) for a range of 16.6 ^{o}C-25.4 ^{o}C temperature and in D0 ($r^2 = 0.13$ at *P<0.05*) for a range of 10.8 ^{o}C-25.9 ^{o}C temperature. A significant response of R_s to temperature in defoliation treatments was probably due to plant/root growth.

Between defoliation treatments, R_s response to temperature in D3 was significantly different from its control C2 (C2-3) (there were three sets of measurements for C2: C2-1 against D1, C2-2 against D2, C2-3 against D3), D1, D2 at *P<0.05* (Fig 5 and Table 7)*,* whereas D1, D2 and C2 showed no significant difference with each other. The greater R_s response to temperature at D3 (third stage of defoliation) suggested that defoliation increased R_s sensitivity to temperature (Fig 5).

Soil moisture accounted for only four per cent of the variation in soil respiration in all the treatments (data not presented), therefore, temperature proved to be the main factor that accounted for variation in soil respiration in the polyhouse experiment.

Discussion

Cleared grasslands and native woodlands had similar average annual rates of soil respiration, equivalent to 263 g C/m^2/yr (964 g CO$_2$/m^2/yr) with measurements taken from inter-canopy and inter-grass areas in woodlands, and inter-grass areas in grasslands. The average rate of soil respiration reported herein for the semi- arid zone was less than that reported for semi-arid woodlands of north Queensland (380 g C/m^2/yr; Holt et al., 1990), tropical savannas and grassland (629 g C /m^2/yr) and temperate grassland (442 g C/m^2/yr) (Raich and Schlesinger, 1992). The reasons may be the differences in climate, chiefly rainfall and temperature, and partly due to the vegetation communities. Russell et al. (2007) reported that vegetation composition, particularly detritus inputs from roots and associated microbial communities are largely responsible for determining CO$_2$ emissions.

This study suggested that conversion of woodlands to open pastures (grasslands) did not increase the rate of total soil respiration, except for CO$_2$ emissions during clearing operations e.g. pulling, fire and initial decomposition of vegetation left after clearing. This contradicts the concerns raised in many studies (Batjes and Sombroek, 1997; Raich and Tufekcioglu, 2000) that increases in CO$_2$ emissions accompany land use change, particularly when converting woodlands to open grasslands. However, the degree of sensitivity of soil respiration to temperature change in woodland and grassland is of concern as discussed later.

Soil respiration response to temperature and moisture may vary in different climatic zones. The Q_{10} ($Q_{10} = e^{\beta_1 T}$) value of 1.42 suggested only little response to temperature in field conditions of central

Queensland. The average Q_{10} value for various ecosystems reported 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) and may have $Q_{10} = 3.5$ (Boone et al., 1998). Whereas, soil moisture, considered a primary factor that limits growth in semi-arid woodlands (Holt et al., 1990; Scholes, 1993), and soil temperature or their interaction with other environmental factors, may affect the rates of soil respiration in the semi-arid climates.

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. Measurements taken during the rainy season indicated a small response of soil respiration to soil moisture ($r^2 = 0.18$) for the successive 2 to 6 day after rain. Under polyhouse experimental conditions, such a response was minimal ($r^2 = 0.04$ for a range of 35-80% volumetric content of water), mainly due to the absence of any wet or dry periods which would have occurred under natural conditions as seen for in-field soil respiration response to rain. Fallon, et al. (2007) suggested that in dry conditions, rainfall seems to control C emissions resulting in lower C stocks. However, our both the polyhouse and in-field experiments indicated a very small response of soil respiration to soil moisture, suggesting there may be other limiting factors such as soil nutrients or soil carbon source/substrate quality that regulate such response.

The contribution of root respiration (herbaceous plants, for 0-60 cm depth) to total soil respiration was greater in cleared (55%) than in uncleared (38%) pastures. Holt et al. (1990) also reported 40% contribution of root respiration to total soil respiration in the dry tropic woodlands. About 17-40 per cent root respiration of total soil respiration in grasslands was also reported by Raich and Tufekcioglu (2000). Our polyhouse experiment provided further detailed information about different components of R_s where respiration from *C. ciliaris* roots contributed about 31-73 percent, rhizosphere about 25-68 percent and root-free soil (microbial) respiration 1.4-5 percent of total soil

respiration. The root biomass and root respiration relationship from the polyhouse experiment suggested that for in-field measurements the differences in root biomass between cleared and uncleared sites (Tables 3 and 4) were largely responsible for minimizing the differences in total soil respiration between treatments.

