REGULAR ARTICLE

The change of soil carbon stocks and fine root dynamics after land use change from a native pasture to a pine plantation

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Abstract A published meta-analysis of worldwide data showed soil carbon decreasing following land use change from pasture to conifer plantation. A paired site (a native pasture with *Themeda triandra* dominant, and an adjacent *Pinus radiata* plantation planted onto the pasture 16 years ago) was set up as a case study to assess the soil carbon reduction and the possible reason for the reduction under pine, including the change in fine root (diameter <2 mm) dynamics (production and mortality). Soil analysis confirmed that soil carbon and nitrogen stocks to 100 cm under the plantation were significantly less than under the pasture by 20 and 15%, respectively. A 36% greater mass of fine root was found in the soil under the pasture than under the plantation and the length of fine root was about nine times greater in the pasture. Much less fine root length was produced and roots died more slowly under the plantation than under the pasture based on observations of fine root dynamics in minirhizotrons. The annual inputs of fine root litter to the top 100 cm soil, estimated from soil coring and minirhizotron observations, were 6.3 Mg dry matter ha^{-1} year^{-1} (containing 2.7 Mg C and 38.9 kg N) under the plantation, and 9.7 Mg ha^{-1} year^{-1} (containing 3.6 Mg C and 81.4 kg N) under the pasture. The reduced amount of carbon, following afforestation of the pasture, in each depth-layer of the soil profile correlated with the lower length of dead fine roots in the layer under the plantation compared with the pasture. This correlation was consistent with the hypothesis that the soil carbon reduction after land use change from pasture to conifer plantation might be related to change of fine root dynamics, at least in part.

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Introduction

Vegetation, soil and oceans can act as carbon sinks. As forests make up large ecosystems, with high

biomass, they can play an important role in mitigating the anthropogenic emissions of CO_2 (Backeus et al. 2005). Hence, reforestation or afforestation of agricultural land has been widely accepted as a means to sequester CO_2 from the atmosphere. Fast-growing tree species, e.g. *Pinus radiata*, accumulate "live" carbon (C) more rapidly than do slow-growing species thereby giving a period of more rapid carbon sequestration into biomass (Cannell 1996).

However, observations have shown that soil C stocks usually decrease after the conversion from pasture to pine plantation (e.g. Gifford 2000; Turner and Lambert 2000; Guo and Gifford 2002) even though large quantities of atmospheric CO_2 can be fixed into tree biomass for a long period of time (Hoen and Solberg 1994). Ecosystem C-sequestration depends on the sum of all carbon pools – soil, litter and biomass – and full C-accounting for CO_2 mitigation purposes should include all these pools.

Belowground primary production is often greater than aboveground production in perennial, native ecosystems (Coleman 1976). The quality of roots is an important factor in the root utilisation by soil biota, and thus in rate of decomposition and associated nutrient cycling. Root litter production thereby feeds back to primary production and is relevant to global C budgets (Zak et al. 2000).

In forests, coarse roots represent most of the standing root crop, but fine roots account for most belowground production (Steinaker and Wilson 2005). Fine root production has been reported to account for approximately half of the C cycled in forests, or up to two thirds of the annual photosynthate consumption (Vogt et al. 1996; Waring et al. 1998). Fine root turnover is of critical importance when assessing nutrient and carbon fluxes in a plant–soil system, as the fluxes below ground might be higher than those above ground (Vogt et al. 1986; Fahey and Hughes 1994; Andersson and Majdi 2005). Root turnover (via mortality) is a major source of soil carbon (McClaugherty et al. 1982; Tate et al. 1993; Steele et al. 1997). On the other hand, Guo et al. (2005) reported that soil C changes were positively correlated with *live* fine root length density in the soil under various species in controlled environments from a 1-year pot study. Accordingly, we hypothesize that change in two aspects of fine root dynamics (the amount of carbon input via production and mortality, and live root surface area involving rhizosphere

processes) may play important roles in the phenomenon of soil carbon loss after land use change from pasture to pine plantation. Furthermore, trends in soil carbon can be better understood through consideration of the linked nitrogen (N) cycle for which root dynamics plays an integral role.

Here we report a field experiment designed to explore the above ideas via a case study. Our objectives for this study are to assess: (1) the changes of soil C and N stocks after pine trees were planted onto a long established native grazed pasture; (2) the change of fine root dynamics in terms of both surface area and potential C and N input via fine root turnover; and (3) the potential linkages between the above changes.

Methods

Site description

The paired site (a native pasture with *Themeda triandra* Forssk. dominant, and an adjacent 16 year old *Pinus radiata* D. Don. plantation) for this study was at Billy Billy, Kowen Forest, ACT, Australia (149° 19′30″E, 35°20′00″S). The site was chosen for its uniformity, lack of any isolated eucalypt trees in the pasture area and because prior study (Gifford 2000) of soil carbon stocks in forests and adjacent pastures in the Australian Capital Territory and New South Wales had found that a paired site along the same boundary of the Kowen forest, about 1 km distant from the present study site, had 67.5 Mg C ha^{-1} to 1 m depth under the native pasture and 62.6 Mg C ha^{-1} under the adjacent pine forest, the difference being consistent with that found in the global meta-analysis of such comparisons (Guo and Gifford 2002). The site has an elevation of 720 m above sea level. From meteorological data for Canberra airport (about 15 km from the field site for this study), average daily temperatures range from 5.7°C in July to 20.4°C in January and the average annual precipitation is 622 mm, and was 519 mm in the study period (a dry year) from April 2003 to March 2004 (Fig. 1). A similar precipitation time-trend was recorded at the field site during the study period, except in November and December, and the annual rainfall was only 464 mm.

