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# Primary production and carbon allocation in relation to nutrient supply in a tropical experimental forest

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## Abstract

**Nutrient supply commonly limits aboveground plant productivity in forests, but the effects of an altered nutrient supply on gross primary production (GPP) and patterns of carbon (C) allocation remain poorly characterized. Increased nutrient supply may lead to a higher aboveground net primary production (ANPP), but a lower total belowground carbon allocation (TBCA), with little change in either aboveground plant respiration (APR) or GPP. Alternatively, increases in nutrient supply may increase GPP, with the quantity of GPP allocated aboveground increasing more steeply than the quantity of GPP allocated belowground. To examine the effects of an elevated nutrient supply on the C allocation patterns in forests, we determined whole-ecosystem C budgets in unfertilized plots of *Eucalyptus saligna* and in adjacent plots receiving regular additions of 65 kg N $ha^{-1}$, 31 kg P $ha^{-1}$, 46 kg K $ha^{-1}$, and macro- and micronutrients. We measured the absolute flux of C allocated to the components of GPP (ANPP, TBCA and APR), as well as the fraction of GPP allocated to these components.**

**Fertilization dramatically increased GPP. Averaged over 3 years, GPP in the fertilized plots was 34% higher than that in the unfertilized controls (3.95 vs. 2.95 kg C $m^{-2}$ $yr^{-1}$). Fertilization-related increases in GPP were allocated entirely aboveground – ANPP was 85% higher and APR was 57% higher in the fertilized than in the control plots, while TBCA did not differ significantly between treatments. Carbon use efficiency (NPP/GPP) was slightly higher in the fertilized (0.53) compared with the control plots (0.51). Overall, fertilization increased ANPP and APR, and these increases were related to a greater GPP and an increase in the fraction of GPP allocated aboveground.**

*Keywords:* aboveground net primary production, carbon budget, ecosystem respiration, gross primary production, leaf respiration, litterfall, soil carbon, soil respiration, total belowground carbon allocation, wood respiration

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## Introduction

Allocation theory suggests that alleviating nutrient limitations to plant growth should shift the relative allocation of carbon (C) away from roots and mycorrhizae, where the photosynthate is used for the capture of nutrients and water, to leaves and stems, where the photosynthate is used for light capture (Cannell & Dewar, 1994; Raich, 1998; McConnaughay & Coleman, 1999). Tests of allocation theory typically have examined the above- and belowground distribution of plant dry matter (Ingestad & Agren, 1991; Albaugh *et al*., 1998; Magill *et al*., 1999; McConnaughay & Coleman, 1999; Giardina & Rhoades, 2001), yet the standing crop represents only a small fraction of the total C expended for the capture of nutrients, water and light. Much of the C that is assimilated by trees is respired, allocated to

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mycorrhizae, exuded by roots or released as above- and belowground litter (Pregitzer *et al*., 1995; Ryan *et al*., 1996, 1997; Law *et al*., 1999). For example, fertilization dramatically increased fine root production and mortality in *Populus* trees, but had little effect on fine root mass (Pregitzer *et al*., 1995). Because of the difficulty in measuring these various fluxes, our understanding of the mechanisms that control these fluxes, and therefore the complete C budget of forests, remains quite limited (Cannell & Dewar, 1994).

Gross primary production (GPP), defined as net photosynthesis summed over an annual time step, can be estimated as the annual sum of C allocated to dry matter production and respiration:

$$\mathrm{GPP} = \mathrm{ANPP} + \mathrm{APR} + \mathrm{TBCA}, \quad (1)$$

where GPP provides the carbohydrates used for all plant processes; ANPP is aboveground net primary production, APR is aboveground plant respiration; and, TBCA is total belowground C allocation (Ryan, 1991). Of the three component fluxes of GPP (Eqn (1)), only ANPP has been intensively characterized across a range of forest types and fertility conditions (Binkley *et al*., 1997; Fisher & Binkley, 2000; Clark *et al*., 2001; Roy and Saugier, 2001). In forests, ANPP is typically nutrient limited (Fisher & Binkley, 2000; Reich & Bolstad, 2001) and existing C budget studies have reported fertilization-related increases in the fraction of GPP allocated to aboveground tissues (Axelsson, 1983; Ryan *et al*., 1996; Keith *et al*., 1997). These shifts are consistent with generally observed declines in root-to-shoot ratios in response to an elevated nutrient supply (Albaugh *et al*., 1998; McConnaughay & Coleman, 1999; Giardina & Rhoades, 2001) and with theoretical considerations of how nutrient supply controls the C partitioning strategies of plants (Cannell & Dewar, 1994). However, the magnitude of observed shifts in the partitioning of GPP to ANPP remains poorly understood, particularly in field studies of whole forests (Ryan *et al*., 1996; Keith *et al*., 1997).

The flux of C allocated to APR can represent a large fraction of GPP and may increase when an elevated nutrient supply also increases the quantity and metabolic activity of living tissues. Alternatively, fertilization may increase ANPP with little effect on APR (e.g. Keith *et al*., 1997). TBCA, the primary source of detrital C to forest soils, also represents a large fraction of GPP (Law *et al*., 1999), and TBCA may increase, decrease or remain unchanged in response to an increased nutrient supply (Haynes & Gower, 1995; Ryan *et al*., 1996; Keith *et al*., 1997; Raich, 1998; Zak & Pregitzer, 1998; Giardina & Ryan, 2002). Overall, detailed estimates of forest GPP are scarce (Ryan *et al*., 1997; Williams *et al*., 1997), particularly for tropical forests (Clark *et al*., 2001; Grace *et al*., 2001), and environmental controls on GPP and the partitioning of GPP between respiratory losses and net primary productivity (NPP) remain poorly understood. Because forests exert a dominant influence over the C balance of the terrestrial biosphere (Atjay *et al*., 1979; Grace *et al*., 1995; Jobbágy & Jackson, 2000), these information gaps currently limit efforts to model terrestrial C cycling accurately.

