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**Christian P. Giardina · Dan Binkley · Michael G. Ryan · James H. Fownes · Randy S. Senock**

# Belowground carbon cycling in a humid tropical forest decreases with fertilization

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**Abstract** Only a small fraction of the carbon (C) allocated belowground by trees is retained by soils in long-lived, decay-resistant forms, yet because of the large magnitude of terrestrial primary productivity, even small changes in C allocation or retention can alter terrestrial C storage. The humid tropics exert a disproportionately large influence over terrestrial C storage, but C allocation and belowground retention in these ecosystems remain poorly quantified. Using mass balance and $^{13}C$ isotope methods, we examined the effects of afforestation and fertilization, two land-use changes of large-scale importance, on belowground C cycling at a humid tropical site in Hawaii. Here we report that in unfertilized plots, 80% of the C allocated belowground by trees to roots and mycorrhizae was returned to the atmosphere within 1 year; 9% of the belowground C flux was retained in coarse roots and 11% was retained as new soil C. The gains in new soil C were offset entirely by losses of old soil C. Further, while fertilization early in stand development increased C storage in the litter layer and in coarse roots, it reduced by 22% the flux of C moving through roots and mycorrhizae into mineral soils. Because soil C formation rates related strongly to rhizosphere C flux, fertilization may reduce an already limited capacity of these forests to sequester decay-resistant soil C.

**Keywords** Ecosystem carbon cycling · Hawaii · Rhizosphere respiration · Soil surface $CO_2$ efflux · Soil carbon formation

C. P. Giardina (✉)
United States Department of Agriculture-Forest Service, North Central Research Station,
410 MacInnes Drive,
Houghton, MI 49931, USA
e-mail: cgiardina@fs.fed.us
Tel.: +1-906-4826303
Fax: +1-906-4826355

D. Binkley · M. G. Ryan
Department of Forest, Rangeland, and Watershed Stewardship and Graduate Degree Program in Ecology, Colorado State University,
Fort Collins, CO 80523, USA

M. G. Ryan
United States Department of Agriculture-Forest Service, Rocky Mountain Research Station,
240, West Prospect Street,
Fort Collins, CO 80526, USA

J. H. Fownes
Department of Natural Resources conservation, Holdsworth Natural Research Center, University of Massachusetts,
Amherst, MA 01003, USA

R. S. Senock
Department of Natural Resources and Environmental Management, University of Hawai'i at Manoa,
Honolulu, HI 96822, USA

## Introduction

Humid tropical forests are among the most productive ecosystems on Earth (Grace et al. 2001; Saugier et al. 2001). These forests exert a disproportionately large influence over terrestrial C cycling, and store 470 Pg of detrital soil C, which exceeds by some 60 Pg the total quantity of soil C stored in temperate and boreal forests combined (Jobbágy and Jackson 2000). Consequently, afforestation of degraded agricultural lands along with intensified management with fertilizers may represent important tools in the tropics for sequestering additional C from the atmosphere (Schulze et al. 2000; Six et al. 2002a, b). The long-term C sink strength of a forest is determined, however, by net changes in the storage of decay resistant C (Schlesinger and Lichter 2001), and controls on belowground C allocation, cycling and detrital C retention remain poorly quantified (Giardina and Ryan 2000, 2002; Clark et al. 2001; Janssens et al. 2001; Rustad et al. 2001; Schlesinger and Lichter 2001; Raich et al. 2002). Methodological constraints have limited direct measurement of total inputs (Giardina and Ryan 2002), and nothing is known about retention efficiencies. Consequently, predicted impacts of global change on soil C

storage remain highly uncertain (Matson et al. 1999; Cox et al. 2000, Holland et al. 2000).

The complexity of belowground C cycling, specifically the many fates of total C allocated belowground by plants and the diverse sources of soil surface $CO_2$ efflux, has emerged as a central obstacle to accurately modeling ecosystem C cycling and its response to environmental change. While an appreciation of this complexity is emerging (Högberg et al. 2001; Schlesinger and Lichter 2001), tools for partitioning belowground C cycling into units that can be used to test basic concepts in plant ecology and to model ecosystem response to global environmental change remain rudimentary.

