

AN EXPERIMENTAL TEST OF THE CAUSES OF FOREST GROWTH DECLINE WITH STAND AGE

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Abstract. The decline in aboveground wood production after canopy closure in even-aged forest stands is a common pattern in forests, but clear evidence for the mechanism causing the decline is lacking. The problem is fundamental to forest biology, commercial forestry (the decline sets the rotation age), and to carbon storage in forests. We tested three hypotheses about mechanisms causing the decline in wood growth by quantifying the complete carbon budget of developing stands for over six years (a full rotation) in replicated plantations of *Eucalyptus saligna* near Pepeekeo, Hawaii. Our first hypothesis was that gross primary production (GPP) does not decline with stand age, and that the decline in wood growth results from a shift in partitioning from wood production to respiration (as tree biomass accumulates), total belowground carbon allocation (as a result of declining soil nutrient supply), or some combination of these or other sinks. An alternative hypothesis was that GPP declines with stand age and that the decline in aboveground wood production is proportional to the decline in GPP. A decline in GPP could be driven by reduced canopy leaf area and photosynthetic capacity resulting from increasing nutrient limitation, increased abrasion between tree canopies, lower turgor pressure to drive foliar expansion, or hydraulic limitation of water flux as tree height increases. A final hypothesis was a combination of the first two: GPP declines, but the decline in wood production is disproportionately larger because partitioning shifts as well.

We measured the entire annual carbon budget (aboveground production and respiration, total belowground carbon allocation [TBCA], and GPP) from 0.5 years after seedling planting through 6½ years (when trees were ~25 m tall). The replicated plots included two densities of trees (1111 trees/ha and 10 000 trees/ha) to vary the ratio of canopy leaf mass to wood mass in the individual trees, and three fertilization regimes (minimal, intensive, and minimal followed by intensive after three years) to assess the role of nutrition in shaping the decline in GPP and aboveground wood production.

The forest closed its canopy in 1–2 years, with peak aboveground wood production, coinciding with canopy closure, of 1.2–1.8 kg C·m⁻²·yr⁻¹. Aboveground wood production declined from 1.4 kg C·m⁻²·yr⁻¹ at age 2 to 0.60 kg C·m⁻²·yr⁻¹ at age 6. Hypothesis 1 failed: GPP declined from 5.0 kg C·m⁻²·yr⁻¹ at age 2 to 3.2 kg C·m⁻²·yr⁻¹ at age 6. Aboveground woody respiration declined from 0.66 kg C·m⁻²·yr⁻¹ at age 2 to 0.22 kg C·m⁻²·yr⁻¹ at age 6 and TBCA declined from 1.9 kg C·m⁻²·yr⁻¹ at age 2 to 1.4 kg C·m⁻²·yr⁻¹ at age 6. Our data supported hypothesis 3: the decline in aboveground wood production (42% of peak) was proportionally greater than the decline in canopy photosynthesis (64% of peak). The fraction of GPP partitioned to belowground allocation and foliar respiration increased with stand age and contributed to the decline in aboveground wood production. The decline in GPP was not caused by nutrient limitation, a decline in leaf area or in photosynthetic capacity, or (from a related study on the same site) by hydraulic limitation. Nutrition did interact with the decline in GPP and aboveground wood production, because treatments with high nutrient availability declined more slowly than did our control treatment, which was fertilized only during stand establishment.

Key words: aboveground productivity; age-related decline; belowground allocation; carbon allocation; *Eucalyptus*; foliar respiration; forest production; leaf area; modeling; nutrition; soil respiration; wood respiration.

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INTRODUCTION

But I have not yet taken into the account the fact that, though the thickness of the layer is less, its superficies, or extent, is greater, as the diameter of the tree increases. Let us compare the three portions of wood. If the diameter at the end of the first fifty years is four, the second fifty, six, and the third fifty, seven, then the amount of wood added each term will be (to omit very minute fractions) twelve and a half, fifteen and a half, and ten respectively. So that, though in the second fifty the rings are twice as near together, yet considerably more wood is produced than in the first, but in the third fifty the tree is evidently enfeebled, and it probably is not profitable (so far as bulk is concerned) to let it grow any more.

—Henry David Thoreau, 1 November 1860

One of the common patterns in the growth of forests is an increase in aboveground wood production early in stand development, followed by a peak near the time when maximum leaf area is achieved (canopy closure). After this peak in production and leaf area, the rate of increase in stand biomass declines by 20–80% over a period of years to centuries (reviewed by Gower et al. 1996, Ryan et al. 1997a). Empirical evidence for the peak and decline of forest productivity dates back to chronosequence studies of forest stands and forestry “growth and yield” studies (reviewed by Assmann 1970, Ryan et al. 1997a), and includes several “ecological” studies in which other components, such as leaf area and leaf production, were also measured (Ryan et al. 1997a). The decline in annual production of wood after canopy closure is quite common (we have not identified any published counter-examples), but because older forestry case studies and chronosequence studies did not manipulate resource availability, we cannot conclude that the decline is inevitable or always occurs.