The sensitivity of soil respiration to temperature was greater for *C. ciliaris* in polyhouse experiment (Fig 5, $r^2 = 0.64$, $Q_{10} = 3.31$) compared to in-field response ($r^2 = 0.13$, Fig 2), may be due to differences in soil, vegetation and climatic (natural wet and dry) conditions that the plants grow in-field and in the polyhouse. Moreover, the average root biomass per unit volume was greater in the polyhouse experiment (6 mg/cm^3) compared to in-field conditions (1 mg/cm^3). The greater sensitivity of soil respiration to temperature in polyhouse conditions was mainly due to the greater root respiration (root respiration was strongly related to root biomass ($r^2 = 0.88$)). This was concluded based on the evidence that compared to grass pots, the control C1 with no grass showed no significant soil respiration response to temperature ($r^2 = 0.07$). Hence, it is suggested that the soil respiration response to temperature was in the main due to root biomass and therefore root respiration response to temperature. Greater sensitivity of root respiration than soil respiration to change in temperature has also been reported before (Boone et al., 1998). If the root respiration were sensitive to temperature, then the greater rate of root respiration could be of concern in cleared pastures for increase in CO_2 emissions with increase in temperature.

Conversion of woodlands to cleared pastures presents a different scenario for microbial activities and for microbial carbon and nitrogen biomass than for total soil respiration where the cleared pastures had lesser rate of microbial activity and lesser MBC and MBN than did the uncleared pastures (Table 3 and 4). Sparling et al. (1994) reported similar observations. For established woodland systems, the lesser microbial activity in relation to their biomass (respiratory quotient) in

E. melanophloia and *A. harpophylla* than that at cleared pastures indicated the potential of these woodlands to optimise the use of soil resources whereas higher respiratory quotient values in woodlands indicate stress response and 'poor soil health' (Sparling, 1997).

The changed pasture composition from a multi-species and multi-storeyed system in native woodlands to monocultures of *C. ciliaris* (predominantly, and with some other species) altered soil biological properties, particularly microbial and root biomass, and their activity. Such a change may further 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). Introduction of exotic grass species such as *C. ciliaris,* and clearing of native vegetation disturb the plant-soil relationship in a particular environment. The different species harbour different microbial communities that affect the ecosystem functions (Bardgett et al., 1999). Substrate quantity and quality, soil microclimate and adaptability of microbes change with the type of vegetation (Kutsch and Dilly, 1999: Russell et al., 2007).

Tree clearing resulted in changes at the macroscopic (vegetation communities: tree, shrubs and pasture plant species) and at the microscopic level (microbial biomass (Tables 3 and 4) and microbial respiration (Fig 1)). These changes alter the ecosystem functions e.g. nutrient availability at cleared and uncleared sites (Sangha et al., 2005; Kaur et al., 2007), quantity and quality of substrate available for microbial decomposition and nutrient return in a system (Sangha et al., 2006). In the present study, the decline in soil biological properties and increases in root biomass in cleared pastures raises concerns for changes in contribution of roots to total soil respiration in response to increase in global temperature.

Acknowledgements

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Tables:

Table 1. Paired treatments for each of *E. populnea*, *E. melanophloia* and *A. harpophylla*.

Treatments	Time since clearing
Cleared	**Recent (5 years)**
Uncleared/intact	Never cleared
Cleared	**Medium (11-13 years)**
Uncleared/intact	Never cleared
Cleared	**Old (33 years)**
Uncleared/intact	Never cleared

Table 2. Various treatments to estimate root respiration in the polyhouse.