The native vegetation was Southern Tableland Grassy Woodland (Keith 2004). However, the native trees had been largely cleared and native grasses, with

Fig. 1 Monthly precipitation at Canberra airport (60 year average and the study period of April 2003–March 2004), and at the field site for the study period
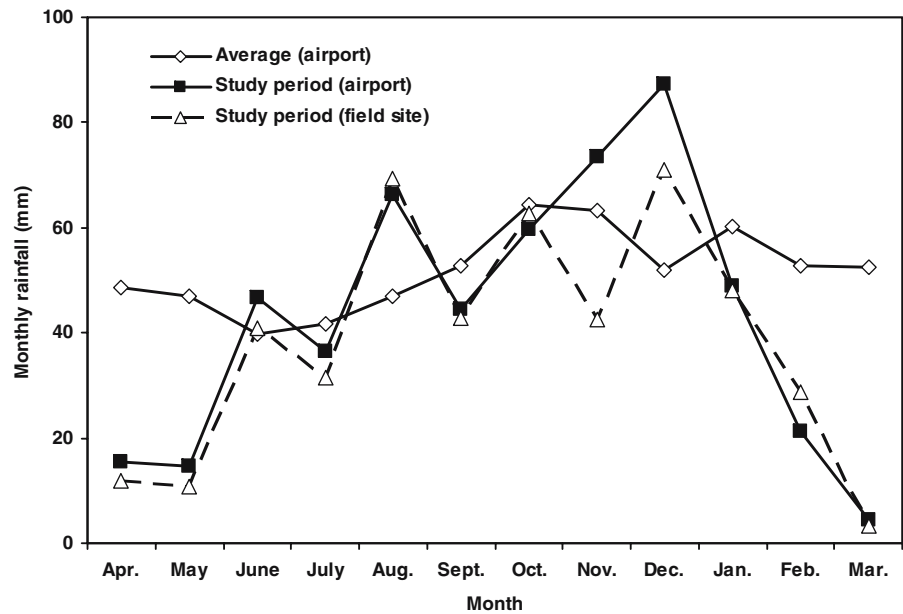
Themeda triandra dominant, have been grazed for more than a century. P. radiata was planted in 1987 onto the native pasture. The pine tree density was 800 trees ha^{-1}, with an average of 25.4 cm diameter at breast height over-bark, and 15.6 m height in 2003. The adjacent pasture continued to be extensively grazed during the study period.

The pasture was a half kilometer-wide strip between a highway and the plantation boundary, which ran parallel to the highway for approximately 2 km from the start of the forest before being intersected by an access lane. The forest ranged from 0.5 to 2 km deep (approximate). Ten plots were set up in the pasture (1×1 m) and in the adjacent plantation (10×12 m) for this study. The plots in the forest were much larger than in the pasture because of the large size of the trees compared with the grass plants. The pasture plots were spaced systematically at 10 m spacing along a transect that ran parallel to the forest-pasture boundary at a distance of 30–40 m. The forest plots were a minimum of 40 m from the forest edge and arranged in staggered rows approximately parallel to the boundary to leave at least 10 m gaps between them.

Soil sampling

The soils at the site are classified as Dermosols having structured B2 horizons and lacking strong texture contrast between A and B horizons (Isbell

1996). Topsoil pH (in calcium chloride) was pH 4.5 increasing to pH 5.6 at 60 cm under both forest and pasture. Topsoil clay content was 21% increasing to 35–40% at 60 cm in both ecosystems. In December 2003, two soil cores were obtained from each plot totaling 20 cores from the pasture and from the plantation. In the plantation, the soil cores were alternately taken within the tree rows, and a quarter-way or halfway between rows since soil (especially topsoil) may have been redistributed via tree establishment operations. Cores were 44 mm in diameter and were taken to as great a depth as possible down to a little beyond 100 cm in order to have the option to compare soil samples of equivalent soil mass (Gifford and Roderick 2003) that may have been required if there had been differences in soil bulk densities under the two ecosystems. The corer was driven in by hydraulics mounted on the back of a tractor. Owing to soil dryness at depth some cores did not reach 100 cm, but all reached beyond 80 cm. Measurement of the depth of the holes and the length of the extracted cores showed that core compaction did not occur. Cores were cut into five segments, 0–10, 10–30, 30–60, 60–100 cm and >100 cm. Each core segment was placed in a separate plastic bag and transported to laboratory.

The soil samples were oven dried for at least 4 days at 80°C, cooled over desiccant silica gel, and weighed. The dried segments were crushed with a

pestle. The crushed soil was not sieved because, for inventory work, in which results are expressed per unit land area, it is important to include gravel and stone as part of the soil profile (Gifford 2000). Roots greater than 1 mm diameter or, if thinner, longer than about 1 cm, were removed with forceps. The crushed soil was thoroughly mixed, poured into a pile on a smooth surface, the pile split in half with a steel ruler, and those piles split twice more to produce 16 piles. A broad spatula was then used to take the necessary amount from random small piles to accumulate the amount needed for grinding and analysis. In this way subsampling avoided biasing the subsample towards coarse or fine material (Gifford 2000). Stones were not large enough for be problematic for this procedure. The soil sub-samples were ground to a fine powder using a large capacity puck-mill. For each core-segment a single small ground subsample was weighed into an aluminium foil cup (20–40 mg) for C and N analysis in a Europa Elemental Analyser (ANCA-SL) using standardized soil as the routine calibration standard. The densities of C and N in the soil in each segment ($kg\ m^{-2}$) were calculated from the %C and %N (mass basis) measured by the elemental analyser, the dry mass of soil in each segment, and the cross sectional area of the corer.

Fine root sampling

For estimating fine root biomass and calibrating minirhizotron data against root mass density and root length density, two further soil cores for fine roots were obtained from each plot at five depths (0–15, 15–30, 30–50, 50–75, 75–100 cm) using a rotating corer fitted with a circular saw bit (diameter 100 mm) from October to November 2003. Twenty cores from the pasture and 20 from the plantation were so obtained. All segments of soil cores were transported back to the laboratory on the same day and stored in a cool room (4°C) until further processing.

