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SHORT COMMUNICATION

# Seasonal patterns of fine-root productivity and turnover in a tropical savanna of northern Australia

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Fine roots and their turnover represent a dynamic aspect of below-ground biomass (BGB) and nutrient capital in forest ecosystems, and account for a significant fraction of net primary productivity (NPP) (Cuevas 1995, Vogt *et al.* 1990). On a weight basis, coarse roots contribute more to total ecosystem biomass than fine roots, but they account for only a small portion of annual root production (Eamus *et al.* 2002). Despite the fact that fine roots may compose less than 2% of total ecosystem biomass, they may contribute up to 40% of total ecosystem production (Vogt *et al.* 1990). Therefore, estimates of root production, like estimates of root biomass, should differentiate between coarse- and fine-root production.

Savannas dominate the northern region of the Australian continent and cover approximately 25% of the total area of Australia. They are an important natural resource and have economic, social, cultural and biodiversity values. Although efforts have been made recently to estimate BGB, net ecosystem production (NEP) and soil $CO_2$ efflux in the savannas (Chen *et al.* 2002, Eamus *et al.* 2001, 2002), the below-ground component, including fine-root dynamics, is still a poorly understood part of the vegetation community. The lack of reliable information about below-ground biological processes including fine-root growth and turnover rate not only limit the accuracy and complete assessment of NPP and carbon dynamics of the tropical savannas, but also may cause wrong inferences about tree ecological and physiological processes (Eamus *et al.* 2002).

The present study quantified fine-root biomass ($B_{fr}$), fine-root net primary production ($NPP_{fr}$) and fine-root turnover rates in the eucalypt open forest savannas in northern Australia. Root ingrowth-bags were used to monitor temporal patterns of fine-root growth and turnover. Root production and turnover were calculated based on measurement of root biomass changes with time as measured using ingrowth-bags. The aims of the study are: (1) to estimate $NPP_{fr}$ and turnover and (2) to describe the pattern of fine-root growth with depth in the soil and observe temporal changes to growth over an annual wet–dry cycle.

The study was carried out at Howard Springs, about 35 km south of Darwin (130°45′E, 12°30′S) in the Northern Territory, Australia. The climate is monsoonal, with a distinct wet season (November–March) and a distinct dry season (April–October). Annual average precipitation is approximately 1600 mm. Almost all precipitation (> 90%) falls in the wet season. Temperatures and solar radiation remain high throughout the year and mean monthly temperatures throughout the year vary only slightly from annual means. Soil was deep red kandosol with an A horizon of well-drained, highly weathered sand, mid-brown in colour and a B-horizon with the colour of reddish brown-yellow. The vegetation in this study site is dominated by *Eucalyptus miniata* Cunn. ex Schauer and *Eucalyptus tetrodonta* F. Muell. The understorey vegetation is dominated by tall $C_4$ grasses, mainly *Sorghum* spp.

At the study site, soil cores were dug to a depth of 50 cm, with soil collected and divided into two depth zones, 0–25 cm and 25–50 cm. All roots were carefully removed, and the resulting root-free soil was used to fill mesh bags. Bags filled with root-free soil were then inserted into holes 7 cm diameter × 50 cm deep. Mesh size (0.3 cm) of the

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stocking-like bag allowed surrounding roots to penetrate relatively easily, but restricted coarse-root ingrowth. Rate of ingrowth of new roots was determined by sequential re-sampling of the mesh bags over time. Fine roots were here defined as those roots having a diameter less than 2 mm.

Two experiments were conducted using root ingrowth-bags. $B_{fr}$ was estimated by establishing a total of 36 bags, starting October 1999 with 12 bags established at each of the three randomly selected locations at the research site. These locations were approximately 500 m from each other. At each sampling time, two bags from each location were taken, giving a total of six bags per sampling. Sampling occurred after incubation periods of 2, 4, 6, 9, 11 and 13 mo and these data will be referred to as the incubation data set and represent the $B_{fr}$ at the time of sampling. A second set of bags was established to estimate fine-root growth rate. Six bags were established at the study site with root-free soil at the start (October 1999). After a set interval, all fine roots were measured within each bag, and then bags, with fresh root-free soil, were put back in the field. Three locations were used, with two bags established at each, giving a total of six bags per sampling. Sampling occurred at 2-mo intervals from October 1999 to January 2001. On each sampling occasion, the root bags were returned to the laboratory, and for each bag root material was sorted into two groups based on their depth in the bag (0–25 cm and 25–50 cm). These data will be referred to as the replacement data set and represent the rate of fine-root growth over the 2-mo interval. All root materials from both treatments were dried at 70 °C until they reached a constant weight.