	Treatment	Abbreviations used in text	No. of pots	Growth period (months)
Control 1	No grass, soil only	C1	5	-
Control 2	No defoliation	C2	3	9
I set	No defoliation	D0	5	4
II set	Defoliation - once	D1	3	6
	Defoliation - twice	D2	3	7.5
	Defoliation - thrice	D3	3	9

Table 3 Root biomass for 0-60 cm depth, microbial biomass carbon (MBC) and nitrogen (MBN), and soil organic carbon for 0-5 cm depth, microbial quotient (%), and respiratory quotient for cleared (recent, medium and old) and uncleared treatments at *E. populnea, E. melanophloia* and *A. harpophylla.*

Parameters	Tree community	Uncleared*	Recent*	Medium*	Old*	LSD#
Root biomass (fibrous roots) (g/0.005 m^3)	*E. populnea*	3.56^d	5.71^b	6.59^a	4.41^c	0.52
	E. melanophloia	2.64^b	3.67^a	2.96^b	2.61^b	
	A. harpophylla	3.74^d	5.74^b	7.18^a	4.95^c	
MBC (mg/kg)	*E. populnea*	349.2^{ab}	447.7^a	339.1^{ab}	178.4^b	240.45
	E. melanophloia	315.5^a	181.0^a	250.0^a	147.1^a	
	A. harpophylla	492.9^a	148.1^b	204.9^b	386.5^{ab}	
MBN (mg/kg)	*E. populnea*	32.1^a	45.4^a	28.4^a	30.2^a	23.48
	E. melanophloia	40.6^a	21.1^b	28.7^{ab}	28.0^{ab}	
	A. harpophylla	47.8^a	20.1^b	19.2^b	47.8^a	
Soil organic carbon (g/kg)	*E. populnea*	11^b	18^a	14^{ab}	11^b	4.97
	E. melanophloia	13^a	12^a	11^a	10^a	
	A. harpophylla	18^a	18^a	14^a	15^a	
Microbial quotient (%)	*E. populnea*	3.26^a	2.49^a	2.42^a	1.62^a	2.716
	E. melanophloia	2.38^a	1.51^a	2.27^a	1.47^a	
	A. harpophylla	2.93^a	0.82^a	1.46^a	2.58^a	
Respiratory quotient (g CO_2/hr per g MBC)	*E. populnea*	0.10^a	0.08^a	0.14^a	0.14^a	0.061
	E. melanophloia	0.12^b	0.23^a	0.16^b	0.22^{ab}	
	A. harpophylla	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 (LSD) of means at *P <0.05*

Table 4. The mean values (± standard error of mean) for microbial (R_{micro}) and root (R_{root}) respiration, root biomass, and soil microbial biomass for carbon (MBC) and nitrogen (MBN) for all the cleared and the uncleared treatments.

	Uncleared	Cleared
R_{micro} (g CO_2/m^2/hr)	0.07(±0.004)*	0.05 (±0.006)
R_{root} (g CO_2/m^2/hr)	0.04 (±0.003)*	0.06 (±0.007)
Root biomass (g/0.005 m^3)	3.31 (±0.21)*	4.87 (±0.53)
MBC (mg/kg)	385.9 (±37)*	253.6 (±37)
MBN (mg/kg)	40.17 (±3.29)*	29.87 (±3.45)

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

Table 5. Soil respiration (g $CO_2/m^2/hr$), soil moisture (SM - % volumetric water content) and temperature (ST- ^oC) before (-3 to-1 day) and after (2-6 day) rainfall.

Days after rain	-3 to -1	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
STx SM							0.276

df = 191

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

Table 6.Total soil (R_s), microbial (root-free soil) (R_{rfs}), rhizosphere (R_{rhizo}) and root (R_{root}) respiration (g $CO_2/m^2/hr$) per soil respiration chamber volume (1885.71 cm^3), and root respiration (R_{root}) per pot (volume 20757 cm^3), per unit root biomass (g), and root biomass (RB) (g) per pot for controls C1 (soil but with no grass) and C2 (with grass, no defoliation), and for plants before (D0) and after successive stages of defoliation (D1-once, D2-twice and D3-thrice) treatments.