The core segments for destructive fine root sampling were soaked in tap water for approximately 30 min. Roots were separated from soil by running water washing through a 1 mm sieve and hand picking. The washed fine roots (<2 mm), dispersed in a transparent tray of water, were scanned at 300 dpi to measure length using WinRHIZO (Regent Instruments Inc. Quebec, Canada), and then oven dried at

70°C before weighing. "Root" here refers to the root material extracted by washing the soil and hand picking. By this definition some of it would actually be dead, though not discernibly so. That does not concern this study as our focus is the transition of root material into soil organic matter whereupon it loses identity as root-strands. We do not regard dead root strands as soil organic matter unless they are too fine to be visible or extractable.

Minirhizotrons

Two minirhizotron tubes (clear acrylic, 180 cm long, 5 cm inner diameter) with heat-inscribed windows (18×13.5 mm) were installed into tightly fitting holes at 45° angles in each plot in both pasture and plantation in April 2002. A steel-mesh enclosure was set up to protect the tops of tubes in each pasture plot from damage by grazing animals. The angle of the tube was directed out of the enclosure such that grazing occurred vertically above the root measurement zones. To allow for settling in and recolonization of fine roots (Joslin and Wolfe 1999; Johnson et al. 2001), minirhizotron observations were not taken until 1 year after their installation.

From April 2003 to April 2004, images were taken fortnightly for each tube from a constant set of four upward-facing windows at each of four depths corresponding to four soil sampling vertical layers, 0–10 (5), 10–30 (20), 30–60 (45) and 60–100 (80) cm, in each minirhizotron tube using a minirhizotron video camera (Bartz Technology, Santa Barbara, California, USA). In both pasture and plantation, 8,320 images were taken from 20 minirhizotron tubes over 26 times in the year.

Images from minirhizotron tubes were analyzed using RooTracker (D. Tremmel, Duke University Phytotron, Durham, North Carolina, USA) for estimating root production (including their length, volume and surface area) and disappearance from the repeated fortnightly measurement of the individual roots in each window. Identification of root death from minirhizotron images is problematic (West et al. 2004) and not a reliable indicator of the start of their transition to soil organic matter. Therefore, we focused on permanent disappearance of fine root (defined as "death" in this study) as that is a practicable criterion for the transition from dead root to soil organic matter via decomposition.

From minirhizotron data, root turnover rate (year^{-1}) was calculated, following Ostonen et al. (2005), as:

$$R_t = P_r/L_r$$

where R_t is the fine root turnover rate (year^{-1}), P_r is annual root length production (mm cm^{-2} window area year^{-1}), L_r is mean fine root length (mm cm^{-2}). Fine root longevity was calculated as the reciprocal of root turnover rate (Ostonen et al. 2005).

To estimate the disappeared stock of root mass per hectare of soil under both pasture and plantation from the standing stock of root length in the minirhizotron images, a direct calibration of volumetric root biomass density in soil cores was made against root length density per unit area of minirhizotron frame determined from images taken on the day closest to the fine root harvest via coring (Johnson et al. 2001; Davis et al. 2004; Steinaker and Wilson 2005). Thus, the cumulative oven dry mass of fine root mortality per hectare in a year (M_m) was approximated as:

$$M_m = M_i(L_m/L_i)$$

where M_i is the instantaneous oven dry mass (Mg ha^{-1}) of fine roots via coring to 1 m, L_m is the cumulative length density (mm cm^{-2}) of disappeared fine roots during the year, and L_i is the live fine root length density (mm cm^{-2}) in minirhizotrons at closest day to the harvest via coring.

Statistical calculations

All data were analyzed with an analysis of variance (ANOVA – GLM procedure using GenStat software– Sixth Edition) between the pasture and plantation to examine statistical differences of soil C and N stocks, and fine roots (both from minirhizotrons and destructive harvesting). Means were separated using a least significant difference test with a probability level of 0.05.

Results

Soil C and N

The dry soil mass in the top 100 cm was very similar between the pasture and the plantation (Table 1). Accordingly, the cumulative mass approach (Gifford

and Roderick 2003) was not needed here for comparing total soil C stocks to that depth. Furthermore, there was no significant difference in soil C and N between the soil cores alternately taken within the tree rows, and a quarter-way or halfway between rows in the plantation. Hence, soil redistribution via tree establishment operations probably did not occur.

Soil C and N stocks were 20 and 15% less respectively under the plantation than under the pasture (Table 1). Soil C or N was less throughout the soil profile (Fig. 2). Thus, soil C and N stocks per unit land area both decreased after the land use change from pasture to plantation. The difference in C/N ratio was not significant (Table 1).

Fine root stock and length, C and N

The mass of fine roots was 36% greater in the soil under the pasture than in the soil under the plantation (Table 1). The main difference in the fine root mass between the two ecosystems was in top 15 cm, with no significant difference at other depths (Fig. 3). However, the length of fine roots was about nine times greater in the soil under the pasture than in the soil under the plantation (Table 1), the difference being significant at all depths (Fig. 3). There was a similar amount of C stored in fine roots in the soil under the two ecosystems, but pine roots had much less N than pasture fine roots did (Table 1). Therefore, the C/N ratio was much higher for pine fine root (70) than for grass fine root (44).

Fine roots monitored via minirhizotrons

Root length production and mortality were many-fold greater in soils under pasture than in the soils under the plantation in the top three depths, especially in the 0–10 cm layer (Table 2). A similar trend was also found in the mean fine root length and fine root turnover rate. Fine root longevity was shorter in the soils under pasture than in the soils under the plantation, especially in topsoil (0–10 cm). Annual root production and mortality decreased with depth in the soil.

In the topsoil, the standing length of fine root increased under both the pasture and the plantation from April 2003 (autumn), reached the maximum in September and October 2003 (early spring) and then started decreasing sharply from the end of October 2003 (Fig. 4a,b).