$B_{fr}$ was calculated as: $B_{fr} = W_{fr}/A_b$, where $W_{fr}$ is mean dry weight of fine root in ingrowth-bags (g), and $A_b$ the cross-sectional area of the bag ($cm^2$). Mean values of $B_{fr}$ were expressed as kg $m^{-2}$ or t $ha^{-1}$. Two calculation methods were used to calculate $NPP_{fr}$, based on the incubation and bag replacement treatments. The first method calculated $NPP_{fr}$ as the difference between maximum and minimum values of biomass using the incubation data series, namely: $NPP_{fr} = B_{frMAX} - B_{frMIN}$, where $B_{frMAX}$ and $B_{fr\,MIN}$ were the maximum and minimum values of $B_{fr}$ during a year, respectively. The second calculation method used the bag replacement data set with $NPP_{fr}$ calculated as the integral of the 2-mo $B_{fr}$ rates: $NPP_{fr} = \Sigma\ (B_{fr})_i$. In the present study, the ratio of annual $NPP_{fr}$ and maximum value of $B_{fr}$ was used to calculate fine-root turnover ($T_{fr}$), as follows: $T_{fr} = NPP_{fr}/B_{frMAX}$. This equation has been the most extensively used method for calculation of root turnover (Gill & Jackson 2000).

$B_{fr}$ was greatest during the mid to late wet season, February to April 2000, declining over the dry season to reach a minimum of approximately 0.6 kg $m^{-2}$ by October, the late dry season (Figure 1a). Differences in

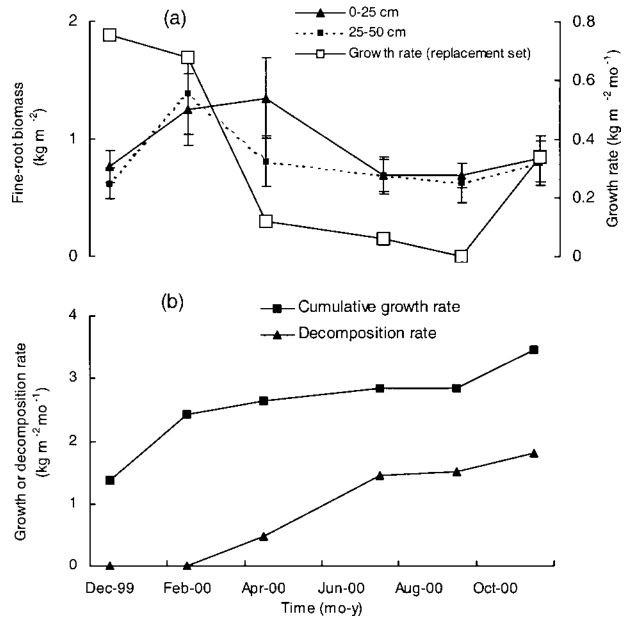


**Figure 1.** (a) Change of fine-root biomass ($B_{fr}$) at the Howard Springs site, plotted over a wet–dry cycle, October 1999 to November 2000. Data were derived from root ingrowth-bags, using the incubation data set and partitioned into soil depths, 0–25 and 25–50 cm. Seasonal patterns of total (0–50 cm) standing fine-root biomass at the Howard Springs site from the incubation ingrowth-bags and fine-root growth rate from the replacement ingrowth-bags. The error bar is standard deviation. Also plotted (b) is cumulative growth rate and calculated decomposition rate.

$B_{fr}$ between the upper and lower soil depth zones were small, except for the late wet season measurement (April 2000) when $B_{fr}$ of the upper zone (0–25 cm) was 1.4 kg $m^{-2}$ while the deeper layer (25–50 cm) was 0.8 kg $m^{-2}$ (Figure 1a). For the duration of the experiment, mean $B_{fr}$ in 0–25 cm and 25–50 cm soil layers was 0.93 and 0.82 kg $m^{-2}$ respectively.

The annual pattern in fine-root production can be illustrated by a single pulse curve (Figure 1a), and is consistent with the wet–dry seasonality of rainfall in this region. In a tropical forest ecosystem in South India, Sundarapandian & Swamy (1996) reported a similar strongly seasonal pattern in fine-root production, with maximum production occurring during the rainy season and minimum in the dry season. Similarly, Fabiao *et al.* (1985) and Cavelier *et al.* (1999) reported that fine-root productivity was limited by water supply during the dry season in a *Eucalyptus globulus* plantation and a semi-deciduous lowland forest.

The reduction in fine-root surface area is matched by the 40% reduction in tree or overstorey LAI that occurs during the transition from the wet to the dry season in these savannas (O'Grady *et al.* 2000). This indicates a balance between leaf area and root surface area or biomass in these eucalypt open forest savannas. The strong relationship between tree leaf area (LA) and fine-root biomass ($B_{fr}$) has been described in a previous study (Eamus *et al.* 2002) ($B_{fr} = 0.68 \ln(LA) - 0.817$) and this functional link is further emphasized by the close and coupled temporal patterns of $B_{fr}$ and LAI. The total root surface area required for adequate water uptake is at least as great as the leaf surface area (Cuevas 1995).