Treatments -defoliation (growth period)	R_s^*	R_{rfs}^*	R_{rhizo}^*	R_{root}^*	R_{root}/pot^*	R_{root}/RB^*	RB/pot^*
C1	0.02^d	0.02^a					
C2-none (9 month)	1.13^a	0.02^a	0.39^b	0.72^a	7.92^a	0.07^a	129.4^a
D0-none (4 month)	0.19^c	0.01^a	0.08^c	0.09^c	1.05^c	0.08^a	11.1^b
D1-once (6 month)	0.76^b	0.01^a	0.38^b	0.37^b	4.07^b	0.09^a	41.3^b
D2-twice (7.5 month)	1.37^a	0.02^a	0.93^a	0.42^b	4.64^b	0.07^a	69.0^b
D3-thrice (9 month)	1.22^a	0.02^a	0.31^b	0.89^a	9.77^a	0.08^a	121.2^a
LSD	0.268	0.025	0.178	0.200	0.021	0.02	41.96

[*] Different superscripts in a column represent significant difference according to least significant difference of means (LSD) at *P = 0.05*

Table 7 Regression analysis results for exponential relationship ($R_s = a + b\ e^{(-k*temperature)}$) between soil respiration and soil temperature for various treatments.

Treatment	a (Intercept)	b (Slope)[#]	k	r^2 *
D1 (Defoliated once)	0.4065	0.00001749	-0.1806	0.64
D2 (Defoliated twice)	0.6278			
D3 (Defoliated thrice)	0.8055			
C2-1 (Control against D1)	0.3711			
C2-2 (Control against D2)	0.7421			
C2-3 (Control against D3)	0.7584			
D0 (no defoliation)	n.s.			
C0 (Control with no plant)	n.s.			

[#] Slopes were not significantly (at *P<0.05*) different across various treatments hence all data had a common slope, meaning that the lines were parallel but with different intercepts.

* for pooled data from defoliation treatments D1, D2, D3 and their controls C2-1, C2-2 and C2-3.

n.s. - no significant response of soil respiration to soil temperature at *P<0.05*.
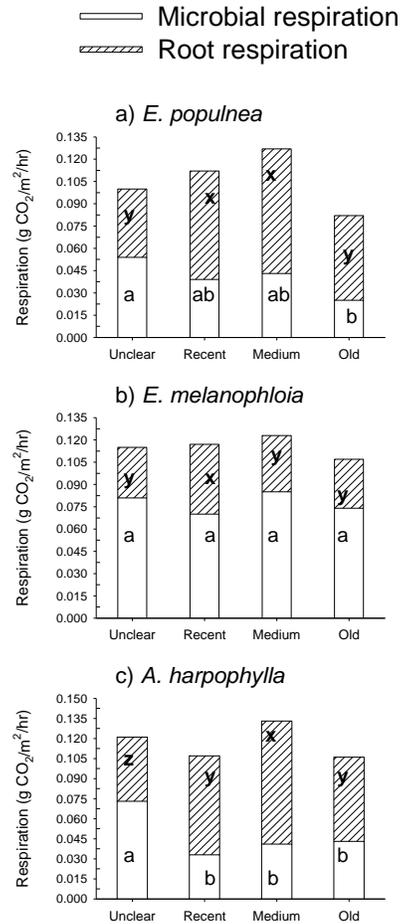
Fig. 1. Soil microbial and root respiration at cleared and uncleared treatments for a) *E. populnea*, b) *E. melanophloia* and c) *A. harpophylla* communities.