In tropical ecosystems, there is increasing interest in how afforestation and intensified management with fertilizers alter ecosystem C cycling. Afforestation projects typically rely on fast growing species and tropical plantation forests now occupy some 50 million ha. About 14 million of these have been planted with trees in the genus *Eucalyptus* (Brown et al. 1997). Because the global demand for forest products is accelerating (Brown et al. 1997), and plantation forests rapidly sequester large quantities of C in aboveground biomass, the tropical land area devoted to plantation forestry is increasing rapidly (Fisher and Binkley 2000). Critically, the economic success of plantation forestry in the tropics is often linked to intensive nutrition management, particularly fertilization (Fisher and Binkley 2000).

While afforestation and fertilization are widespread in the tropics, and substantial information is available on the aboveground impacts of these practices, data on belowground effects are scarce (Giardina and Ryan 2002). We used a C-balance approach and measurements of soil surface $CO_2$ efflux, aboveground litterfall, litter layer C content, and C content and $^{13}C$:$^{12}C$ of mineral soil to examine how afforestation and fertilization, two contemporary changes of global significance (Bashkin and Binkley 1998; Matson et al. 1999), alter the belowground processes controlling soil surface $CO_2$ efflux and soil C storage. Specifically, we used these data and tools to: (1) partition soil surface $CO_2$ efflux into three component fluxes, (2) quantify total belowground C allocation (TBCA), (3) estimate the fraction of TBCA that is retained as new soil C, and (4) quantify the impact of increased nutrient supply on these processes.

## Materials and methods

### Research site

The research site is located at 350 m elevation on the windward side of the Island of Hawaii (19°50′28.1″N, 155°7′28.3″W). The site receives an average annual rainfall of 3.6 m with no dry season. Mean annual temperature for the site is 21°C with little seasonal variation. Soils (Typic Hydrudands) are derived from volcanic ash and are moderately acidic (pH of 5–6 in water). Sugarcane agriculture was practiced on the site for 83 years with biannual harvesting, plowing and fertilization. Cultivation ended in 1993, and 1 year later, the site was plowed and herbicide applied to eliminate remnant cane and weedy grasses. In May 1994, eighteen 30 m×30 m plots were planted with 4-month old *Eucalyptus saligna* seedlings at either 1 m×1 m or 3 m×3 m densities. To assure successful establishment, all plots received 155 kg N $ha^{-1}$, 65 kg P $ha^{-1}$, 130 kg K $ha^{-1}$, 60 kg Ca $ha^{-1}$, 12 kg Mg $ha^{-1}$, and 5 kg $ha^{-1}$ micronutrient mix at planting and at 7 months. After month 7, three randomly selected plots at each density began receiving quarterly additions of 56 kg N $ha^{-1}$, 24 kg P $ha^{-1}$, 46 kg K $ha^{-1}$, plus annual additions of 125 kg Ca $ha^{-1}$, 58 kg S $ha^{-1}$, 23 kg Mg $ha^{-1}$, and 10 kg $ha^{-1}$ micronutrient mix. Three plots at each density received no additional fertilization and served as unfertilized controls (Binkley and Resh 1999; Giardina and Ryan 2002). The remaining six plots became part of a delayed fertilization experiment that is reported elsewhere (Giardina et al. 2003). The 18 plots were organized into three randomized blocks, with each block containing one of the six combinations of fertility (control, continuous fertilization, and delayed fertilization) and planting density (1×1 m and 3×3 m). By the start of the study in January 1996, all plots had closed canopy, trees were 12 m tall, and stands were producing 20–30 Mg wood $ha^{-1}$ $year^{-1}$. Throughout the study, understory vegetation was controlled with herbicides.

We used ANOVA with block, fertility and planting density as main fixed effects to assess treatment differences in above and belowground C cycling. For each comparison between fertilized and control plots, 2 years of annual estimates were averaged across years by plot, such that we compared 2-year means. Interaction of the fertilization and spacing treatment were not significant for any measure. All analyses were performed with the GLM univariate procedure in SPSS (SPSS, Chicago, Ill., USA), and an $\alpha = 0.05$ was used to protect against Type I errors.