Table 1 The stocks of soil C, soil N and fine roots (<2 mm) in top 100 cm soil under a native pasture and an adjacent 16-year-old pine plantation

Ecosystem	Soil				Fine roots				
	Mass (Mg ha^{-1})	C (Mg ha^{-1})	N (Mg ha^{-1})	C:N	Mass (Mg ha^{-1})	Length (km ha^{-1})	C (Mg ha^{-1})	N (Mg ha^{-1})	C/N
Pasture	13922 (172)	71.6 (2.1)	6.7 (0.3)	10.2 (0.5)	6.0 (0.6)	335907 (22808)	2.2 (0.2)	0.0502 (0.0062)	44 (1)
Plantation	14004 (194)	57.3 (2.0)	5.6 (0.3)	9.9 (0.4)	4.4 (0.3)	37554 (1074)	1.9 (0.1)	0.0272 (0.0016)	70 (1)
Significance	ns	**	**	ns	*	***	ns	**	**

SEM in parenthesis following the mean ($n=20$)

ns Not significant

*Significant at $P<0.05$

**Significant at $P<0.01$

***Significant at $P<0.001$

Under the pasture, fine root production in topsoil (0–10 cm) peaked in April (autumn), but in the 30–60 cm layer peaked in October (mid spring; Fig. 4c). In the plantation, there were two main peaks in April and September (early spring) and the production in the 10–30 cm layer fluctuated similarly with the topsoil (Fig. 4d).

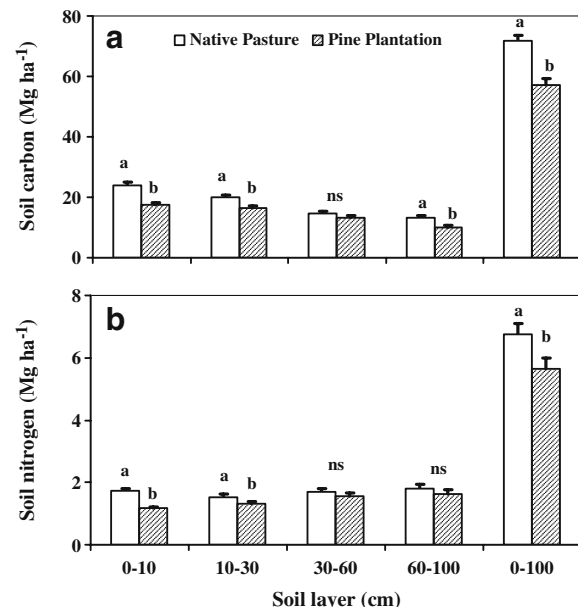Fine root mortality in the topsoils under both the pasture and the plantation peaked in November (late

Fig. 2 Carbon (**a**) and nitrogen (**b**) stocks in soil under a native pasture and an adjacent 16 year old pine plantation [*error bars* represent SEM; the stock denoted with different letters in same soil layer are significantly different ($P<0.05$) by Duncan grouping; $n=20$]

spring; Fig. 4e,f). Not much root activity (production or mortality) was found in the soil beyond 60 cm in depth.

The annual inputs of fine root litter

From fine root monitored in minirhizotrons and from the harvest via coring, it was estimated that 6.3 Mg ha^{-1} year^{-1} (with 2.7 Mg C and 38.9 kg N) was contributed to soil under the plantation and 9.7 Mg ha^{-1} year^{-1} (with 3.6 Mg C and 81.4 kg N) to the soil under the pasture via fine root mortality.

The correlation between fine root dynamics and soil carbon change

The soil carbon content difference between the plantation and the pasture correlated with differences in several attributes of fine root dynamics (i.e. total accumulated root, new root production and root mortality in the study period) monitored in minirhizotrons, especially root mortality (Fig. 5). The average amount of annual carbon loss in each layer of the soil profile following the land use change was positively correlated with the change in each of the attributes of annual fine root dynamics, in the same layer, particularly with the mortality volume (i.e. mass input) (*3* in Fig. 5b).
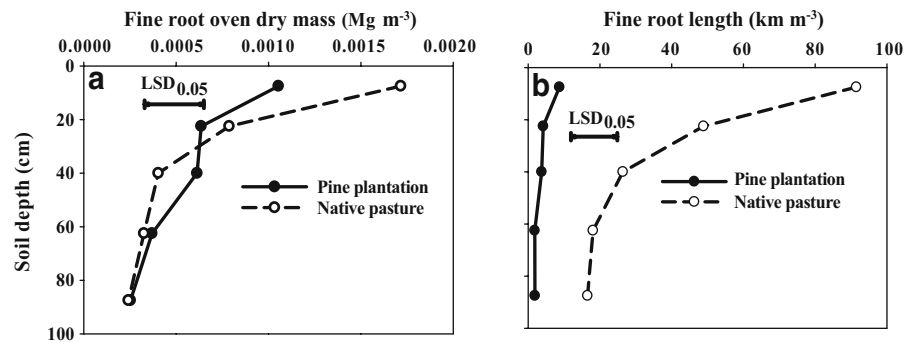
Discussion

Steinaker and Wilson (2005) concluded that the invasion of grassland by trees has many ecosystem-level effects, including changes in root/shoot ratios, temporal and

Fig. 3 The distribution of fine root mass (**a**) and length (**b**) in soil under a native pasture and an adjacent 16-year-old pine plantation (*n*=20)

spatial patterns of root production, litter quality, soil microbial biomass, and soil organic C and N dynamics. Similar effects should occur after planting pine trees into pasture.

Results from this experimental study are consistent with the finding from a meta-analysis of worldwide data (Guo and Gifford 2002) that soil C stocks usually decrease after land use change from pasture to pine (conifer) plantation (Table 1, Fig. 2). While this present case-study, being at a single adjacent-pair site owing to project funding limitations, certainly should not be generalized uncritically to all soil types, climates and grass-conifer comparisons, the correspondence of its observations on soil C stocks at the site involved with the results of the global meta-analysis gives weight to

regarding the findings as providing worthwhile hypotheses for formulating project plans for future comparisons in other environments. The statistical analyses should be viewed in that light.