In the earliest exploration of a mechanism, this decline in wood growth was attributed primarily to an unexplained decline in carbon assimilation by the canopy (gross primary production, GPP; all symbols are defined in the Appendix), and secondarily to a slight increase in respiration by woody tissues (Möller et al. 1954). After the mid-1950s, the expectation of increasing rates of autotrophic respiration began to receive stronger support in the literature. Odum (1956) postulated that community-level production reaches a steady state with succession, either increasing from low rates during primary succession, or declining from high rates early in secondary succession. In both cases, Odum (1956) postulated that plant respiration increases with time until the rate of biomass accumulation in a system approaches zero. Yoda et al. (1965) advanced the idea that the ratio of net primary production (NPP) to GPP should differ in stands of different ages because

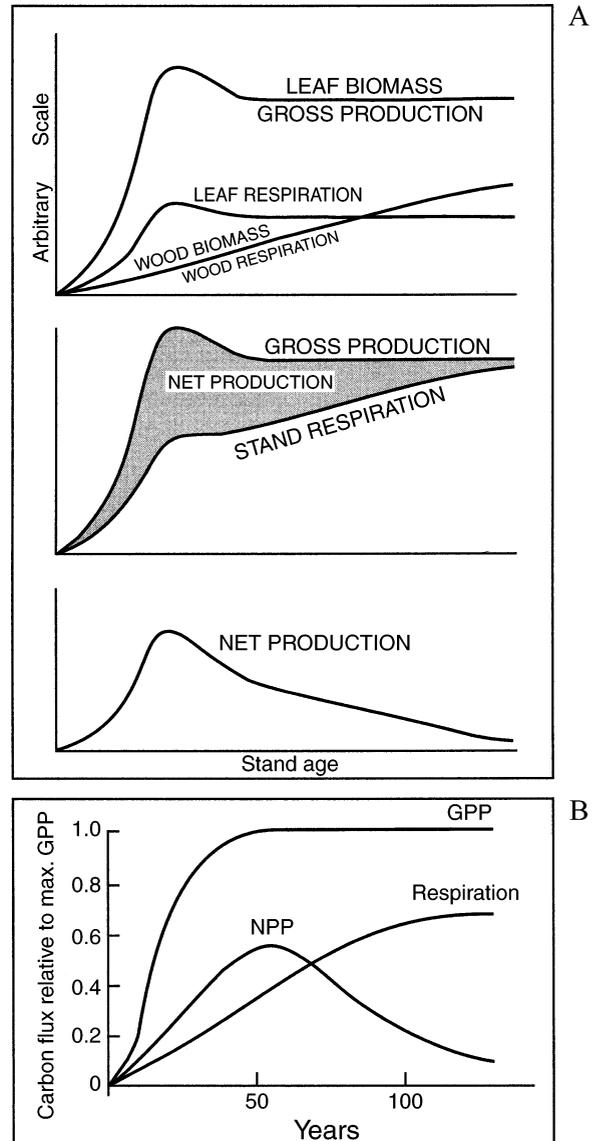


FIG. 1. (A) Classic expectation of increasing net production in forests with age, followed by decline. The transient peak in gross production was attributed to an expected decline in leaf area (from Kira and Shidei 1967). (B) A reinterpretation of the classic pattern (modified from Barnes et al. 1998).

leaf biomass stays constant while woody biomass and woody respiration increase. Kira and Shidei (1967) used measurements of woody respiration in temperate and tropical forests (Yoda et al. 1965, Yoda 1967), to develop the hypothesis that wood production declines primarily because of increasing respiration losses as forests accumulate biomass (Fig. 1A). A secondary cause was hypothesized to be declining GPP as leaf biomass declined to steady state from its maximum level at canopy closure (Fig. 1A). At the same time, Whittaker and Woodwell (1967) proposed a similar ex-

planation with an alternative mechanism: woody respiration was best modeled by surface area, and woody surface area : leaf area increased with stand development.

The motivation for the Kira and Shidei (1967) hypothesis in Fig. 1A is unclear. Respiration rates reported by Yoda (1965) and Yoda et al. (1967), measured with potassium hydroxide absorption of cut stems, are very similar to in situ measurements of woody respiration from CO₂ efflux outside bark. For example, Yoda's rates for temperate species (0.06–0.03 μmol C·kg C⁻¹·s⁻¹ for stems averaging 5–10 cm in diameter) were similar to those of other temperate species (Ryan et al. 1994, 1997b). The only chronosequence data cited by Yoda et al. (1965), Kira and Shidei (1967), and Whittaker and Woodwell (1967) were those of Möller et al. (1954), who measured woody respiration and showed that it was only a very minor contributor to NPP decline. Kira and Shidei (1967) and Yoda et al. (1965) may have been impressed by the dramatic change in wood : leaf biomass with stand development, and perhaps their scaling method may have overestimated the contribution of woody respiration, as they estimated a ratio of woody respiration to GPP of 26% (Kira et al. 1967), compared with ratios <10% found in subalpine and boreal forests (Ryan and Waring 1992, Ryan et al. 1997b).

Regardless of the fact that it contradicted the only measurements of respiration and production for a chronosequence available at the time, Kira and Shidei's (1967) general model of stable gross primary production and increasing respiration has been cited in a wide range of journal articles and textbooks as the mechanism for age-related decline (Odum 1971, Kimmins 1987, Brewer 1988, Long and Smith 1992). The idea that respiration should increase with stand age has been so well accepted that some authors no longer cite the original sources for the model, and consider that respiration is the sole explanation of decreasing stem growth, with no contribution from declining GPP (e.g., Waring and Schlesinger 1985, Barnes et al. 1998; see Fig. 1B).