The objective of this study was to use a C budget approach (Eqn (1)) to examine how an increased nutrient supply alters the following processes: GPP; the absolute fluxes of C allocated to ANPP, APR and TBCA; and the partitioning of GPP to ANPP, APR and TBCA. We used experimental plots of *Eucalyptus saligna* Smith in Hawai'i, planted at two densities (1 by 1 m or 3 by 3 m) and receiving two levels of fertilization (unfertilized control or regular additions of complete fertilizer) to test the following hypotheses: (1) the C flux to TBCA declines with fertilization and the decline in TBCA is matched by an increase in ANPP (Ryan *et al*., 1996; Keith *et al*., 1997); (2) fertilization increases leaf area index (LAI), which increases light capture, canopy photosynthesis and therefore GPP (Landsberg, 1997); (3) fertilization increases canopy N content and tree growth rates, which leads to a higher APR; (4) fertilization increases the fraction of GPP that is allocated aboveground (Cannell & Dewar, 1994); and (5) fertilization does not alter the fraction of GPP allocated to NPP and respiration (Ryan *et al*., 1996; Waring *et al*., 1998). The simple, replicated ecosystems examined here provided a unique opportunity to test basic tenets of allocation theory. These forests also represent one of the most rapidly increasing cover types in the tropics – managed plantation forests. Planted *Eucalyptus* forests now cover more than 14 million ha of the tropics and sub-tropics (Brown *et al*., 1997), with very high growth rates and profitability increasing the land-base in these forests.

## Materials and methods

### *Site description*

This study was conducted in a 2.5 ha experimental forest of *E. saligna* near Pepe'ekeo on the Island of Hawai'i (19°50′28.1″N, 155°7′28.3″W). The elevation for the site was 350 m. Over the 4 years of this study, the mean annual air temperature was 20.3 °C and the mean annual precipitation was 3.5 m. The soils are deep (>2 m) and are classified as Typic Hydrudands. The site was cropped with sugarcane from ca. 1910 to 1993, one year prior to the establishment of the forest plots in May 1994. During sugarcane cultivation, management included biannual applications of 85 kg N $ha^{-1}$,

75 kg P ha$^{-1}$, 110 kg K ha$^{-1}$, and after 1955, 700 kg ha$^{-1}$ of lime (Binkley & Resh, 1999).

In May 1994, eighteen 30 by 30 m plots, organized into three completely randomized blocks, were planted with seedlings at a 1 by 1 m or 3 by 3 m planting density. Prior to planting, the site was plowed and herbicide was applied to control the regenerating cane and colonizing weeds. To assure successful establishment, all plots were fertilized at planting (planting holes) and at 7 months (broadcast application) with a total of 310 kg N ha$^{-1}$ as urea, 130 kg P ha$^{-1}$, 260 kg K ha$^{-1}$, 125 kg Ca ha$^{-1}$, 58 kg S ha$^{-1}$, 23 kg Mg ha$^{-1}$ and 10 kg ha$^{-1}$ Granusol micro-nutrient mix (5% Mn, 5% Zn, 5% Fe, 5% S, 1.5% Cu, and 0.5% B) over the two applications (Binkley & Resh, 1999). After the second application of fertilizer, three fertility treatments were established: a 'Continuous Fertilization' treatment designed to avoid any nutrient limitations to growth where three plots at each spacing immediately began receiving quarterly applications of N, P, K and annual applications of Ca, S, Mg and micronutrients; a 'Control' treatment where 3 plots at each spacing received no additional fertilizer after month 7; and a 'Delayed Fertilization' treatment where three plots at each spacing were managed as Control plots from month 7 until April 1998, after which the six plots began receiving quarterly applications of 65 kg N ha$^{-1}$ as urea, 31 kg P ha$^{-1}$, 46 kg K ha$^{-1}$, and annual additions of 125 kg Ca ha$^{-1}$, 58 kg S ha$^{-1}$, 23 kg Mg ha$^{-1}$ and 10 kg ha$^{-1}$ Granusol micro-nutrient mix. Understory weeds in all the plots were controlled with glyphosate herbicide. All measurements (except when requiring canopy access) were taken within the interior 10 by 10 m area of the 1 by 1 m plots (20 m buffer) and the interior 15 by 15 m area of the 3 by 3 m plots (15 m buffer).

Because we wished to examine how increased fertility in the established forest stands alters C allocation patterns, this study reports C budget comparisons for the Control and Delayed Fertilization treatments during a 1-year pretreatment period (1997) and during a 3-year post-treatment period (1998–2000). The results from the Continuous Fertilization treatment and age-related changes in the forest C budgets will be examined in a subsequent paper.

### *Carbon budget overview*

Gross Primary Production can be estimated using a C budget approach where relevant fluxes are either measured directly or, when direct measurement alone is not sufficient, estimated by a combination of direct measurement and mass balance (Ryan, 1991; Ryan *et al*., 1996). This approach is well suited for estimating GPP in the experimental forest plots at our research site because process rates are rapid (Binkley & Ryan, 1998; Giardina & Ryan, 2002), soil C stores are relatively homogeneous (Binkley & Resh, 1999), plot size is large (30 by 30 m) and measurements were taken for multiple years. In addition, overstory vegetation was of a single age and species and the climate is relatively constant throughout the year (Townsend *et al*., 1995).

To arrive at our estimates of GPP (Eqn (1)), we measured ANPP, the annual total of aboveground dry matter production (in kg C m$^{-2}$ yr$^{-1}$), as annual leaf, twig, fruit and bark litterfall plus annual wood mortality plus the annual change in leaf, branch, bark and wood biomass:

$$\mathrm{ANPP} = F_A + F_W + \Delta C_C + \Delta C_W, \qquad (2)$$

where $F_A$ is the flux of C associated with aboveground leaf, twig, fruit and bark litterfall, $F_W$ the flux of C associated with tree mortality, $\Delta C_C$ the increment in the C content of live leaves in the canopy, and $\Delta C_W$ the increment in the C content of aboveground branches, bark and wood. These fluxes can be summarized as leaf NPP (the sum of $\Delta C_C$ and the leaf component of $F_A$) and aboveground wood NPP (the sum of $F_W$, $\Delta C_W$ and the fruit and woody components of $F_A$).