Soil C/N ratio did not differ between the pine and native grassland plots, soil N stocks also being less under the pine. C and N processes may be mutually regulated by each other via the close coupling between C and N cycles during ecosystem transitions (Gifford 1992; Luo et al. 2006). Therefore, trends in soil C may be better understood through consideration also of the N cycle, since N cycling seems to play an important role in C cycling. While this paper is about C stocks and fine root dynamics, associated N data are reported here, the results being combined with other results in a

Table 2 Annual fine root production, annual fine root mortality, mean fine root length, fine root turnover, and fine root longevity per unit area of minirhizotron window in soils under a native pasture and an adjacent 16-year-old pine plantation

| Ecosystem	Layer (cm)	Annual production (mm cm^{-2} year^{-1})	Annual mortality (mm cm^{-2} year^{-1})	Mean length (mm cm^{-2})	Turnover rate (year^{-1})	Longevity (year)
Native pasture	0–10	25.0 (3.1)	25.7 (2.8)	6.8 (0.5)	3.7 (0.4)	0.27 (0.02)
	10–30	5.5 (0.4)	5.1 (0.3)	2.2 (0.2)	2.5 (0.3)	0.40 (0.03)
	30–60	5.3 (0.2)	1.6 (0.2)	2.3 (0.3)	2.3 (0.2)	0.43 (0.04)
	60–100	0.3 (0.1)	0.1 (0.0)	0.1 (0.0)	2.5 (0.1)	0.40 (0.01)
	0–100	5.3 (0.3)	4.7 (0.2)	1.8 (0.2)	2.9 (0.3)	0.35 (0.01)
Pine plantation	0–10	4.9 (0.5)***	5.0 (0.4)***	2.0 (0.1)***	2.4 (0.3)**	0.42 (0.03)**
	10–30	2.6 (0.4)**	1.9 (0.3)**	1.2 (0.1)**	2.1 (0.1)*	0.48 (0.03)*
	30–60	0.5 (0.1)**	0.3 (0.0)*	0.3 (0.1)***	1.7 (0.1)*	0.59 (0.04)*
	60–100	0.4 (0.0)ns	0.1 (0.0)ns	0.2 (0.0)ns	1.7 (0.0)*	0.59 (0.04)**
	0–100	1.3 (0.1) ***	1.0 (0.1) ***	0.6 (0.1) ***	2.1 (0.3) **	0.48 (0.02)**

SEM in parenthesis following the mean (*n*=20)

ns Not significant

*Significant at *P*<0.05 in each layer between the two ecosystems

**Significant *P*<0.01 in each layer between the two ecosystems

***Significant at *P*<0.001 in each layer between the two ecosystems
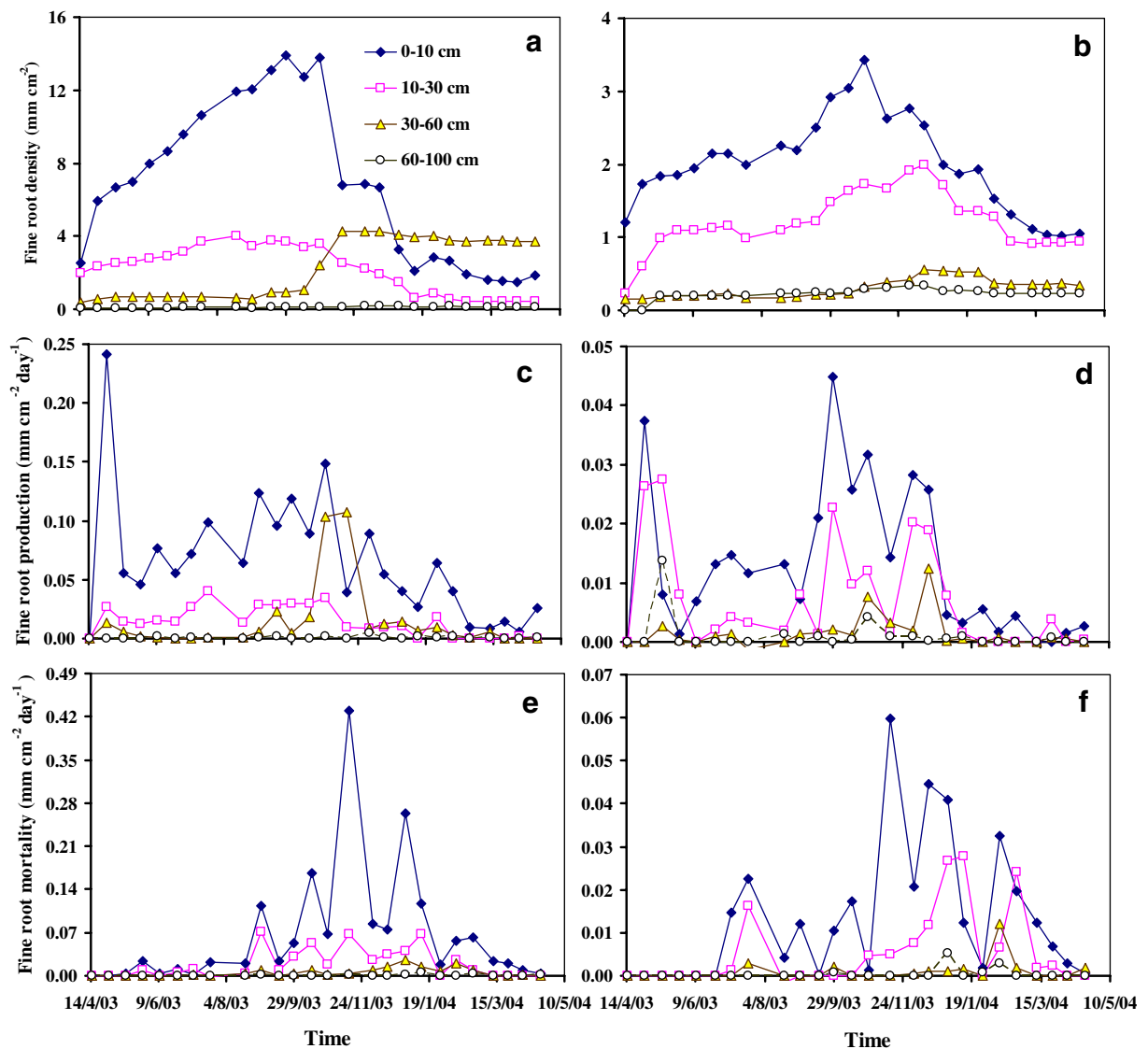
Fig. 4 Fine roots monitored fortnightly via minirhizotrons: the live length density under a native pasture (**a**) and under a 16-year-old pine plantation (**b**); the daily length production under the pasture (**c**) and under the plantation (**d**); and the daily length mortality under the pasture (**e**) and under the plantation (**f**)

modeling investigation of role of the coupled N cycle at the site (Kirschbaum et al. 2007).