### Partitioning the belowground carbon cycle

Soil surface $CO_2$ efflux consists of C released from respiring roots, mycorrhizae, and organisms inhabiting rhizosphere and bulk soils:

$$F_S = F_{AL} + F_{SOC} + F_{RM} + F_{BL} \quad (1)$$

where $F_S$ is soil surface $CO_2$ efflux; $F_{AL}$ is the flux of $CO_2$ from decomposing aboveground litter (mostly leaves and small branches for young forests); $F_{SOC}$ is the flux of $CO_2$ from decomposing detrital C in bulk mineral soil; $F_{RM}$ is the flux of $CO_2$ from respiring roots and mycorrhizae; and $F_{BL}$ is the flux of $CO_2$ from rhizosphere metabolism of root and mycorrhizal exudation and litter turnover. To develop annual $CO_2$ flux estimates for the different components of Eq. 1, we measured $F_S$ and $F_{AL}$ monthly in 1996 and 1997 using standard methods (see below).

Because of land-use change at our site, several approaches were required to measure $F_{SOC}$. In 1910, our research site was converted from primary forest to sugarcane agriculture, which was practiced until 1993. In 1994, we replanted the site back to forest. Eight decades of cultivating sugarcane, a grass that uses the $C_4$ photosynthetic pathway, altered the $^{13}C$:$^{12}C$ of detrital inputs to soil such that quantifiable pools of old, forest-derived $C_3$-C and young, sugarcane-derived $C_4$-C were present in soil at the beginning of this study. In previous work at this site (Binkley and Resh 1999), the 18 plots of even-aged trees were sampled in 1994 at three locations and two depths (0–0.15 and 0.15–0.3 m). Soil C content and $^{13}C$:$^{12}C$ were analyzed as described below in our methods section. In 1994, after 80 years of sugar cane cultivation, soil C in 0–0.3 m was 8.9 kg C $m^{-2}$ (SD=0.3), 30% of which was derived from $C_4$ vegetation (Binkley and Resh 1999). From 1994 to 1997 (2.5 years), $C_4$-C declined from 2.6 to 2.1 kg C $m^2$, while $C_3$-C increased from 6.2 to 6.7 kg C $m^{-2}$. Nearly all change was in the top 0.15 m, where $C_4$-C declined from 1.5 to 1.0 kg C $m^{-2}$.

Following afforestation in 1994, $F_{SOC}$ therefore had three potential C sources: >80-year-old C that originated from the native, pre-1910 forest; 2 to 80-year-old sugarcane C; and 0 to 4-year-old, *E. saligna*-derived soil C. For our calculations, we assumed zero C mass loss for >80-year-old forest C during our study—an assumption that is supported by the following data. First, the

measured mean mass loss rate for pre-1910 forest C during eight decades of cultivation was 0.22 Mg C $ha^{-1}$ $year^{-1}$ (Binkley and Resh 1999; Giardina and Ryan 2000), which is within the measurement error of the other fluxes in Eq. 1. Second, because 0.22 Mg C $ha^{-1}$ $year^{-1}$ represents a mean from 1910 to 1993, and mass loss rates typically decline with time (Paul and Clark 1996), 0.22 Mg C $ha^{-1}$ $year^{-1}$ likely over-estimates the mass loss rate for pre-1910 forest C during our study. Because a portion of soil C lost under cultivation likely was caused by erosion, the 0.22 Mg C $ha^{-1}$ probably overestimates mean soil C decomposition rate for the cultivation period. Following planting of the site back to $C_3$ forest, standard-mixing equations and $^{13}C$:$^{12}C$ and total C content data for mineral soils were used to quantify the annual change in sugarcane C in soil (Vitorello et al. 1989; Bashkin and Binkley 1998; Binkley and Resh 1999). Specifically, $F_{SOC}$ of sugarcane origin was estimated as $[-1 \times (\Delta C_{SOC4}/\Delta t)]$ where $C_{SOC4}$ is soil C of sugarcane origin, and $\Delta t$ is the 2.5 years between 1994 and 1997 measurements of soil C content and $^{13}C$:$^{12}C$ (see below).