This well-accepted model of growth decline as a result of increasing respiration has never been tested by following the carbon budget of individual stands over time. Stand growth and woody respiration have been estimated in just two chronosequence studies (with unreplicated stands), and neither supported the model. Möller et al. (1954) reported that the decline in wood increment in forests of European beech was related primarily to a decline in GPP with age; tree respiration remained a constant proportion of GPP as the wood increment declined. Ryan and Waring (1992) found that declining growth in an older stand of lodgepole pine led to lower respiration associated with stem growth, which largely offset modest increases in the maintenance respiration of the accumulating wood biomass. Indirect evidence against the respiration model has

come from growth analysis of spacing trials, where trees at wider spacings had higher wood : leaf ratios (and potentially more woody respiration per unit photosynthetic capacity), yet continued to grow and had higher production per unit leaf area than trees at closer spacings with lower wood : leaf ratios (Fownes and Harrington 1990, Harrington and Fownes 1995).

If respiration does not increase enough to explain the decline in wood growth in older stands, what other mechanisms might be responsible? Gower et al. (1996) and Ryan et al. (1997a) reviewed two other possibilities: (1) declining nutrition with stand development as nutrients are sequestered in biomass, resulting in increased allocation belowground; and (2) declining photosynthesis.

Decreasing nutrient supply has been supported by some previous studies and refuted in others (Ryan et al. 1997a). Model analyses predict that nutrient availability should decline with stand development as nutrients are immobilized in woody biomass (Murty et al. 1996, Murty and McMurtrie 2000). However, the lodgepole pine (*Pinus contorta*) ecosystem used for the simulations did not show decreased nutrient availability with stand age (Olsson et al. 1997). The literature suggests that no consistent pattern of nutrient availability with stand development exists (Ryan et al. 1997a).

The hypothesis that increasing belowground production offsets aboveground wood production is supported by an unreplicated comparison of a young and an old stand of Pacific silver fir, *Abies amabilis* (Grier et al. 1981). In this study, root production and relative belowground allocation were higher in the older stand. It was also supported by a model analysis incorporating fine-root biomass data from Scots pine (*Pinus sylvestris*) chronosequences (Magnani et al. 2000). It was not supported by an unreplicated pair of slash pine (*Pinus elliotii*) stands (Gholz and Fisher 1982, Gholz et al. 1986), where belowground production was higher in the older stand, but represented a lower proportion of NPP. Nor was it supported in a replicated chronosequence in lodgepole pine (Smith and Resh 1999), where both NPP and belowground production declined in the oldest stands.

Declining photosynthesis was first suggested by Möller et al. (1954), who estimated GPP as the sum of NPP and respiration. Möller et al. (1954) offered that a "more and more unfavorable water balance" was the mechanism causing the decline. Ryan and Waring (1992) also suggested reduced photosynthesis, after photosynthesis in an older forest modeled from climate and leaf area was much greater than measurements. Five potential mechanisms to explain a decline in GPP with stand development are: (1) hydraulic limitation (Yoder et al. 1994, Ryan and Yoder 1997), where protection of the water conducting system through maintenance of a constant minimum leaf water potential forces lower stomatal conductance; (2) lower leaf area caused by abrasion (Putz et al. 1984, Marchand et al.

1986, Long and Smith 1992, Rudnicki et al. 2003); (3) genetic programming (Greenwood 1989, Haffner et al. 1991); (4) reduced leaf area or photosynthetic capacity caused by declining nutrient availability; or (5) reduced foliar growth and perhaps photosynthesis because of reduced turgor pressure with tree height (Woodruff et al. 2004).

Generally, these explanations for declining GPP have been observed in individual trees, and are not explicitly linked with a decline in wood production. However, the evidence for any of these mechanisms is sparse. Hydraulic limitation reduces stomatal conductance or photosynthesis in some tall trees (Yoder et al. 1994, Hubbard et al. 1999), but not all (Phillips et al. 2001, Barnard and Ryan 2003). Stem hydraulic conductance declined as NPP declined in Scots pine (Mencuccini and Grace 1996*a, b*), but stand-level stomatal conductance or photosynthesis were not measured. Loss of leaf area is common with stand development after canopy closure, but productivity losses are generally greater than can be attributed to leaf area decline (Ryan et al. 1997*a*). The growth of scions from different-aged trees grafted to young rootstock varied with scion age, suggesting a link between tree age and physiology (Greenwood 1989); however, evidence of differences in photosynthetic capacity with tree size is sparse.

Fast-growing tropical plantations offer an opportunity to test the mechanisms that control the trend in stand growth over time because measurements can be made over the course of stand development, and nutrient availability and stand structure are easily manipulated. These plantations accumulate wood at rates of 0.5–2.0 kg·m⁻²·yr⁻¹, and commonly peak in wood growth between 3 and 5 years, when stem biomass is 3–5 kg/m² (1.5–2.5 kg C/m²; Lugo et al. 1988, Fownes and Harrington 1990, Binkley et al. 1997).