The fine root biomass was 26% less under pine than under the pasture, while N in the fine root pool was 54% less, but the 13% difference in root C was not significant (Table 1). However, fine roots are the sub-annually dynamic part of the root system (Vogt et al. 1986) while coarse roots do not die and decompose for many years or decades. Therefore, the lesser amount in fine root under pine could affect the soil C and N stocks directly via the exchange between fine roots and soil.

Considering our prior observation that soil C change was positively correlated with live fine root length density (or surface area; Guo et al. 2005), attention focuses particularly on the potential importance of fine root length that was nine times higher under the pasture than under the pine (Table 1).

Most herbaceous plant roots are located in the top few centimetres of the soil (Jackson et al. 1996). This allows for efficient uptake of water and nutrients from soil surface layers, which are often characterised by accumulation of organic matter and by relatively large
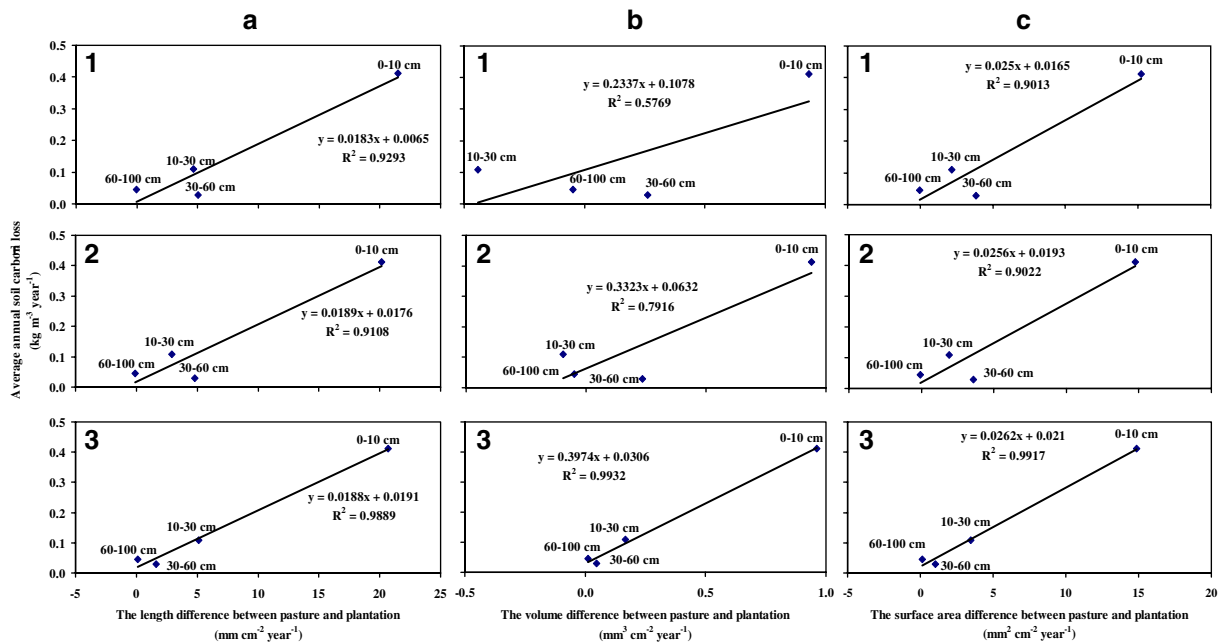
Fig. 5 The correlations between the average annual carbon mass lost after land use change from a native pasture a 16-year-old pine plantation in each layer of the soil profile and the differences between the pasture and the plantation in; column **a**, the root length production rate; column **b**, the root volume production rate; and column **c** the root surface area production rate; for the net accumulated fine root production rate – i.e. new root production minus mortality (in row *1*); for total new fine root production rate (in row *2*); and for fine root death rate (in row *3*)

amounts of available nutrients (Trettin et al. 1999). In the current study, there were high (mass and length) densities of fine roots in the topsoil layers both under the pasture and the plantation, and there was a gradual density decrease with depth in the soil (Fig. 3). Similar patterns of vertical biomass distribution have been reported in other studies (e.g. Grier et al. 1981; Yin et al. 1989; Persson et al. 1995; Janssens et al. 2002; Claus and George 2005). In addition, longevity of roots in the topsoil was shorter than in the deeper soil (Table 2), an effect also found by others (e.g. Kosola et al. 1995; Wells et al. 2002; Baddeley and Watson 2005). Consequently, the turnover rate was faster in the topsoil than deeper down the profile (Table 2).

We were unable to determine using minirhizotron technology whether there was significant root activity in the surface litter layer. Contact between minirhizotron tube and litter is too loose and variable at the surface for the approach to work. However, in this system the relatively low rainfall meant that the litter layer is too dry most of the time for roots to survive. Hence we are assuming that root activity in the forest floor litter is of minor significance at this site. However, it may well be of greater significance in wetter climes.

There are many factors that may affect the life span of a root (Majdi et al. 2005). The unusually dry late-summer/autumn periods (Fig. 1) may have had some impact on fine root turnover in this study. In their study on *Quercus robur* L. and *Pinus sylvestris* L., Konopka et al. (2005) indicated that midsummer root growth cessation was a common phenomenon in trees growing in regions with hot or dry summer climates, and summer drought was the likely reason for the high fine root mortality during summer. In our study, however the peak fine root mortality in the topsoil under both the pasture and the plantation occurred in November 2003 (Fig. 4e and f) before the summer drought started (Fig. 1). In addition, fine root production in both pasture and forest peaked in April (Fig. 4c and d), which was a dry autumn month. Consequently, the drought may have played only a limited role in the difference of fine root turnover between the two ecosystems.