The invasive methods used to estimate root respiration at the ecosystem scale typically ignore exudation and mycorrhizae and disrupt the delicate connections between roots, mycorrhizae and soil (Högberg et al. 2001). Consequently, $F_{SOC}$ of *E. saligna* origin, the third potential source of $F_{SOC}$, cannot be distinguished reliably from the decomposition of new, *E. saligna*-derived belowground litter and exudation ($F_{BL}$), and neither flux can be distinguished reliably from mycorrhizal and root respiration ($F_{RM}$). We therefore re-expressed Eq. 1 as:

$$F_S = F_{AL} + F_{SOC4} + [F_{RM} + F_{BL} + F_{SOC3}] \quad (2)$$

where $F_{SOC4}$ is the annual flux of $CO_2$ derived from decomposing sugarcane soil C, calculated as above, and $[F_{RM} + F_{BL} + F_{SOC3}]$ is the annual rhizosphere C flux—that flux of C moving through the rhizosphere of *E. saligna* trees including decomposition of new, *E. saligna*-derived soil C. From measures of $F_S$, $F_{AL}$ and $F_{SOC4}$, we used Eq. 2 to estimate $[F_{RM} + F_{BL} + F_{SOC3}]$ as: $F_S - F_{AL} - F_{SOC4}$ (Fig. 1).

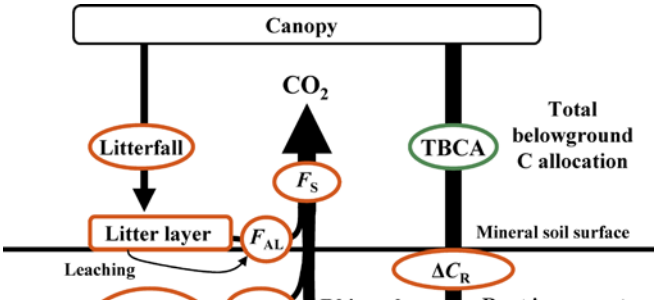


**Fig. 1** Conceptual summary of our mass balance-based approach for examining the belowground C fluxes contributing to soil surface $CO_2$ efflux and their origin in total belowground C allocation and aboveground litterfall. Fluxes or pools that are presented in orange were measured or estimated directly while fluxes presented in green were estimated indirectly by difference using Eqs. 2, 3 and 4, as described in the text. Because the decomposition of C leached from aboveground litter cannot be distinguished from heterotrophic decomposition of that litter, and the formation of new soil C was not related significantly to $F_{AL}$, we assumed that all C leached from aboveground litter was labile and decomposed soon after leaching, and assigned this $CO_2$ to $F_{AL}$. For a definition of terms, please see Eqs. 2, 3 and 4 in the text

We also used a mass balance-based approach to estimate TBCA, defined as the total quantity of C allocated belowground by trees for the construction and maintenance of roots and mycorrhizae including exudation and litter turnover (Giardina and Ryan 2002). Conservation of mass dictates that TBCA must either be released as $CO_2$, change C storage in roots and soils, or be eroded or leached from the site. In a detailed analysis, Giardina and Ryan (2002) estimated that DOC + DIC loss from our site is <1% of TBCA. In general, erosion and leaching losses of C are negligible in closed canopy forests on level topography (Richter et al. 1999). Therefore, annual TBCA at our site can be described as:

$$TBCA = [F_{RM} + F_{BL} + F_{SOC3}] + [\Delta C_R] + [\Delta C_{SOC3}/\Delta t] \quad (3)$$

where $\Delta C_R$=annual C increment in root biomass, $\Delta C_{SOC3}$=change in soil C derived from *E. saligna* trees, and $\Delta t$=2.5 years. We estimated $\Delta C_R$ by sampling annually for fine roots with a soil corer, and by estimating coarse root increment with allometrically based annual estimates of aboveground biomass and an equation relating aboveground wood + bark biomass and coarse root biomass >2 mm (root biomass = aboveground wood + bark biomass × 0.19). This equation was established for closely related *E. grandis* × *urophylla* trees in Brazil, and it accurately predicted coarse root biomass (>2 mm) for two harvested *E. saligna* trees at our site (±5%). Notably, above and belowground standing stock allometries appear to be generally insensitive to nutrition variables (reviewed in Giardina and Ryan 2002). This lack of sensitivity likely relates to the support function served by coarse roots. In contrast, shorter-lived tissues such as fine roots and mycorrhizae serve to acquire nutrients and water, and allocation of C to these tissues will be more sensitive to changes in nutrient or water supply. Further, because it is coarse root increment that is captured in Eq. 3, not standing biomass, even a 30% error in this allometry would affect our TBCA estimates by <2%.