Our objective was to test the hypotheses that might explain the decline in stand growth in a longitudinal study of an experimental forest of fast-growing *Eucalyptus saligna*:

- 1) GPP remains high after maximum leaf area is reached, but aboveground wood growth declines as a result of a shift in partitioning from wood production (1a) to respiration as woody biomass accumulates (Kira and Shidei 1967, Whittaker and Woodwell 1967), (1b) to belowground production (Grier et al. 1981, Gower et al. 1996) or (1c) to some combination of these or other sinks, such as higher foliage turnover.
- 2) GPP declines with stand age as a result of physiological or structural changes (Möller et al. 1954, Ryan and Waring 1992), and the decline in aboveground wood production is proportional to the decline in GPP. A decline in GPP could be driven by reduced canopy leaf area and photosynthetic capacity resulting from increasing nutrient limitation (Gower et al. 1996), reduced leaf area from

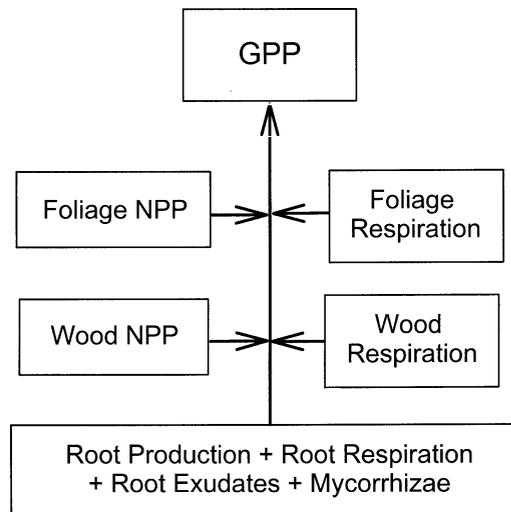


FIG. 2. Estimating gross primary production as the sum of the components of aboveground production and respiration and total belowground carbon allocation.

increased abrasion between tree canopies (Putz et al. 1984, Marchand et al. 1986, Long and Smith 1992, Rudnicki et al. 2003), reduced photosynthetic capacity from ontogenetic changes in gene expression (Greenwood 1989, Haffner et al. 1991), reduced foliar expansion from lower turgor pressure (Woodruff et al. 2004), or reduced photosynthetic performance from hydraulic limitation of water flux as tree height increases (Yoder et al. 1994, Ryan and Yoder 1997).

- 3) GPP declines with stand age (as a result of one or more of the processes listed in hypothesis 2), but the decline in wood production is disproportionately larger because partitioning also shifts.

In framing our study, we considered all components of the basic production equation:

$$\text{NPP} = \text{GPP} - R_A \quad (1)$$

where R_A is autotrophic respiration. Because NPP for aboveground wood (ANPP_w) is 10–30% of GPP, we expanded Eq. 1 as follows:

$$\text{ANPP}_w = \text{GPP} - \text{NPP}_F - R_w - R_F - \text{TBCA} \quad (2)$$

where NPP_F is foliage NPP, R_w is aboveground woody respiration, R_F is foliar dark respiration, and TBCA is total belowground carbon allocation (the sum of root production and respiration and carbon flow to mycorrhizae and root exudates).

We measured all of the components of Eq. 2 for replicated developing stands and estimated GPP by summing the other five components (Fig. 2). We tested these hypotheses by determining whether GPP remained constant after canopy closure, and whether R_w , TBCA, or the fraction of GPP used by these components increased over time. We also examined the in-

PLATE 1. Aerial view of the 30×30 m plots at 18 months. Closed-canopy plots were planted at 1×1 m spacing; more open plots were planted at 3×3 m spacing. A gully/buffer strip winds through the middle of the plantation. Photo credit: R. S. Senock.



teraction of nutrition with these hypotheses by maintaining high nutrient availability and determining whether GPP and ANPP_w declined, and by restoring high nutrient availability after the decline began and determining whether GPP and ANPP_w recovered to peak levels. Finally, we examined the causes of a potential decline in GPP by changing nutrition and by measuring leaf area, photosynthetic capacity, and any hydraulic limitation (in a related study; Barnard and Ryan 2003).

METHODS

Site description

The study site ($19^{\circ}50'28.1''$ N, $155^{\circ}7'28.3''$ W) is a 4-ha experimental forest of *Eucalyptus saligna*, 13 km northeast of downtown Hilo, Hawaii, at 350 m elevation. Mean annual temperature is 21°C , with an average annual rainfall of ~ 4000 mm (Binkley et al. 1992). Rainfall and photosynthetically active radiation are distributed uniformly throughout the year, but the winter months tend to be wetter and cloudier, and have shorter daylight periods. For the years 1995–1999 (some data were missing for 2000), rainfall averaged 3460 mm/yr, temperature averaged 21.2°C , and photosynthetically active radiation averaged $10\,700$ mol photons $\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. There was no discernible trend among years for these three variables.