Assuming that when fine roots die no C or N is first resorbed into the live plant (Nambiar 1987; Gordon and Jackson 2000), it was calculated that fine root mortality contributed much less C and N to the soil under the plantation (2.7 Mg C ha^{-1} year^{-1} and 38.9 kg N ha^{-1} year^{-1}) than to the soil under pasture

(3.6 Mg C ha^{-1} year^{-1} and 81.4 kg N ha^{-1} year^{-1}). As root turnover (or mortality) is a major source of soil carbon (McClaugherty et al. 1982; Tate et al. 1993; Steele et al. 1997), a decrease of soil carbon stocks may be expected. Additionally, the rate of decomposition of pine root litter to humus was much slower than the decomposition of grass root litter to humus (Guo et al. 2006), as would be expected given the higher N content of the grass roots than the pine roots. Together these changes were shown, by a whole-ecosystem C and N-turnover modeling analysis (Kirschbaum et al. 2007), to be a major cause of the decline of soil carbon stocks after land use change from the pasture to the plantation. Most of the nitrogen that did not accumulate in soil organic matter under the forest accumulated in tree biomass.

From a study on the invasion of grassland by *Populus tremuloides* trees, Steinaker and Wilson (2005) thought the enhancement of aboveground litter-N inputs to the soil surface after invasion was relatively unimportant because belowground processes dominated both systems (fine roots accounted for 80 and 92% of the total forest and grassland litter production, respectively). However, the changes in the C and N inputs from above ground litter after afforestation were more important in the current study given the substantial reduction of the fine root litter fraction of total litter mass from 93 to 60%, litter C from 92 to 55%, and litter N from 90 to 51% after planting pine trees into pasture. This contrast between *Populus* and *Pinus* results may be caused by the different characteristics of fine root dynamics between tree species (i.e. broadleaf vs. conifer), and may further affect soil C change. Planting broadleaf trees into pasture had little effect on soil C stocks (Guo and Gifford 2002). Cuevas et al. (1991) found that the amount of aboveground litter was more than 35 times the dead root fraction in a tropical pine (*Pinus caribaea*) plantation, whereas for a paired broadleaf secondary forest, the standing stock of dead roots was higher than aboveground litter stock.

Our exploratory pot study involving the same dominant species and topsoils as in this study, showed low live root length or low live root surface area as correlating better than the rate of C input from dead root as a cause of soil C loss under pine over the one year period after planting (Guo et al. 2005). However, in this field study, 16 years after pine establishment, it was fine root mortality (expressed as either length, volume

or surface area, *3* in Fig. 5a–c), more than properties of the standing stock of fine root (*1* in Fig. 5a–c) or the formation of live root (*2* in Fig. 5a–c), that had the strongest correlation down the soil profile with difference in soil C stocks between the two ecosystems. Thus, while differences between pine and native grassland in fine root dynamics do indeed seem to contribute substantially to the causes of soil C decline under pine following grassland, as hypothesised, we cannot distinguish yet the relative contributions of differences in rate of dead root litter input to the soil and differences in rhizosphere processes that relate to live root surface area may be involved. Our data do not allow clear discrimination between these two options. Any future comparisons among sites will be more informative than comparisons between depths within sites. Nevertheless, the huge (fivefold) difference between plantation and pasture in fine root length production and mortality in the top (0–10 cm) soil layer (Table 2) presumably plays a role in the significant decline of soil carbon stocks in this layer after the land use change from the pasture to the plantation.

In conclusion, soil C and N stocks were 15–20% lower under the pine than under the adjacent pasture 16 years after the land use change from the pasture to the plantation for this paired site consistent with the results of a global meta-analysis. Consistent with our hypothesis, slower fine root dynamics (production and mortality) were found in the soils under the plantation than in the soils under the pasture. Much less C and N via fine root death was contributed to soils under the plantation than to soils under the pasture, especially in the topsoil (0–10 cm), where more C and N were lost than lower in the soil profile. The data from these root studies alone do not allow the C-input role of changed fine root dynamics to be distinguished from the potential role of live root surface area properties fostering organic matter stabilization or organic matter exudation. To address the latter, studies on changes following land use change in the ratio of active to slow turnover soil C pools and in soil aggregate stability may be required.

References

Andersson P, Majdi H (2005) Estimating root longevity at sites with long periods of low root mortality. Plant Soil 276:9–14

Backeus S, Wikstrom P, Lamas T (2005) A model for regional analysis of carbon sequestration and timber production. For Ecol Manag 216:28–40

Baddeley JA, Watson CA (2005) Influences of root diameter, tree age, soil depth and season on fine root survivorship in *Prunus avium*. Plant Soil 276:15–22

Cannell MGR (1996) Forests as carbon sinks mitigating the greenhouse effect. Commonw For Rev 75:92–99

Claus A, George E (2005) Effect of stand age on fine-root biomass and biomass distribution in three European forest chronosequences. Can J For Res 35:1617–1625

Coleman DC (1976) A review of root production processes and their influence on biota in terrestrial ecosystems. In: Anderson JM, MacFadeyen A (eds) The role of terrestrial and aquatic organisms in decomposition processes. Science Publications, Oxford, UK, pp 417–434

Cuevas E, Brown S, Lugo AE (1991) Aboveground and belowground organic-matter storage and production in a tropical pine plantation and a paired broadleaf secondary forest. Plant Soil 135:257–268

Davis JP, Haines B, Coleman D, Hendrick R (2004) Fine root dynamics along an elevational gradient in the southern Appalachian Mountains, USA. For Ecol Manag 187:19–34

Fahey TJ, Hughes JW (1994) Fine-root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. J Ecol 82:533–548