We estimated APR, the annual total of C respired by leaves and aboveground wood during the construction and maintenance of cellular structures and for phloem loading and the maintenance of ion gradients (Cannell & Thornley, 2000), as the sum of construction ($L_{RC}$) and maintenance respiration ($L_{RM}$) for the foliage and total respiration for aboveground wood ($W_R$):

$$\mathrm{APR} = L_{RC} + L_{RM} + W_R. \qquad (3)$$

Finally, we used a mass balance-based approach (Raich & Nadelhoffer, 1989; Giardina & Ryan, 2002) to estimate TBCA, the annual total of the C sent belowground for the production and maintenance of roots and mycorrhizae and the C released as root exudates or biomass turnover. Because all the C allocated belowground must either be respired, transported off site or stored, TBCA can be estimated from the following equation:

$$\mathrm{TBCA} = F_S + F_E - F_A + \Delta C_S + \Delta C_R + C_L, \qquad (4)$$

where $F_S$ is the soil surface $CO_2$ efflux, $F_E$ the flux of the C transported off the site by leaching of the dissolved organic and inorganic C or by erosion, $\Delta C_S$ the change in the C content of mineral soil, $\Delta C_R$ the increment in the C content of root biomass (coarse + fine), and $\Delta C_L$ the change in the C content of the litter layer. To estimate TBCA, litterfall ($F_A$) is subtracted from $F_S$ because $F_S$ includes the C released from decomposing aboveground litter. The aboveground litter that does not decompose within the measurement period will

increase $C_L$ for that period. Conversely, the litter layer material that decomposes within the measurement period will lower $C_L$. All the components of Eqn (4) were measured or estimated except for $F_E$, which is typically $\ll 1\%$ of TBCA in closed canopy forests (Giardina & Ryan, 2002). Because ranges of root herbivores are small and the consumed C should be respired or retained in the measurement area, we expect that root herbivory will not influence TBCA estimates.

Leaf level isoprene emission from trees at our site was measured in May 2000 (Funk *et al*., 2002). Because the estimated canopy isoprene flux between July 1999 and June 2000 was 1.2 to 3.9% of ANPP in the Continuously Fertilized and Control plots, respectively (Funk *et al*., unpublished results), we did not include these loses in our stand C budget. We did not estimate monoterpene flux for our stands because monoterpene emissions for Eucalyptus species are typically much lower than isoprene emissions (He *et al*., 2000).

*Aboveground net primary production*

The components of ANPP (leaf plus wood NPP) were estimated from Eqn (2). Aboveground litter ($F_A$) was collected monthly from eight 0.186 $m^2$ traps per plot that were placed on the forest floor. Litterfall, which consisted mostly of leaves with some twigs, bark and very occasional fruits, was composited by plot, oven-dried at 70 °C to a constant weight, and separated into leaves and branches plus bark plus fruit for weighing. We assumed that all litter was 50% C, based on the mean C content of fresh leaves (50.6%) and wood (48.2%). To account for leaf litter decomposition between collections in our estimates of litterfall, we used a measured decay rate for senescent leaves from the fertilized and unfertilized plots of 0.0095 $day^{-1}$ where the leaf litter = measured leaf litterfall × 1.14 (Giardina & Ryan, 2002). The decomposition of branch, bark and fruit litter between collections was assumed to be zero. The leaf litter data were used to estimate leaf NPP while the twig, fruit and bark data were used to estimate wood NPP.

We estimated the change in canopy mass ($\Delta C_C$) using monthly measures of LAI. Synchronous above and below canopy measurements were made in the post-treatment period with two identical LAI-2000 Plant Canopy Analyzers (LiCor, Lincoln, NE, USA); the above-canopy sensor was located in an open field approximately 50 m from the forest plots and aligned in the same direction as the below-canopy sensor. In all years, LAI was sampled at 18 stratified points across the measurement area of each plot with the goal of maximizing canopy coverage within each plot. The measurements were made under overcast and calm conditions; in months when LAI could not be measured because of rain or sunny conditions, the monthly value was estimated using linear interpolation from the adjacent monthly measurements. In 1998, the sampling was modified to adjust for higher canopies and increased area covered by the sensor.

To correct LAI-2000-based estimates for leaf overlap and clumping, we conducted two harvests to establish a relationship between the tree leaf area and diameter at 1.4 m (diameter at breast height, or DBH). In January 1996, the total mass (wet weight) of leaves plus attached branches $<1$ cm was measured for two randomly selected trees that were harvested from each of the 18 experimental plots ($n = 36$). In the laboratory, the leaf + branch subsamples were stripped of leaves; the leaves and branches were then weighed separately, and the leaf area of the stripped leaves was measured with a LiCor 3100 Leaf Area Meter (LiCor, Lincoln, NE, USA). The leaf area per kg leaf (wet weight) and leaf/twig wet weight were then used to estimate the total leaf area per tree from the total leaf + branch weight per tree. The resulting relationship between leaf area and DBH was used to estimate the LAI of the measurement area in each of the 18 plots at the time of harvest. The LAI-2000-based LAI estimates at the time of harvest were then compared with and corrected to the allometrically determined LAI for each plot, resulting in the following relationship: $\mathrm{LAI} = \mathrm{LAI} - 2000 \times 1.54 + 0.93$. This relationship is similar to previous correction factors developed for other Eucalypt forests (*E. nitens*, Cherry *et al*., 1998). A second leaf area harvest in August 1999 of all 23 trees in an adjacent Continuously Fertilized 3 by 3 m plot that was not part of this study (Binkley *et al*., 2002) yielded an estimate of LAI that was within 15% of our allometrically corrected LAI-2000 value.

To estimate the change in the woody biomass ($\Delta C_W$), we estimated woody biomass (boles + branches) quarterly using diameter measurements at DBH for all living trees inside the measurement area of each plot, and an allometric equation between DBH and woody biomass (woody biomass (kg) = $0.0662 \times (\mathrm{DBH})^{2.5}$, $R^2 = 0.99$, $P < 0.001$, $n = 57$) that was developed for this experimental forest. Mortality ($F_W$), which never exceeded 1% of woody biomass production, was added back to quarterly production estimates.

Our approach underestimates ANPP where herbivory or decomposition in the canopy prevents litter from being measured (Clark *et al*., 2001). These errors were likely small at our site because no leaf herbivory was observed during the regular tower measurements of canopy leaves or while processing leaf litterfall samples, and senesced leaves were rarely retained in the canopy.