The slope is modest ($<5\%$) and the soils are >2 m deep, acidic (pH 5–6 in water), thixotropic, isothermic Typic Hydruclands in the Kaiwiki series (Binkley and Resh 1999). Sugarcane was cropped on the site for >80 years, with harvesting every two years, followed by planting a new crop or letting a new crop develop from stem sprouts. From about 1920 onward, routine management of the soil included applications every two years of 85 kg N/ha, 75 kg P/ha, and 110 kg K/ha. After 1955, 700 kg/ha of lime was also added every two years. In 1993, the last sugarcane crop was harvested about one year before the planting of *Eucalyptus* seedlings. The site was fallow for about nine months,

and then, in February of 1994, was plowed to turn under the developing vegetation (mostly C_4 grasses). Three months later, new regrowth was killed with a broadcast application of glyphosate herbicide (Roundup, Monsanto Company Agricultural Products, St. Louis, Missouri, USA). *Eucalyptus saligna* seedlings were grown for six months in a greenhouse from a single, open-pollinated seed stock. Prior to planting in May 1994, seedlings were selected for uniform size (~ 0.20 – 0.25 m in height).

Experimental design

The plantation contains eighteen 30×30 m plots (see Plate 1). The experimental design had two levels of tree spacing (1×1 m or 3×3 m) equal to 10000 trees/ha (“high density,” HD) or 1111 trees/ha (“low density,” LD) at planting, and three levels of fertilization (“control,” C; “high fertilization,” HF; or “restore fertility,” RF), organized in three randomized blocks. The two spacings were designed to vary the ratio of leaf area : woody tissues, and to vary the timing of canopy closure. The three fertilization regimes were designed to test the role of changes in nutrient limitation over time. All plots received N + P + K + S + Ca + Mg in planting holes (at a 1×1 m interval, including the treatment with trees planted at 3×3 m intervals), followed by a broadcast application of the same at 7 months. Total fertilizer application received during these two applications (representing current rates for operational plantations) was: 310 kg N/ha as urea, 130 kg P/ha and 125 kg Ca/ha as triple-superphosphate, 260 kg K/ha as potassium chloride, and 100 kg/ha of Granusol 2GB5 micronutrient fertilizer (5% Mn, 5% Zn, 5% Mg, 5% Fe, 1.5% Cu, and 0.5% B; API Technologies, Kingdom of Prussia, Pennsylvania, USA). The high-fertilization treatment was designed to prevent nutrient limitations on *Eucalyptus* growth; from age 7 months to the end of this study, HF plots received quarterly applications of 65 kg N/ha, 31 kg P/ha, and 46 kg K/ha, and annual additions of 125 kg

Ca/ha, 58 kg S/ha, 23 kg Mg/ha, and 100 kg micro-nutrients/ha (Binkley and Resh 1999). The restore-fertility treatment was designed to eliminate nutrient limitation after growth peaked and began to decline, and received the same fertilizer application as control plots until April of 1998 (age 4 years), after which the application rates matched the high-fertilization additions. All non-*Eucalyptus* vegetation was controlled by application of Roundup. All measurements were made inside a 10 × 10 m interior plot in the HD treatments (100 trees) and inside a 15 × 15 m interior plot for the LD treatments (25 trees).

Meteorological data

Meteorological data were collected from a clearing ~300 m upwind of the site. Variables measured included: photosynthetically active radiation (LI-COR LI190SB, LI-COR, Lincoln Nebraska, USA), precipitation (Campbell Scientific TE525, Campbell Scientific, Logan, Utah, USA), air temperature and relative humidity (Campbell Scientific CS500), and soil temperature at 10 cm (copper-constantan thermocouple). Measurements were taken every 10 seconds, and summed totals or averages were stored every 15 minutes.

Ecophysiological measurements

Photosynthetic capacity.—We periodically assessed photosynthetic capacity to determine whether the spacing and fertility treatments and stand age altered the biochemical potential of foliage to fix carbon. We used two methods to estimate photosynthetic capacity: measuring maximum assimilation (A_{\max}) rates and estimating maximum carboxylation velocity ($V_{c_{\max}}$). A_{\max} or $V_{c_{\max}}$ were measured on 1–2 fully expanded leaves at four positions within the canopy: 4–5 leaves in from the terminal bud of the upper, middle, and lower crown thirds, and 4–5 leaves out from the point of shoot attachment in the lower third of the crown. Scaffolding towers in one C and HF plot in each planting density were used to access foliage. Measurements were made with a PPSystems CIRAS-1 (PPSystems, Haverhill, Massachusetts, USA) in open-system mode. For A_{\max} , CO_2 efflux was measured at $\text{CO}_2 = 360 \mu\text{mol/mol}$, high humidity ($D < 0.5 \text{ kPa}$), and saturating light (photosynthetically active radiation $> 1200 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, generated by an artificial light source). For $V_{c_{\max}}$, measurements were made under the same light and humidity conditions, but with intercellular CO_2 concentration varying from 0 to $250 \mu\text{mol/mol}$. Measurements were made on overcast days in January, May, September, and December of 1995, October 1996, February 1998, and September of 1999. Sample foliage was harvested, measured for leaf area with a LI-COR 3000A/3050A leaf area meter, dried at 70°C for 48h, and analyzed for N content with a LECO CHN analyzer (LECO, St. Joseph, Michigan, USA).