High rates of fine-root growth occurred from October 1999 to February 2000 (early to mid wet season, Figure 1a) with growth rates declining sharply over the dry season and reaching zero by the September 2000 sampling date. Following September/October, there was a rapid increase of $B_{fr}$ prior to the wet season of 2000/2001 (Figure 1a). For each sampling period, decomposition rate was estimated as the difference between cumulative growth rate and $B_{fr}$. Cumulative growth rate represents the total fine-root productivity over a measurement period and this amount minus current standing crop biomass gives the total $B_{fr}$ lost to decomposition for each sampling period. The result of these calculations is given in Figure 1b and shows decomposition rates as zero during the wet season but increasing steadily over the dry season, with a sharp increase at the end of the wet season (March–May).

Previous studies have indicated a large range in estimates $NPP_{fr}$, and this range may have resulted from the different methods used. It is surprising that there was a 2.5-fold difference in term of fine-root production between the two methods (Table 1). In the present study, there was a single, wet–dry seasonal pulse of fine-root growth (Figure 1a), and the maximum–minimum method may yield the more accurate estimate. If there is a difference in physical properties inside and outside the ingrowth-bags due to the reconstruction of root-free soil, the incubation treatment will make a single error in the calculation while the replacement method has the potential to repeat the error over the duration of the experiment. Therefore, the value of 14.3 t $ha^{-1}$ $y^{-1}$ may provide the more accurate estimate of fine-root production for northern Australian savannas.

The value of $NPP_{fr}$ in the present study is much greater than the range reported for tropical forests (1.0–11.2 t $ha^{-1}$ $y^{-1}$; Priess *et al.* 1999, Visalakshi 1994), and various temperate forests (1.4–11.5 t $ha^{-1}$ $y^{-1}$; McClaugherty *et al.* 1982, Usman *et al.* 1999). The $NPP_{fr}$ estimate from this study also lies at the high end of the range given for drought-deciduous woodlands, which is 5–19 t $ha^{-1}$ $y^{-1}$ (Menaut & Cesar 1979).

**Table 1.** Net primary production of fine roots (t $ha^{-1}$ $y^{-1}$) of different soil layers in eucalypt forest savanna of northern Australia.

| Methods | Season | 0–25 cm | 25–50 cm | Total (0–50 cm) |
|---|---|---|---|---|
| $NPP_{fr} = \Sigma (B_{fr})_i$ | dry | 3.1 | 3.1 | 6.2 |
| | wet | 14.0 | 14.5 | 28.5 |
| | total | 17.1 | 17.6 | 34.7 |
| $NPP_{fr} = B_{frMAX} - B_{frMIN}$ | total | 6.6 | 7.7 | 14.3 |

**Table 2.** Fine-root turnover ($y^{-1}$) in eucalypt open forest savannas of northern Australia estimated from the three methods of calculation, using either $B_{frMAX}$, $B_{frMIN}$, $B_{frMEAN}$.

| | $B_{frMAX}$ | $B_{frMIN}$ | $B_{frMEAN}$ |
|---|---|---|---|
| $NPP_{fr} = 14.3$ t $ha^{-1}y^{-1}$ | 0.54 | 1.09 | 0.73 |
| $NPP_{fr} = 34.7$ t $ha^{-1}y^{-1}$ | 1.31 | 2.65 | 1.78 |

Using the maximum–minimum $B_{fr}$ method ($NPP_{fr} = B_{frMAX} - B_{frMIN}$) (Table 1), $NPP_{fr}$ at this site was 1.43 kg $m^{-2}$ $y^{-1}$ or 14.3 t $ha^{-1}$ $y^{-1}$. Of this amount, 46% was in the 0–25 cm soil layer and 54% in the 25–50 cm soil layer. However, if the replacement data set was used to calculate $NPP_{fr}$ ($NPP_{fr} = \Sigma (B_{fr})_i$) the value was 34.7 t $ha^{-1}$ $y^{-1}$. Approximately 82% of $NPP_{fr}$ occurred during the wet season and 18% occurred during the dry season (Table 1) as calculated using by the replacement data set. Based on the concept of turnover ($NPP_{fr}/B_{fr}$), values of fine-root turnover in the forest savannas were calculated and ranged from 0.54 to 1.78 $y^{-1}$ (Table 2), indicating a turnover time of 0.6–1.9 y.

The fine-root turnover of this study was 0.54–1.09 $y^{-1}$, depending on the method of estimation (see Table 2). These estimates are within the range of root turnover for savannas (0.35–1.56; Devidas & Puyravaud 1995, Singh 1993). This is a high rate of turnover, as would be expected given the high $NPP_{fr}$ and suggests that the $B_{fr}$ of this savanna be completely turned over in less than two seasonal cycles.

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