*Aboveground plant respiration*

We assumed that leaf construction respiration ($L_{RC}$) equaled 25% of leaf NPP (Penning de Vries, 1975; Sprugel *et al*., 1995), where leaf NPP equals the leaf component of total litterfall ($F_A$) plus a change in foliage mass in the canopy ($\Delta C_C$). We estimated leaf maintenance respiration (foliage dark respiration, or $L_{RM}$) by periodically measuring $CO_2$ efflux at night from intact and attached leaves. To do this, scaffold towers were constructed just outside the interior measurement area of 1 by 1 m and 3 by 3 m Control and Continuous Fertilization plots (four total plots). We assumed that in the pretreatment period, the Delayed Fertilization plots were similar to the Control plots (Table 1); in the post-treatment period, we assumed that the Delayed Fertilization plots were similar to the Continuous Fertilization plots. The flux was measured with Plexiglas mixing chambers attached to a PPSystems CIRAS-1 (PPSystems, Haverhill, MA, USA) in open system mode. The chambers were fit with neoprene seals to prevent air leaks, and the air seal was monitored continuously during each measurement with an in-line flow meter. Foliage dark respiration was measured between 21:00 and 02:00 hours on fully expanded leaves from four positions in the canopy:

**Table 1** Pre-treatment (year 1) differences between the control (C) and fertilized (F) plots for components of aboveground net primary production, aboveground plant respiration and total belowground carbon allocation; the terms are defined in the Materials and methods and Appendix

| Measure | Component | Treatment | Mean kg C $m^{-2} yr^{-1}$ | SE | *P* |
|---|---|---|---|---|---|
| ANPP | | C | 1.05 | 0.058 | 0.41 |
| | | F | 1.11 | 0.069 | |
| | $F_A$ | C | 0.43 | 0.022 | 0.96 |
| | | F | 0.42 | 0.035 | |
| | Wood NPP | C | 0.81 | 0.063 | 0.37 |
| | | F | 0.86 | 0.048 | |
| | Leaf NPP | C | 0.24 | 0.016 | 0.86 |
| | | F | 0.25 | 0.027 | |
| | LAI* | C | 4.93 | 0.33 | 0.99 |
| | | F | 4.93 | 0.36 | |
| APR | | C | 0.97 | 0.049 | 0.38 |
| | | F | 0.98 | 0.057 | |
| | $L_{RC}$ | C | 0.06 | 0.004 | 0.73 |
| | | F | 0.06 | 0.007 | |
| | $L_{RM}$ | C | 0.49 | 0.028 | 0.90 |
| | | F | 0.50 | 0.028 | |
| | $W_R$ | C | 0.42 | 0.020 | 0.88 |
| | | F | 0.43 | 0.028 | |
| TBCA | | C | 1.94 | 0.151 | 0.21 |
| | | F | 1.72 | 0.128 | |
| | $F_S$ | C | 2.20 | 0.093 | $<0.01$ |
| | | F | 2.01 | 0.051 | |
| | $C_S$ | C | −0.02 | 0.100 | 0.81 |
| | | F | −0.06 | 0.119 | |
| | $C_R$ | C | 0.16 | 0.012 | 0.64 |
| | | F | 0.17 | 0.009 | |
| | $C_L$ | C | 0.04 | 0.014 | 0.69 |
| | | F | 0.03 | 0.015 | |
| GPP | | C | 3.96 | 0.207 | 0.54 |
| | | F | 3.81 | 0.171 | |

*Units for LAI are $m^2 m^{-2}$.

four to five leaves in from the terminal bud of the upper, middle and lower one-third crown, and four to five leaves out from the point of shoot attachment in the lower one-third crown. The measurements were made four times in 1995, once in October 1996 and once in February 1998.

The relationship between foliage dark respiration rate ($\mu mol\,m^{-2}\,s^{-1}$) and foliar N content ($mmol\,m^{-2}$) differed between the Control and Fertilization treatments, but not between seasons or years (Ryan *et al*., unpublished results). Therefore, in the post-treatment period we used separate $L_{RM}$ coefficients ($a$) for the Control and Fertilization treatments (5.16 and 4.21 mmol C (mol foliar N)$^{-1}$ s$^{-1}$, respectively). For the pretreatment period, we assumed that the $L_{RM}$ coefficient from the Control plot applied to all the stands. All estimates of $L_{RM}$ were corrected of 20 °C using a $Q_{10}$ of 2 (mean annual temperature = 20.3 °C).

Our estimates of $L_{RM}$ and therefore GPP do not include dark foliar respiration in the daytime, and were determined with $L_{RM}$ coefficients and canopy N content:

$$L_{RM} = N_C \times a \times (\text{seconds of darkness in 1 year}), \quad (5)$$

where $N_C$ is the annual average total N content of the forest canopy ($mol\,N\,m^{-2}$) and $a$ is the dark respiration coefficient (see above). $N_C$ was estimated from allometrically corrected measures of LAI, and direct measures of the specific leaf area and leaf [N] of leaves sampled periodically from the canopy towers and from the 36 trees harvested in 1998. The tissue [N] was determined for leaf subsamples on a Leco 1000 CHN Element Analyzer (Leco Corporation, St Joseph, MI, USA).

We measured wood respiration through the bark four to five times per year in 1996 and 1997, and in March 1999, July 2000 and May 2001. In 1996 and 1999, we measured $CO_2$ efflux at two locations (offset by 90°) at DBH for 5–15 trees per plot in one plot per treatment combination, and also at 3 and 6 m above the ground for four to five trees in six plots with canopy access towers. In 2000, we measured 5–10 trees per plot at DBH on all the 18 plots at our site and on 18 trees at 3 and 6 m in six plots with towers. For these measurements, we again used Plexiglas mixing chambers fit with neoprene seals to prevent air leaks and attached to a PPSystems CIRAS-1 in open system mode. The seals between the chambers and tree bark were checked continuously with an in-line flow meter.

To estimate stand level woody respiration ($W_R$), we expressed our respiration measurements relative to the wood biomass contained in a tree cylinder of the same height and at the same height as the respiration chamber. The volume of the cylinder was estimated from the diameter of the cylinder at the point of measurement on the tree while wood specific gravity was determined from the allometry trees that were periodically harvested at our site. Woody respiration was then estimated as a specific respiration rate for that measurement period (mol C (mol C)$^{-1}$ s$^{-1}$) × annual average $C_W$ (C in the aboveground woody biomass estimated from DBH) × $3.154 \times 10^7$ (the number of seconds in 1 year). Again, the measurements were adjusted to 20 °C using an assumed $Q_{10}$ of 2.

### *Total belowground carbon allocation*

Soil surface $CO_2$ efflux and mineral soil temperature at 0.10 m depth were measured monthly at 15 points along transects running diagonally through the interior measurement area of each plot using a PPSystems CIRAS-1 with a standard, unmodified PPSystems soil respiration chamber. In a previous study, we directly compared our measurements of $F_S$ with measurements taken with a LiCor soil chamber operating with the LiCor 6400, as described by Janssens *et al*. (2000), and found no difference between the systems (Giardina & Ryan, 2002). Because $F_S$ did not vary with the time of day during two diurnal measurement periods, and the diurnal soil temperatures in our closed canopy forests varied by $<2$ °C, monthly $F_S$ was estimated as the measured rate (kg C m$^{-2}$ s$^{-1}$) × the number of seconds in the measurement month. The annual estimates were achieved by summing the monthly estimates.