$V_{c_{\max}}$ was estimated by a nonlinear regression fit to the Farquhar et al. (1980) photosynthesis equation (the initial slope of the photosynthesis–intercellular CO_2 response curve). Concurrent measurements of A_{\max} and $V_{c_{\max}}$ in September and December 1995 showed that A_{\max} and $V_{c_{\max}}$ were highly and linearly related ($r^2 = 0.85$, $P < 0.001$) and that the relationship between A_{\max} and $V_{c_{\max}}$ did not differ with canopy position, tree density, or fertility. Therefore, to examine trends in photosynthetic capacity through time, we estimated A_{\max} from $V_{c_{\max}}$ when A_{\max} was not directly measured.

Foliage respiration rates.— CO_2 efflux was measured between 2100 and 0200 hours on 1–2 fully expanded leaves at the same four positions within the canopy previously described under *Photosynthetic capacity*. We also measured CO_2 efflux on expanding foliage in the upper one third of the crown. CO_2 efflux was measured at ambient CO_2 concentration with plexiglass mixing chambers attached to a PPSystems CIRAS-1 in open-system mode. Chambers were fit with neoprene seals to prevent air leaks, and the air seal was checked continuously during each measurement with a Cole-Parmer A32460-42 in-line flow meter (Cole-Parmer Instrument Company, Vernon Hills, Illinois, USA). Measurements were made in January, May, September, and December of 1995, October of 1996, and February of 1998. Sample foliage was harvested, measured for leaf area with a LI-COR LI-3000A/3050A leaf area meter, dried at 70°C for 48h, and analyzed for N content with a LECO CHN analyzer. Respiration rates were measured at an average temperature of 20.7°C (range of 15.4 – 23.6°C). We corrected respiration rates to 20°C using an assumed Q_{10} of 2.

Foliar nutrients.—We periodically measured foliar nutrient concentrations to assist in estimating foliar dark respiration for the canopy, to assess the effectiveness of our nutrient treatments, and as an index of photosynthetic capacity. We estimated nutrient concentrations for the canopy by subsampling a well-mixed pile of all of the foliage taken from the 1–2 trees per plot harvested for the allometric equations. These samples were taken in December 1994 and in August of 1995, 1996, and 1998. Foliage samples were analyzed for C, H, and N using a LECO CHN analyzer (LECO, St. Joseph, Michigan, USA), and subsamples (other than the 1998 samples) were digested (in a H_2SO_4 and H_2O_2 solution) and analyzed by inductively coupled plasma spectroscopy for K, Ca, Mg, and Al by the Colorado State University Soil Testing Laboratory. This lab also analyzed the digests for P concentration using an automated colorimetric method. To assess whether these whole-canopy samples were representative of the canopies at other times, we sampled foliage every 3–6 months at five diagnostic positions in one plot per treatment from scaffold towers: the four positions described under *Photosynthetic capacity* and expanding foliage in the top third of the canopy. These samples generally coincided with measurements of

photosynthetic capacity and foliar respiration, but nutrient samples were sometimes collected without measuring physiology. These “diagnostic” samples were analyzed for C, H, and N using a LECO CHN analyzer.

Wood respiration rates.—We measured wood respiration as CO₂ efflux through bark using plexiglass mixing chambers fit with neoprene seals attached to a PPSystems CIRAS-1 in open-system mode. Measurements were made 4–5 times per year in 1996 and 1997, and in March 1999, July 2000, and May 2001. From 1996 to 1999, measurements were made in one C and HF plot in each planting density (four plots total). We measured CO₂ efflux on 10 trees/plot at 1.37 m and on 4 trees/plot at 3 m and 6 m above the ground. At each height on each tree, CO₂ efflux was measured at two locations (offset by 90°). In 2000, we measured 5–10 trees/plot at 1.37 m on all 18 plots and at 10 m and 20 m on 18 trees in six plots. In 2001, we measured 6 trees/plot at 1.37 m on all 18 plots. To estimate growth occurring during the measurement period, we measured diameter, *D*, to 0.05 cm 30–50 days before and after the respiration measurement. We expressed respiration measurements on the basis of biomass by scaling respiration to a cylinder with height equal to chamber height and multiplying that volume by the specific gravity of wood from trees harvested for the tree allometric equation, which we will describe. Wood growth for the same cylinder was estimated from the diameter change and specific gravity.

Foliage height profiles.—We measured the vertical distribution of leaf area at stand ages of 17, 29, 41, and 53 months to assess how canopy structure changed with stand development. The relative distribution of leaf area was estimated using the zoom-lens technique of MacArthur and Horn (1969) and Aber (1979), with a viewfinder matrix of 20 points. Measurements of canopy profiles were made at 15 sampling points along a transect in each plot of one randomly selected block. Absolute leaf area profiles were calculated from the relative profiles and the total leaf area during that period from the LAI-2000 measurements, corrected with Eq. 4, which follows.

C pool and flux estimation

Carbon budget overview.—We estimated all of the major components of an annual carbon budget, and estimated gross primary production (GPP) as the sum of five components (illustrated in Fig. 2; see Möller et al. 1954, Ryan 1991, Ryan et al. 1996). These components were: ANPP_w, aboveground net primary production in wood (includes bark and branches); NPP_F, aboveground net primary production in foliage; *R*_w, aboveground wood respiration; *R*_F, aboveground foliage dark respiration; and TBCA, total belowground carbon allocation (includes coarse and fine root production and respiration, root exudates, and plant carbon used by mycorrhizae). Our estimate of GPP excludes the contribution to foliage dark respiration during the

light period. This definition of GPP approximates the carbon flux that would be measured from cuvette measurements on every leaf in the canopy from sunrise to sunset. We used this definition of GPP because the use of excess energy from light-harvesting reactions makes foliage dark respiration in the light difficult to estimate correctly (Kirschbaum and Farquhar 1984). This estimate of GPP is used by some physiologically based models of forest carbon cycling (e.g., Forest and Biome BGG, Running and Coughlan 1988), and is sometimes called net photosynthesis (Ryan et al. 1997b). Practically, including or excluding foliage dark respiration in the light only alters the magnitude of GPP, not the relationship among treatments.