Because of land-use changes at our site, $\delta^{13}C$ mass spectrometry of 1994 and 1997 soils and the assumption of zero change in pre-1910 forest C allowed us to quantify the formation rate of new, *E. saligna*-derived soil C ($\Delta C_{SOC3}/\Delta t$). Combining Eqs. 2 and 3, the annual TBCA flux therefore can be estimated as:

$$TBCA = F_S - F_{AL} - F_{SOC4} + [\Delta C_R] + [\Delta C_{SOC3}/\Delta t] \quad (4)$$

## Soil C decomposition

Land-use changes at our research site and standard-mixing equations (Vitorello et al. 1989; Binkley and Resh 1999) permitted annual $F_{SOC4}$ and $\Delta C_{SOC3}$ to be determined from measurements of the change in $^{13}C$ natural abundance, total C content, and bulk density of soils sampled in April 1994 immediately prior to planting and in January 1997. Total C content and $^{13}C$:$^{12}C$ of soil was measured to 0.30 m depth near three permanently marked points per plot. Previous studies at nearby sites under similar vegetation with similar soils have shown soil C below 30 cm to be extremely stable (Torn et al. 1997; Bashkin and Binkley 1998), and so were not examined. Soil $^{13}C$:$^{12}C$ was measured with a VG isochrom-NA stable isotope ratio mass spectrometer (Binkley and Resh 1999). Soil C derived from sugarcane was calculated as: $\%C_4\text{–}C = (\delta - \delta o / \delta c - \delta o) \times 100$, where $\delta$ is the $\delta^{13}C$ of the soil sample, $\delta o$ is the $\delta^{13}C$ of soil samples with no C from $C_4$ plants, and $\delta c$ is the mean $\delta^{13}$ C of $C_4$ sugarcane leaves + roots. The % $C_3$-C was estimated by difference. We used $\delta o$=−25.5‰ and $\delta c$=−11.5‰, which were measured from C in native forest soils and sugarcane material both from nearby sites (Binkley and Resh 1999). In a preliminary sensitivity analysis for application of $C_3/C_4$ mixing models to afforested cane fields in Hawaii, Bashkin and Binkley (1998) found that for adjacent sites even relatively large variation in end member $^{13}C$:$^{12}C$ ($\delta^{13}C$ of −8.5 to −14.5‰ for cane material) would have minor (~3%) effects on estimates of soil C partitioning into $C_3$ and $C_4$ sources. To estimate a mean annual rate of change for $C_3$-C formation and $C_4$-C decomposition [i.e., $(\Delta C_{SOC3}/\Delta t)$ and $(\Delta C_{SOC4}/\Delta t)$], we divided change in $C_3$-C or $C_4$-C by 2.5 year—the time between 1994 and

1997 measurements. Little change in soil C stocks was observed in this period. However, afforestation resulted in significant increases in $C_3$ derived soil C, as revealed by isotope analyses, while the loss of $C_4$ plant inputs to soil resulted in a significant decline in $C_4$ derived soil C (Binkley and Resh 1999).

### Soil surface $CO_2$ efflux

We measured $F_S$ and soil temperature (0.1 m depth) monthly through 1996 and 1997 at 15 stratified points per plot with a portable infra-red gas analyzer (PPSystems CIRAS-1, Haverhill, Mass., USA) attached to a soil respiration chamber (area = 7,800 $mm^2$) and operating as a closed-system (Giardina and Ryan 2002). These measures, which were nearly identical to those obtained at this site with a LiCor 6400 IRGA attached to a LiCor chamber (LiCor, Lincoln, Neb., USA), were used to establish a mean annual flux rate for the 1996–1997 study period, as discussed in Giardina and Ryan (2002).