Litter layer mass ($C_L$) was measured from eight 0.186 m$^2$ samples per plot in January from 1996 to 1999. The litter layer was not measured in 2000, but had changed little after 1998, suggesting that the mass had stabilized (Giardina & Ryan, 2002). The samples were composited by plot, dried at 70 °C to a constant weight, separated into the leaf and twig plus branch plus bark components, and weighed separately. We assumed a 50% C content for the litter layer material.

A change in the biomass of coarse roots was estimated from the change in aboveground biomass (measured quarterly) using a regression between coarse root biomass (>2 mm) and aboveground biomass (Giardina & Ryan, 2002), where coarse root biomass (kg) = $0.19 \times C_W$ (kg). Because changes in fine root biomass were $<0.02$ kg C m$^{-2}$ yr$^{-1}$ from 1995 to 1999 (Giardina & Ryan, 2002), and fine root biomass was ~5% of total root biomass, we assumed zero net annual change in the pool of fine root C.

Soil C was measured to a depth of 0.30 m at three permanently located sites per plot in May 1994 and in January 1997 (Binkley & Resh, 1999), and again for all plots in January 2000 (D. Binkley, unpublished results). For annual estimates of TBCA, we assumed that the rate of change in soil C was constant across these two periods. From earlier work at nearby sites with similar

soils and land use (Bashkin & Binkley, 1998), we expect that soil C below 0.30 m changed little over the course of this 4-year study (Post & Kwan, 2000; Giardina & Ryan, 2002). A full uncertainty analysis of measurement error for the components of our TBCA budget is presented in Giardina & Ryan (2002).

### *Mycorrhizal colonization rates*

In March 2000, we examined mycorrhizal colonization rates for fine roots in the plots at our site by collecting ten 0–0.20 m depth cores per plot, and compositing cores by plot. The cores were immediately refrigerated, and 4 days later, all visible live fine roots were hand picked from soils, washed with $H_2O$ and $H_2O_2$, and stained with trypan blue (Phillips & Hayman, 1970). The colonization rates for arbuscular and ecto-mycorrhizae were determined by direct observation. The fruiting bodies in all plots were dominated by *Laccaria fraterna* and *Scleroderma verrucosum*.

### *Light interception*

In September 1999 (peak annual LAI) and May 2000 (mean annual LAI), an AccuPAR PAR-80 ceptometer (Decagon Devices Inc., Pullman, WA, USA) was used to estimate canopy radiation interception at 100 stratified points in each plot. Above-canopy PAR levels (μmol $PAR\,m^{-2}$) were measured in an adjacent open field immediately before and after each plot was examined for below-canopy PAR levels. All the measurements were taken under cloudless and windless conditions between 10:30 and 13:30 hours, HST. To assess reproducibility, 4 plots were measured three times in September 1999, and the plot means were found to vary by $<3\%$.

### *Statistical analysis*

We used an analysis of variance (block, fertility treatment and tree spacing were the main fixed effects) to assess the treatment differences in GPP, ANPP, APR, TBCA, constituent components of these measures, CUE, LAI and canopy light interception. The annual estimates of these measures were compared for the pre-treatment data, while for post-treatment stands, 3 years of annual estimates were averaged across years by plot, and 3-year means were compared. We determined the statistical differences between treatments for the fraction of GPP allocated to ANPP, APR or TBCA by estimating fractions for each plot (again, 3-year means), and then statistically comparing the means in an ANOVA. Because the interaction of fertilization and spacing treatment was significant only for LAI and $L_{RC}$, we present means that are pooled across spacing treatments. These analyses were performed with the GLM univariate procedure in SPSS (SPSS, Inc., Chicago, IL, USA). In our comparisons, $\alpha = 0.05$ was used to protect against Type I errors.

## Results and discussion

We used the C budget approach described above to test our five hypotheses. Specifically, we quantified the total flux of C associated with each of the components of GPP (Eqns (1)–(4)). We then used these data to examine the influence of nutrient supply on the fraction of GPP that is allocated to ANPP, APR and TBCA. The block effects were significant only for APR in the pretreatment period ($P = 0.03$), indicating that the site was initially homogeneous. In the post-treatment period, the $P$-values for block effects were consistently $>0.5$.

### *Aboveground net primary production*

In the year prior to the first application of fertilizer (the pretreatment period), ANPP represented 28% of GPP and no component of ANPP differed between treatments (Table 1). Total litterfall ($F_A$), leaf NPP and LAI averaged $0.43\,kg\,C\,m^{-2}\,yr^{-1}$, $0.24\,kg\,C\,m^{-2}\,yr^{-1}$, and $4.93\,m^2\,m^{-2}$, respectively. Wood NPP was 3.5 times higher than leaf NPP and averaged $0.83\,kg\,C\,m^{-2}\,yr^{-1}$. The pretreatment ANPP ($1.08\,kg\,C\,m^{-2}\,yr^{-1}$) was within the range of values published for managed Eucalypt forests in the humid tropics (Binkley *et al*., 1997).

Our stands were strongly nutrient limited, and, as has been shown elsewhere in Hawai'i (Binkley *et al*., 1992; Herbert & Fownes, 1995; Binkley & Giardina, 1997; Binkley *et al*., 1997; Giardina *et al*., 2000), ANPP responded to fertilizer additions. Post-treatment leaf NPP, wood NPP and ANPP were 55%, 100% and 85% higher, respectively, in the fertilized plots than in the control plots, while LAI increased by 37% (Table 2, Fig. 1). The fraction of GPP allocated to ANPP increased from 26% in the control plots to 36% in the fertilized plots ($P < 0.01$). By comparison, ANPP represented 30% of GPP in unfertilized Australian *Pinus radiata* stands and 38% of GPP in fertilized stands (Ryan *et al*., 1996). Fertilization in an *E. pauciflora* forest in Australia increased from 25% to 30% the fraction of GPP allocated to ANPP (Keith *et al*., 1997). Notably, for water-limited *P. ponderosa* forests in Oregon, USA, ANPP was 15% of GPP (Law *et al*., 1999).

The increase in litterfall in the fertilized plots related to increased canopy mass (Table 2) rather than to increased foliar turnover rates (litterfall/canopy mass), which did not differ between treatments ($1.79\,kg\,C\,kg^{-1}\,C$ across plots; $P = 0.23$). This result is consistent with observations that leaf [N] did not vary among the

fertility treatments (Funk *et al*., unpublished results). The response of wood NPP to fertilization was substantially larger than the response of leaf NPP in both absolute and relative terms, indicating an increase in the fraction of GPP allocated to wood production. Fertilization increased wood NPP : GPP from $0.17 \pm 0.02$ (mean and SE) to $0.26 \pm 0.02$ ($P < 0.01$), but had a minor effect on leaf NPP : GPP ($0.09 \pm 0.004$ for control and $0.10 \pm 0.009$ for fertilized plots).