We estimated ANPP_w from the annual increment in plot-level standing biomass (estimated from allometric equations and annual measurements of tree diameter) plus twig litterfall plus annual mortality. NPP_F was estimated using annual foliage litterfall, corrected for any change in foliage standing stocks. *R*_F and *R*_w were estimated from periodic measurements of CO₂ efflux and biomass (*R*_w) or foliage biomass and foliar N concentration (*R*_F). TBCA was estimated using a carbon balance approach (Giardina and Ryan 2002). See Table 1 for a description of the equations used for the carbon balance.

In 1998, six plots were established for testing the hydraulic limitation hypothesis (Barnard and Ryan 2003). All received the HF fertility regime, and three each had either the low or high stem density treatments. We report ANPP_w and NPP_F for these plots in year 6 to assess whether differences in environment over time could have caused the decline in ANPP_w.

Aboveground woody biomass and woody net primary production.—Woody biomass (in bark, boles, and branches) was estimated annually for each plot using an allometric equation between diameter measurements at 1.37 m (in centimeters) and woody biomass (in kilograms) developed for this study:

$$\text{woody biomass} = 0.0662(\text{diameter})^{2.5}. \quad (3)$$

Here, SEE = 1.16 kg, *r*² = 0.99, *P* < 0.001, *n* = 57. Trees used to develop Eq. 3 were randomly sampled from the 10-m buffer area of each plot, periodically throughout the study. Diameters were measured every 2–3 months for trees in the measurement area of each plot, and biomass for the plot was calculated as the sum of the biomass for each tree from Eq. 3. Allometry did not differ among treatments or over time. ANPP_w was estimated as the annual biomass increment, plus twig and bark litterfall and plus mortality during the year (mortality was <1% of ANPP_w).

Leaf area, leaf biomass, and foliage net primary production.—Leaf area index (LAI) was measured monthly using a LAI-2000 canopy analyzer (LI-COR, Lincoln, Nebraska, USA.) at 18 locations in each plot. We measured tree leaf area and diameters in January 1996, to correct LAI-2000 estimates for leaf overlap and

TABLE 1. Equations used in estimating the carbon fluxes.

Component (kg C·m ⁻² ·yr ⁻¹)	Derivation	Measurement frequency	Equation
ANPP _w	dbh	2–3 mo	12 mo/yr × (Biomass _{t2} – Biomass _{t1} + Mortality)/(no. months); biomass = 0.48 kg C/kg × 0.0662 D ^{2.5} (D is diameter)
NPP _F	litterfall, leaf biomass	monthly for litterfall; 2–3 mo for LAI-2000	{Litterfall × 1.14 (decomposition correction) + (LAI-2000 × 1.54 + 0.93) × kg/m ² (specific leaf area, treatment-specific)} × 0.5 kg C/kg
R _w	wood biomass, respiration/biomass	2–3 mo for biomass, 3–12 mo for respiration	Biomass × Respiration/biomass (by treatment and year) × 0.85 (temperature correction)
R _F	canopy biomass, canopy N, respiration/N	2–3 mo for biomass, 1–2 yr for N, 1–12 mo for respiration	Biomass C × kg N/kg C × kg C respiration/kg N (different for C and HF or RF treatments) × 0.93 (temperature correction)
TBCA	soil respiration, litterfall, dbh, soil C, litter C	monthly for soil respiration and litterfall, 2–3 mo for dbh, 3 yr for soil C, 1 yr for litter C	TBCA = 12 mo/yr × (soil respiration – litterfall) + 0.22 × (biomass _{t2} – biomass _{t1}) × 0.5 kg C/kg + (soil C _{t2} – soil C _{t1})/years + (litter C _{t2} – litter C _{t1})/years

Note: See Appendix for definition of components.

clumping. Total mass (wet mass) of leaves + attached branches <1 cm was measured for two randomly selected trees harvested from the buffer area in each of the 18 experimental plots ($n = 36$ trees). In the laboratory, leaf + branch subsamples were stripped of leaves, leaves and branches were separately weighed, and leaf area of the stripped leaves was measured with a LI-COR 3100 Leaf Area Meter (LI-COR, Lincoln, Nebraska, USA). These measurements were used to estimate leaf area per tree from measured leaf + branch mass (wet). A relationship between tree leaf area and diameter for the entire experiment was used to estimate leaf area index (LAI) of the measurement area in each of the 18 plots at the time of harvest. LAI estimates from the LAI-2000 at the time of harvest were corrected to the allometrically determined LAI for each plot:

$$\text{LAI} = \text{LAI-2000} \times 1.54 + 0.93. \quad (4)$$

This relationship is similar to previous correction factors developed for eucalypts (Cherry et al. 1998). In August 1999, we harvested all surviving trees ($n = 23$) in a LD-HF plot, removed and weighed every leaf, and measured leaf area for a subsample (Binkley et al. 2002). For this plot, measured LAI was within 15% of the LAI-2000 value estimated using Eq. 4. Leaf biomass was estimated from LAI using mass per leaf area for each treatment estimated from the trees harvested throughout the experiment. Mass per leaf area averaged 0.0744 kg/m² for the treatments with 1 × 1 m spacing, and 0.104 kg/m² for the treatments with 3 × 3 m spacing.