### Aboveground litter decomposition flux

Our estimates of annual $F_{AL}$ were derived from monthly measures of aboveground litterfall collected with litter traps placed on the ground at eight points per plot. Because aboveground litter that does not decompose during the measurement period increases litter layer mass, annual measures of litter layer mass were used to estimate the fraction of litterfall that was stored in the litter layer. A leaf litter decomposition study was used to adjust litterfall for C loss (microbial decomposition, leaching) between collections (Giardina and Ryan 2002). Again, these measures were used to establish a mean annual flux rate for the 1996–1997 period.

## Results and discussion

Application of the approach described in Fig. 1 to our site revealed a remarkably tight coupling between TBCA and soil surface $CO_2$ efflux. In unfertilized plots, 80% of the C allocated belowground by trees was returned to the atmosphere as $CO_2$ within 1 year. As a consequence of the rapid cycling of current assimilates through the plant-soil system, 72% of soil surface $CO_2$ efflux was derived from belowground C sources with ecosystem residence times of <1 year (Fig. 2). When $F_{AL}$ is included, new assimilates accounted for 90% of soil surface $CO_2$ efflux across plots, with decomposing sugarcane soil C ($F_{SOC4}$) contributing the remaining 10%.

In line with findings for temperate coniferous forest (Richter et al. 1999; Schlesinger and Lichter 2001), afforestation at our site increased the accumulation rate of detrital C in the litter layer and in live biomass but resulted in no detectable increase in detrital C storage in mineral soil (Fig. 2). While increases in new, *E. saligna*-derived soil C were large at our site, these increases were offset by similarly large losses of old, sugarcane C in soil (Binkley and Resh 1999). Further, in the short period since afforestation, fertilization had little impact on the C balance of mineral soils at our site. Slightly lower $F_{SOC4}$ in fertilized plots (−2.4±1.1 and −1.4 ±0.5 Mg C $ha^{-1}$ $year^{-1}$ for control and fertilized plots, respectively; $P$= 0.47) was offset by slightly lower

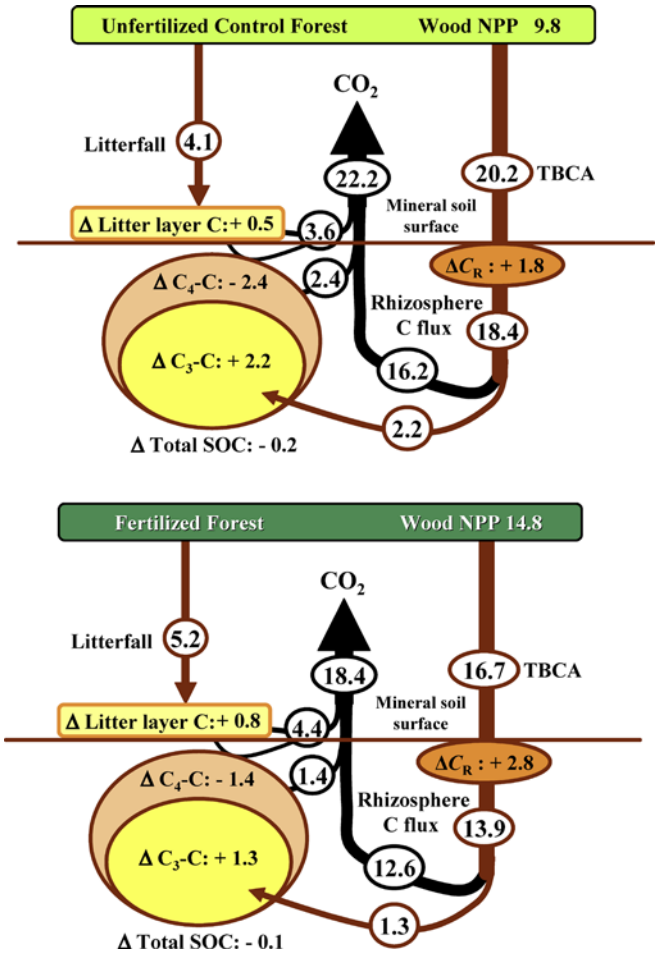


**Fig. 2** Annual belowground C budget for unfertilized control (*top*) and fertilized (*bottom*) stands. Values (Mg C $ha^{-1}$ $year^{-1}$) represent treatment means from 2 or 2.5 years of data for each plot. *Brown flux arrows* or *brown circled pools* represent the movement or storage of organic C (e.g., assimilates, litter, soil organic C). *Black flux arrows* represent the movement of $CO_2$. Standard errors for all fluxes and pools are reported in the text

formation rates of new soil C (2.2±1.1 and 1.3 ±0.6 Mg C $ha^{-1}$ $year^{-1}$; $P$ = 0.41).