### *Aboveground plant respiration*

Prior to fertilization, APR represented 25% of GPP, with no component of APR differing between treatments (Table 1). Throughout the study, $L_{RM}$ represented a large portion of the forest C budget (0.49–0.72 kg C $m^{-2}$ $yr^{-1}$); $L_{RM}$ was eight times larger than $L_{RC}$ and in the post-treatment period, it was twice the total woody respiration ($W_R$; Tables 1 and 2). In the post-treatment period, APR increased from $25 \pm 1.2$% of GPP in the control plots to $29 \pm 1.7$% of GPP in the fertilized plots ($P < 0.01$; Table 2), with $L_{RC}$, $L_{RM}$ and woody respiration all increasing relative to the control plots. In a previous study of *P. radiata*, fertilization increased partitioning of the GPP to APR (from 29% to 41% for control and fertilized; Ryan *et al*., 1996). In contrast, fertilization of *E. pauciflora* forest did not alter the fraction of GPP allocated to APR (44% of GPP for

**Table 2** Post-treatment (years 2–4) differences between the control (C) and fertilized (F) plots for components of aboveground net primary production, aboveground plant respiration and total belowground carbon allocation; the terms are defined in the Materials and methods and Appendix

| Measure | Component | Treatment | Mean kg C $m^{-2}$ $yr^{-1}$ | SE | $P$ |
|---|---|---|---|---|---|
| ANPP | | C | 0.75 | 0.058 | $<0.01$ |
| | | F | 1.39 | 0.047 | |
| | $F_A$ | C | 0.37 | 0.005 | $<0.01$ |
| | | F | 0.53 | 0.019 | |
| | Wood NPP | C | 0.50 | 0.055 | $<0.01$ |
| | | F | 1.00 | 0.052 | |
| | Leaf NPP | C | 0.25 | 0.007 | $<0.01$ |
| | | F | 0.39 | 0.018 | |
| | LAI* | C | 4.73 | 0.25 | $<0.01$ |
| | | F | 6.46 | 0.49 | |
| APR | | C | 0.72 | 0.041 | $<0.01$ |
| | | F | 1.12 | 0.043 | |
| | $L_{RC}$ | C | 0.06 | 0.002 | $<0.01$ |
| | | F | 0.10 | 0.004 | |
| | $L_{RM}$ | C | 0.49 | 0.027 | $<0.01$ |
| | | F | 0.72 | 0.040 | |
| | $W_R$ | C | 0.16 | 0.010 | $<0.01$ |
| | | F | 0.31 | 0.011 | |
| TBCA | | C | 1.47 | 0.107 | 0.82 |
| | | F | 1.42 | 0.182 | |
| | $F_S$ | C | 1.55 | 0.050 | 0.04 |
| | | F | 1.64 | 0.062 | |
| | $C_S$ | C | 0.16 | 0.098 | 0.72 |
| | | F | 0.07 | 0.186 | |
| | $C_R$ | C | 0.10 | 0.010 | 0.02 |
| | | F | 0.20 | 0.011 | |
| | $C_L$ | C | 0.05 | 0.007 | 0.94 |
| | | F | 0.05 | 0.017 | |
| GPP | | C | 2.95 | 0.142 | $<0.01$ |
| | | F | 3.95 | 0.180 | |

*Units for LAI are $m^2$ $m^{-2}$.

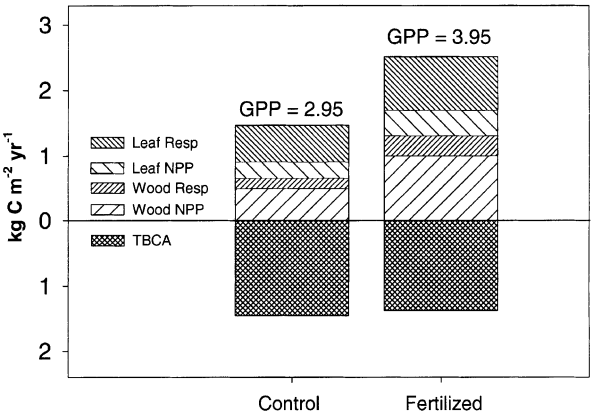


**Fig. 1** Gross primary production (mean of three years of postfertilization data) in unfertilized and adjacent fertilized stands of *E. saligna* in Pepe'ekeo, Hawai'i, and the constituent above and belowground components (see the Appendix for term definitions).

both treatments; Keith *et al*., 1997). For the *P. ponderosa* forest in Oregon, APR represented 23% of GPP (Law *et al*., 1999).

In our study, the fertilizer-related increases in the components of APR were driven by a 22% increase in canopy N content of fertilized stands, which resulted in substantially higher maintenance costs for leaves, and also by higher measured growth rates, which resulted in higher construction costs for leaves and wood (Hypothesis 3). Reflecting the high [N] and N content of leaves relative to wood, $L_{RM}$ dominated APR, but was still substantially lower than soil surface $CO_2$ efflux (Tables 1 and 2).

Our estimates of APR are associated with measurement and scaling uncertainty. Our allometrically corrected, LAI-2000-based estimates of LAI of an adjacent Continuous Fertilization stand were 15% higher than determined by direct harvest. Because the LAI measures were used to estimate canopy N content, and therefore $L_{RM}$, our estimates of $L_{RM}$ may be overestimated. We also assumed that leaf respiration rates in the Delayed Fertilization plots were similar to those measured in the Continuous Fertilization plots – because LAI did not differ between the treatments (Ryan *et al*., unpublished results), we do not expect that this assumption resulted in a significant error or any bias.

Our estimates of woody biomass, which were used to estimate $W_R$, were very precise (see wood ANPP Methods above). However, our approach may have underestimated $W_R$ if a fraction of wood respired $CO_2$ was not released through the bark of tree stems, but instead was transported to the canopy and re-fixed. A detailed analysis (Ryan *et al*., unpublished results) revealed that from 1.5% to 3% of the GPP might be derived from refixed $CO_2$, which is too small to change our conclusions.