Gifford RM (1992) Interaction of carbon dioxide with growth-limiting environmental factors in vegetation productivity: implications for the global carbon cycle. Advances in Bioclimatology 1:24–58

Gifford RM (2000) Changes in soil carbon following land use changes in Australia. National Greenhouse Gas Inventory Development Project, Canberra, ACT, Australia, 118 pp

Gifford RM, Roderick ML (2003) Soil carbon stocks and bulk density: spatial or cumulative mass coordinates as a basis of expression? Glob Chang Biol 9:1507–1514

Gordon WS, Jackson RB (2000) Nutrient concentrations in fine roots. Ecology 81:275–280

Grier CC, Vogt KA, Keyes MR, Edmonds RL (1981) Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. Can J For Res 11:155–167

Guo LB, Gifford RM (2002) Soil carbon stocks and land use change: a meta analysis. Glob Chang Biol 8:345–360

Guo LB, Halliday MJ, Siakimotu SJM, Gifford RM (2005) Fine root production and litter input: its effects on soil carbon. Plant Soil 272:1–10

Guo LB, Halliday MJ, Gifford RM (2006) Fine root decomposition under grass and pine seedlings in controlled environmental conditions. Appl Soil Ecol 33:22–29

Hoen HF, Solberg B (1994) Potential and economic efficiency of carbon sequestration in forest biomass through silvicultural management. For Sci 40:429–451

Isbell RF (1996) The Australian soil classification. CSIRO Publishing, Melbourne, Australia, 144 pp

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED (1996) A global analysis of root distributions for terrestrial biomes. Oecologia 108:389–411

Janssens IA, Sampson DA, Curiel-Yuste J, Carrara A, Ceulemans R (2002) The carbon cost of fine root turnover in a Scots pine forest. For Ecol Manag 168:231–240

Johnson MG, Tingey DT, Phillips DL, Storm MJ (2001) Advancing fine root research with minirhizotrons. Environ Exp Bot 45:263–289

Joslin JD, Wolfe MH (1999) Disturbances during minirhizotron installation can affect root observation data. Soil Sci Soc Am Proc 63:218–221

Keith DA (2004) Ocean shores to desert dunes: the native vegetation of New South Wales and the ACT. The Department of Environment and Conservation, Hurstville NSW 2220, Australia, 353 pp

Kirschbaum MUF, Guo LB, Gifford RM (2007) Observed and modelled soil carbon and nitrogen changes after planting a *Pinus radiata* stand onto former pasture. Soil Bio Biochem (in press)

Konopka B, Yuste JC, Janssens IA, Ceulemans R (2005) Comparison of fine root dynamics in Scots pine and pedunculate oak in sandy soil. Plant Soil 276:33–45

Kosola KR, Eissenstat DM, Graham JH (1995) Root demography of mature citrus trees – the influence of *Phytophthora nicotianae*. Plant Soil 171:283–288

Luo Y, Hui D, Zhang D (2006) Elevated CO_2 stimulates net accumulations of carbon and nitrogen in land ecosystems: a meta-analysis. Ecology 87:53–61

Majdi H, Pregitzer K, Moren AS, Nylund JE, Agren GI (2005) Measuring fine root turnover in forest ecosystems. Plant Soil 276:1–8

McClaugherty CA, Aber JD, Melillo JM (1982) The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 63:1481–1490

Nambiar EKS (1987) Do nutrients retranslocate from fine roots? Can J For Res 17:913–918

Ostonen I, Lohmus K, Pajuste K (2005) Fine root biomass, production and its proportion of NPP in a fertile middle-aged Norway spruce forest: comparison of soil core and ingrowth core methods. For Ecol Manag 212:264–277

Persson H, Vonfircks Y, Majdi H, Nilsson LO (1995) Root distribution in a Norway spruce (*Picea abies* (L.) Karst.) stand subjected to drought and ammonium-sulfate application. Plant Soil 169:161–165

Steele SJ, Gower ST, Vogel JG, Norman JM (1997) Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol 17:577–587

Steinaker DF, Wilson SD (2005) Belowground litter contributions to nitrogen cycling at a northern grassland–forest boundary. Ecology 86:2825–2833

Tate KR, Ross DJ, O'Brien BJ, Kelliher FM (1993) Carbon storage and turnover, and respiratory activity, in the litter and soil of an old-growth southern beech (*Nothofagus*) forest. Soil Biol Biochem 25:1601–1612

Trettin CC, Johnson DW, Todd DE (1999) Forest nutrient and carbon pools at Walker Branch Watershed: changes during a 21-year period. Soil Sci Soc Am Proc 63:1436–1448

Turner J, Lambert M (2000) Change in organic carbon in forest plantation soils in Eastern Australia. For Ecol Manag 133:231–247

Vogt KA, Grier CC, Vogt DJ (1986) Production, turnover, and nutrient dynamics of aboveground and belowground detritus of world forests. Adv Ecol Res 15:303–377

Vogt KA, Vogt DJ, Palmiotto PA, Boon P, Ohara J, Asbjornsen H (1996) Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187:159–219

Waring RH, Landsberg JJ, Williams M (1998) Net primary production of forests: a constant fraction of gross primary production? Tree Physiol 18:129–134

Wells CE, Glenn DM, Eissenstat DM (2002) Changes in the risk of fine-root mortality with age: a case study in peach, Prunus persica (Rosaceae). Am J Bot 89:79–87

West JB, Espeleta JF, Donovan LA (2004) Fine root production and turnover across a complex edaphic gradient of a Pinus palustris–Aristida stricta savanna ecosystem. For Ecol Manag 189:397–406

Yin XW, Perry JA, Dixon RK (1989) Fine-root dynamics and biomass distribution in a Quercus ecosystem following harvesting. For Ecol Manag 27:159–177

Zak DR, Pregitzer KS, King JS, Holmes WE (2000) Elevated atmospheric CO_2, fine roots and the response of soil microorganisms: a review and hypothesis. New Phytol 147:201–222