Overall, our study may represent a best-case scenario for sequestration of decay-resistant C in tropical soils. The volcanic soils examined here have a high capacity to stabilize C (Torn et al. 1997); and TBCA at our site was large (Giardina and Ryan 2002). Further, *Eucalyptus* is the most widely planted genus in the tropics (Brown et al. 1997; Fisher and Binkley 2000) and, 80+ years is a long time period for continuous, mechanized agriculture in the tropics. We caution that generalizing our results to other tropical sites is complicated by the great diversity of soils supporting tropical afforestation efforts and by the many tree species used.

Fertilizers increasingly are being used in the tropics to manage forest productivity (Fisher and Binkley 2000), and in line with allocation theory (Cannell and Dewar 1994), fertilization at our site increased aboveground plant productivity but reduced belowground C cycling. Fertilization increased aboveground wood productivity (9.8±0.5

and 14.8±0.8 Mg C $ha^{-1}$ $year^{-1}$ ; mean±1 SE for control and fertilized plots, respectively; $P<0.01$), total litterfall (4.1±0.2 and 5.2±0.3 Mg C $ha^{-1}$ $year^{-1}$; $P<0.01$), C accumulation in the litter layer (0.5±0.1 and 0.8 ±0.1 Mg C $ha^{-1}$ $year^{-1}$; $P<0.01$), and the contribution of $F_{AL}$ to $F_S$ (16.7±0.9% and 24.2±1.8%; $P<0.01$). In contrast, fertilization reduced by 22% the quantity of current assimilates that moved through the rhizosphere (16.2±2.0 and 12.6±0.5 Mg C $ha^{-1}$ $year^{-1}$; $P<0.01$). This reduction in rhizosphere C flux relates to a 17% reduction in TBCA (20.2±1.6 and 16.7±1.2 Mg C $ha^{-1}$ $year^{-1}$; $P<0.01$) coupled with a 56% increase in coarse root increment (1.8±0.1 and 2.8±0.2 Mg C $ha^{-1}$ $year^{-1}$; $P<0.01$). Together, these changes led to an 18% reduction in soil surface $CO_2$ efflux (22.2±1.0 and 18.4 ±0.7 Mg C $ha^{-1}$ $year^{-1}$; $P<0.01$; Fig. 2). Observations of greatly reduced mycorrhizal colonization of fine roots in fertilized stands and slightly lower fine root biomass (Giardina and Ryan 2002; Giardina et al. 2003) support an allocation-based explanation for reduced belowground C cycling.

Root and mycorrhizal exudation and turnover are important detrital sources for soil C formation (Jobbágy and Jackson 2000). However, the conversion efficiency of TBCA into new mineral soil C, defined here as the fraction of TBCA that remains in soil in detrital form, is poorly quantified. Across our plots, the formation rate of new, *E. saligna*-derived soil C [that is, ($\Delta C_{SOC3}$ / $\Delta t$)] was strongly and linearly related to rhizosphere C flux (Fig. 3; $r^2=0.59$; $P<0.01$; $n=12$). Further, the efficiency with which total belowground inputs [TBCA-($\Delta C_R$)] were converted into new soil C was slightly lower in fertilized plots, but not significantly so (112±59 g C $kg^{-1}$C and 77 ±43 g C $kg^{-1}$C for control and fertilized plots, respectively; $P=0.87$; $n=6$). Consequently, the segregation of soil C formation rates by fertility along the regression line of Fig. 3 along with slightly lower TBCA conversion efficiency in fertilized plots suggest that fertilizer related reductions in rhizosphere C flux were responsible for lower soil C formation rates. Because $F_{SOC4}$ was lower in fertilized plots—in agreement with evidence that fertilization slows decomposition (Agren et al. 2001)—more rapid decomposition of new soil C cannot explain lower soil C formation rates in these plots.