### *Total belowground carbon allocation*

In the pretreatment period, $F_S$ was significantly higher in control than in fertilized plots (Table 1). This pretreatment difference (0.19 kg $C\,m^{-2}\,yr^{-1}$, or about 8.6% of $F_S$ in the control plots) did not persist into the post-treatment period, during which the soil surface $CO_2$ efflux ($F_S$) was 6% higher in the fertilized plots (Table 2). Soil temperatures were slightly warmer in control plots (20.3 °C vs. 19.9 °C), ruling out a temperature-based explanation for the post-treatment difference. More likely, a higher $F_S$ in fertilized plots related to a higher aboveground litterfall, which averaged 0.53 kg $C\,m^{-2}\,yr^{-1}$ for the fertilized plots compared with 0.37 kg $C\,m^{-2}\,yr^{-1}$ for the control plots (Table 2). Overall, these estimates of $F_S$ and $F_A$ are similar to other managed Eucalypt forests in Hawai'i (Binkley & Ryan, 1998), but are notably higher than estimates for unmanaged mature forests in the humid tropics (Raich & Nadelhoffer, 1989; Raich, 1998; Clark *et al*., 2001).

To estimate TBCA, $F_A$ is subtracted from $F_S$, and in the post-treatment period, TBCA was 4% lower in the fertilized plots (but not significantly so, Table 2), despite a higher soil surface $CO_2$ efflux. There were significant and sizable changes in the components of TBCA. In control plots, coarse root increment ($\Delta C_R$) accounted for $7 \pm 0.8$% of TBCA, but accounted for $16 \pm 3.1$% of TBCA in the fertilized plots. Conservation of mass dictates that the observed increase in the fraction of TBCA allocated to coarse root increment in fertilized plots (plus likely increases in coarse root respiration) combined with a slightly lower TBCA must be offset by a large decrease in the fraction of TBCA allocated to fine root litter production, fine root respiration and exudation, and C used by mycorrhizae. We do not have data on fine root production or turnover, but we observed dramatic reductions in fine root mycorrhizal colonization rates ($11 \pm 1.2$% for fertilized roots compared with $37 \pm 5.8$% for control roots; $P < 0.01$) – a reasonable (Cannell & Dewar 1994) and apparently persistent (Giardina & Ryan, 2002) response to an elevated nutrient supply in a high rainfall environment.

In line with Hypothesis 1, fertilization decreased the fraction of GPP allocated belowground: in the control plots, TBCA was twice ANPP and made up $50 \pm 1.9$% of GPP, but in fertilized stands, TBCA equaled ANPP and made up $35 \pm 3.5$% of GPP (Tables 1 and 2, Fig. 1). The increase in coarse root biomass in the fertilized plots is consistent with a reduction in the C allocated to fine roots because coarse roots primarily serve a support function, the need for which increases with stand size

and age (Albaugh *et al*., 1998; King *et al*., 1999). A greater coarse root increment in the fertilized plots does not suggest that whole-tree allometry was sensitive to the fertilization, only that trees grew faster in the fertilized plots.

Whether an increased nutrient supply decreases or increases TBCA has implications for terrestrial C storage because TBCA is the dominant source of the detrital C to mineral soil. Raich & Nadelhoffer (1989) examined mature temperate and tropical forests and found that TBCA increased exponentially with litterfall (their surrogate for ANPP). Similarly, TBCA in *Metrosideros polymorpha* forests growing on soils of varying fertility varied in concert with ANPP (Raich, 1998). In contrast, TBCA in an N-limited *P. radiata* plantation was 29% lower in stands that had been fertilized 5 years earlier with 400 kg N $ha^{-1}$ (7.1 vs. 10.4 Mg $ha^{-1}$ $yr^{-1}$; Ryan *et al*., 1996), and in phosphorus-limited *E. pauciflora* stands in Australia, the addition of 500 kg P $ha^{-1}$ reduced TBCA by 16% (2.9 vs. 3.8 Mg $ha^{-1}$ $yr^{-1}$; Keith *et al*., 1997). Taken together, these studies suggest that TBCA in unmanaged forests may increase with ANPP over broad productivity gradients, but that responses of TBCA to fertilization may be negative and overall more variable. However, longer-term data are needed across forests and site conditions to resolve these contrasting trends.

In line with Hypothesis 4, fertilization at our site decreased the fraction of GPP allocated to TBCA from 45% to 30%. In *P. radiata*, fertilization with N decreased the fraction of GPP allocated to TBCA from 41% to 22% (Ryan *et al*., 1996). In contrast, Keith *et al*. (1997) found small changes in response to the fertilization with P; TBCA decreased from 30% to 26% of GPP. Because tropical forest productivity is as commonly limited by N as by P (Fisher & Binkley, 2000), the individual roles of N and P supply as regulators of C allocation in tropical forests warrants further examination. Notably, at the nutrients poor and water-limited site in Oregon, TBCA was 61% of GPP (Law *et al*., 1999), suggesting that on marginal sites, allocation responses to fertilization and irrigation may be quite large.

### *Gross primary production*

Gross primary producation estimated for our experimental forest plots ranged from 2.95 to 3.96 kg C $m^{-2}$ $yr^{-1}$, which is comparable to GPP estimates for the control and fertilized *P. radiata* stands in Australia (2.5 and 3.4 kg C $m^{-2}$ $yr^{-1}$, respectively; Ryan *et al*., 1996). Our GPP estimates are higher than those estimated for the control and fertilized *E. pauciflora* in Australia (1.7 kg C $m^{-2}$ $yr^{-1}$ for both the treatments; Keith *et al*., 1997), and for temperate and boreal conifer forests (0.8–1.1 kg C $m^{-2}$ $yr^{-1}$; Ryan *et al*., 1997; Law *et al*., 1999). The high GPP of our experimental forest plots likely relates to a year-round growing season, moderately fertile soils, and a high LAI and light capture.

In the post-treatment period, GPP in our fertilized plots was 34% or 1.00 kg C $m^{-2}$ $yr^{-1}$ higher than in control plots (Tables 1 and 2, and Fig. 1). In line with Hypothesis 2, fertilization resulted in a 37% increase in LAI (Table 2, $P<0.01$), a 22% increase in $N_C$ (from 0.010 to 0.012 kg N $m^{-2}$; $P<0.01$), a 13% increase in canopy light interception (from 75% to 85%; $P=0.06$) and a 33% increase in the efficiency with which light was converted into the GPP (from 0.33 to 0.44 mol C $mol^{-1}$ absorbed PAR; $P=0.01$). The much larger increase in light use efficiency than light interception suggests that changes in resource use efficiency can exert a larger influence on stand productivity than an altered resource capture.