Different letters on lined (root respiration) and empty (microbial respiration) bars represent significant difference at P<0.05 between treatments within a tree community corresponding to similar bars.
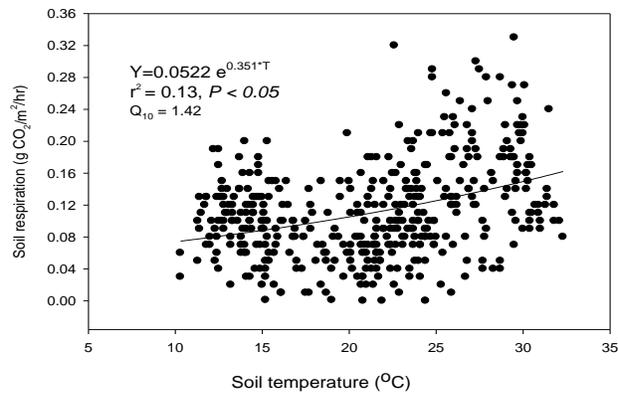
Fig. 2. Soil respiration as a function of soil temperature, data collected throughout a year at all cleared and uncleared sites for *E. populnea, E. melanophloia* and *A. harpophylla* communities.
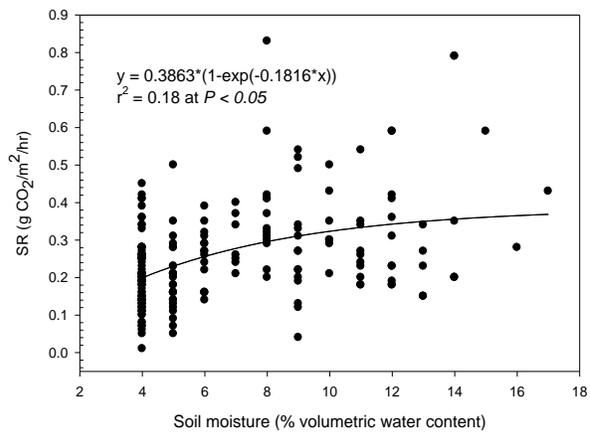
Fig. 3. Soil respiration as a function of soil moisture (before and after rainfall event) at the oldest cleared and uncleared sites for *E. populnea*, *E. melanophloia* and *A. harpophylla* communities.
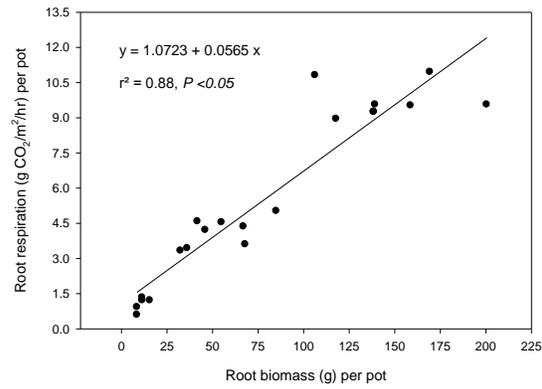
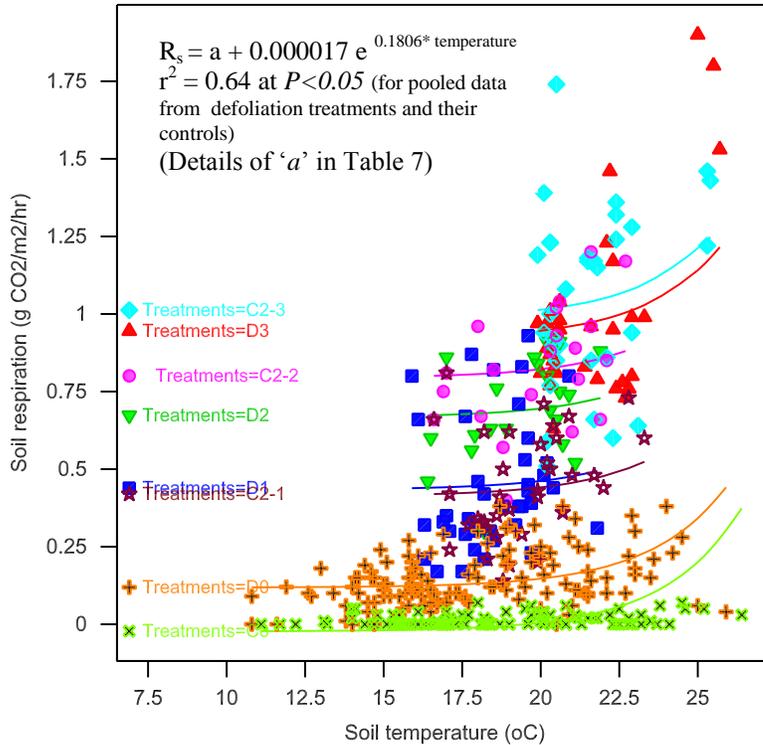Fig. 4. Root respiration and root biomass relationship for *C. ciliaris.*

Fig 5. Soil respiration response to soil temperature for defoliation treatments and their corresponding controls (graph reproduced from Genstat):
D1 (defoliated once) and control C2-1 (treatment labels are overlapping in plot)
D2 (defoliated twice) and control C2-2
D3 (defoliated thrice) and control C2-3
D0 (no defoliation)
C0 (control with no grass) (treatment labels C0 and D0 are overlapping in plot)