The increases in aboveground litterfall associated with fertilization may offset in part the effects of fertilization-related reductions in TBCA on soil C formation (Fig. 3). In a previous study, Bernhard-Reversat (1999) estimated that ~25% of mass loss during *Eucalyptus* leaf litter decomposition relates to leaching of soluble compounds out of the senesced leaf. At our site, a 25% leaching rate for decomposing leaf litterfall would translate to just under 1 Mg $ha^{-1}$ $year^{-1}$ for control plots and just over 1 Mg $ha^{-1}$ $year^{-1}$ for fertilized plots. Assuming that the conversion efficiency of leaf leachates into soil C is twice that of TBCA, such that ~20% of leached leaf C is not respired within the year but instead leads to the formation of 0.2 Mg SOC-C $ha^{-1}$ $year^{-1}$, then approximately 10% of the observed new soil C formation rate would have an

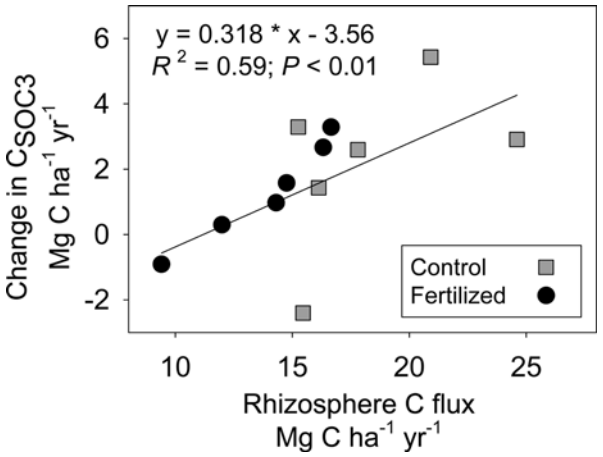


**Fig. 3** The relationship between rhizosphere C flux ($F_{RM} + F_{BL} + F_{SOC3}$) and the formation rate of new soil C ($\Delta C_{SOC3}/\Delta t$). Rhizosphere C flux was estimated as in Eq. 2 while ($\Delta C_{SOC3}/\Delta t$) was estimated using standard $^{13}C$ isotope methods

aboveground source. A small contribution of leaf litter leaching to mineral soil C formation is supported by the following analyses. We identified strong relationships between rhizosphere C flux and both soil surface $CO_2$ efflux ($r^2=0.79$; $P<0.01$; $n=12$) and formation rates of new soil C (Fig. 3). In contrast relationships between formation rates of new soil C and aboveground litterfall ($r^2=0.15$; $P=0.10$; $n=12$) or soil surface $CO_2$ efflux ($r^2=0.38$; $P=0.03$; $n=12$) were weak, suggesting that belowground inputs exert a larger influence over soil C formation than do aboveground inputs. From these analyses, we suggest that soil surface $CO_2$ efflux and aboveground productivity measures are inadequate for inferring the belowground processes controlling soil C formation and storage.

In contrast to agricultural systems where fertilization appears to increase C storage in mineral soil (Schlesinger 1999), our findings suggest that forests may respond to fertilization by decreasing the flow of assimilates to the belowground processes leading to soil C formation. Notably, C storage increased in the litter layer and in aboveground biomass, and these increases offset fertilizer related reductions in belowground C cycling.

In line with findings from temperate grassland and boreal forest (Craine et al. 1999; Högberg et al. 2001), our results show that most soil surface $CO_2$ efflux in humid tropical forests may be derived from C with very short ecosystem residence times, and these short residence times explain low observed rates of soil C accumulation. Further, our findings suggest that global trends of increased fertilizer use (Fisher and Binkley 2000) and atmospheric nutrient deposition (Matson et al. 1999) may have neutral or negative effects on soil C storage in tropical forests—even where nutrient additions increase plant productivity and C storage in living biomass. These findings have important but largely overlooked implications for modeling how global-scale changes in soil nutrient supply and afforestation alter C storage.

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