Fertilization dramatically altered the partitioning of GPP to ANPP, APR and TBCA. Because TBCA flux was similar across plots, a higher ANPP and APR in fertilized plots resulted in a very large increase in the fraction of GPP allocated aboveground (Fig. 1). Fertilization increased the ANPP : GPP from $26\pm1.6\%$ to $36\pm2.3\%$ ($P<0.01$) and APR : GPP from $25\pm1.2\%$ to $29\pm1.7\%$ ($P<0.01$), while the additions lowered the TBCA : GPP from $50\pm1.9\%$ to $35\pm3.5\%$ ($P<0.01$). As a result, TBCA : (ANPP + APR) – a whole ecosystem analog of root : shoot – was substantially higher in control than in fertilized plots ($1.01\pm0.08$ and $0.57\pm0.08$; $P<0.01$). Overall, aboveground increases were driven by a higher GPP and an increase in the fraction of GPP allocated aboveground.

Ryan *et al*. (1996) and Keith *et al*. (1997) used similar C budget approaches to estimate the response of forest GPP to fertilization, but stand level responses to fertilization in these two studies were quite different. In *P. radiata*, as with *E. saligna* in Hawai'i, fertilization with N increased GPP and shifted the partitioning of GPP aboveground (Ryan *et al*., 1996). In contrast, fertilization with P alone in the *E. pauciflora* forest did not change GPP (Keith *et al*., 1997), but did lower the fraction of GPP allocated to TBCA with commensurate increases in ANPP. These different outcomes may be explained by the nutrients limiting aboveground net primary production at these sites. Complete fertilization in our study (N, P, K plus macro and micronutrients) and N fertilization of *P. radiata* led to increases in LAI, canopy N content and GPP, while fertilization of *E. pauciflora* with P alone did not alter the canopy characteristics or photosynthesis.

In line with Hypothesis 5, the fraction of GPP allocated to dry matter production (i.e., the carbon

use efficiency or NPP/GPP, estimated here as [ANPP + 0.50 × TBCA]/GPP) was similar for the fertilized plots (0.53 ± 0.01 and 0.51 ± 0.01; $P < 0.01$). This estimate of CUE is similar to previous findings for the control and fertilized *P. radiata* stands in Australia (0.49; Ryan *et al*., 1996), but higher than the control and fertilized *E. pauciflora* stands in Australia (0.42; Keith *et al*., 1997), and the pine stands in Oregon (0.45; Law *et al*., 1999). Overall, these studies suggest that changes in the climate, species or edaphic factors may exert a greater influence on CUE than changes in nutrient supply within an individual site.

Soil surface $CO_2$ efflux ($F_S$) and APR are the two main sources of ecosystem respiration in forest, and in the pretreatment period, $F_S$ represented 68% of ecosystem respiration. This finding agrees with findings from temperate and boreal forests where $F_S$ can represent from 50% to 70% of ecosystem respiration (Law *et al*., 1999). Notably, the belowground contribution to ecosystem respiration is overestimated if accounting reflects the fact that litterfall ($F_A$) originates in the canopy. If $F_A$ is subtracted from $F_S$ and is added to APR, then in the first year of this study above and belowground sources contributed equally to ecosystem respiration. In the post-treatment period, fertilization decreased the contribution of soil surface $CO_2$ efflux to ecosystem respiration (from 68% to 59%; $P < 0.01$). Again, if $F_A$ is subtracted from $F_S$ and is added to APR, then belowground sources represented 40% of ecosystem respiration in the fertilized plots and 52% in the control plots. Overall, fertilization clearly can alter how ecosystem respiration is partitioned between above and belowground sources.

## Conclusions

The substantial increase in anthropogenic inputs of N to forests over the last century (Vitousek *et al*., 1997), and the sensitivity of forest productivity to an altered nutrient supply (Vitousek & Howarth, 1991; Jaramillo & Sanford, 1995; Fisher & Binkley, 2000) have led to predictions that forest productivity and ecosystem C storage are increasing in response to the alleviation of nutrient limitations to plant growth (Townsend *et al*., 1996; Holland, 1997). In our experimental forest plots, fertilization increased GPP, and higher LAI, canopy N content, light interception and efficiency of light use in fertilized plots all explained the increase in GPP. Fertilization increased ANPP by 85% and APR by 57%, and aboveground increases were driven by a 34% increase in GPP and a 28% increase in the fraction of GPP allocated aboveground. The slightly larger increase in ANPP compared with the increase in APR in fertilized stands resulted in a small increase in CUE (NPP/GPP). Despite the lack of a significant change in TBCA, fertilization dramatically altered the components of TBCA: coarse root increment and likely associated respiratory processes were larger in the fertilized plots while the C flux to fine roots (fine root respiration, exudation and litter turnover; mycorrhizae) was lower.

Tropical forests exert a disproportionately large influence on terrestrial C cycling, and fertilizer use in the tropics will soon exceed that in temperate regions (Matthews, 1994) with important but uncertain implications for plant productivity and ecosystem C storage (Matson *et al*., 1999). For example, the reduction in C allocated to fine roots in our fertilized plots may negatively impact soil C storage even while NPP is higher. Because C budget research in native tropical forests is challenging (Clark *et al*., 2001), we suggest that the simple forests examined here may serve as tractable model ecosystems for examining the various factors that control the primary production and patterns of C allocation in native forests. Further, experimental forests are often managed as plantation forests, which are an increasingly important component of tropical and temperate landscapes.

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## Appendix

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|---|---|
| GPP | gross primary production |
| NPP | net primary production |
| ANPP | aboveground net primary production |
| APR | aboveground plant respiration |
| TBCA | total belowground carbon allocation |
| CUE | carbon use efficiency |
| LAI | leaf area index |
| DBH | diameter at breast height |
| $F_A$ | aboveground twig, bark, fruit and leaf litter fall |
| $F_W$ | tree mortality |
| $C_W$ | carbon content of aboveground wood |
| $C_C$ | carbon content of live leaves in the canopy |
| $L_{RC}$ | leaf construction respiration |
| $L_{RM}$ | leaf maintenance respiration |
| $a$ | leaf maintenance respiration coefficient |
| $N_C$ | nitrogen content of the canopy |
| $W_R$ | wood construction respiration |
| $F_S$ | soil surface $CO_2$ efflux |
| $F_E$ | carbon that is transported off the site by leaching or erosion |
| $C_S$ | carbon content of mineral soil |
| $C_R$ | carbon content of root biomass (coarse + fine) |
| $C_L$ | carbon content of the forest floor |