Aboveground litter was collected monthly from eight 0.186-m² traps per plot that were placed on the forest floor. Litterfall was composited by plot, oven-dried at 70°C to constant mass, and separated into leaves, branches, and bark for weighing. We assumed that litter was 50% carbon, based on the mean carbon content of

fresh leaves (50.6%) and wood (48.2%). We corrected for litter decomposition between collections, using a decay rate for senescent leaves measured on site (0.0095/day) and assumed that litterfall was uniformly distributed throughout the month (leaf litterfall = measured leaf litterfall × 1.14; Giardina and Ryan [2002]). Decomposition of branch and bark litter between collections was assumed to be zero. NPP_F was estimated as annual leaf litterfall, plus any annual difference in foliage biomass. Any underestimation of NPP_F from herbivory or leaf retention in the canopy was probably very small because no leaf herbivory was observed, and senesced leaves were rarely retained in the canopy.

Aboveground plant respiration.—We estimated the maintenance component of R_F using periodic measurements of CO₂ efflux from foliage at night to develop a relationship between R_F and foliar N, and extrapolated rates to the plot using LAI and foliar N concentration. We assumed that the growth respiration component of R_F was 25% of the carbon content of NPP_F (Penning de Vries 1975, Sprugel et al. 1995). Because the relationship between CO₂ efflux and foliar N differed by fertility treatment, but not by tree density or year (see *Results*), we estimated common foliar dark respiration maintenance coefficients separately by treatment: control (5.16 mmol C (mol foliar N)⁻¹ s⁻¹) and high fertility (4.21 mmol C (mol foliar N)⁻¹ s⁻¹); both at 20°C. For the restore-fertility treatment, we assumed the control coefficient applied during ages 1–3 years, and that the high-fertility coefficient applied after the HF fertility regime was initiated at age 4 years.

Nitrogen content of the canopy was estimated from monthly estimates of LAI and direct measures of specific leaf area and leaf N concentration from the trees harvested in 1994, 1995, 1996, and 1998. We assumed that canopy N content and specific leaf area for 1997 equaled those measurements in 1996, and that canopy

N content and specific leaf area for 1999 and 2000 equaled those in 1998. The maintenance component of R_F was then estimated as the product of the maintenance coefficient and canopy N, scaled to a month and summed for the year. We adjusted R_F for temperature (average annual night temperature was 19.0°C) using an assumed Q_{10} of 2. Our estimates R_F and GPP do not include dark foliar respiration in the daytime.

We estimated R_W as average annual aboveground woody biomass \times rate per biomass (which varies by treatment and year). We used these simple, biomass-based rates for each treatment for extrapolating from the chamber to the stand, because growth and maintenance coefficients generally did not vary with height on tree, fertility, or density treatments, but did vary with time. We estimated rates for age 4 by linear interpolation. We adjusted R_W for temperature (average annual temperature was 21°C) using an assumed Q_{10} of 2.

Total belowground carbon allocation.—TBCA was estimated using a carbon balance approach (Giardina and Ryan 2002) in which

$$\text{TBCA} = F_S - F_A + \Delta(C_S + C_L + C_R)/\Delta t \quad (5)$$

where F_S is soil surface CO_2 efflux, F_A is aboveground litterfall, and C_S , C_L , and C_R are carbon stored in soil, roots, and litter, respectively. F_S and mineral soil temperature at 0.10 m depth were measured monthly at 15 points on a transect running diagonally through the interior measurement area of each plot using a PPSys-tems CIRAS-1 with a standard, unmodified PPSys-tems soil respiration chamber (no screen in the chamber). In a previous study, we directly compared our measurements of F_S with measurements taken with a LI-COR soil chamber operating with the LI-COR 6400, (as described by Janssens et al. 2000), and found no difference between systems (Giardina and Ryan 2002). Because F_S did not vary with time of day during two diurnal measurement periods, and diurnal soil temperatures in our closed-canopy forests varied by $<2^\circ\text{C}$, we did not correct for temperature effects and simply scaled our average rate for the plot to a monthly rate. Methods for estimating F_A have been described.

C_L was estimated from eight 0.186-m² subsamples per plot in January from 1996 to 2000. There was no litter layer in 1995; the litter layer was not measured in January 2001 (for change over the year 2000), but had changed little after 1998, suggesting that mass had stabilized. In January 2002, the litter layer averaged 0.32 kg C/m² (Binkley et al. 2004), compared to an average of 0.30 kg C/m² in January 2000. Samples were composited by plot, dried at 70°C to constant mass, separated into leaf and twig, branch, and bark components, and weighed. We used carbon content of 51% (the average of measurements in January 1997 and January 2002) for litter layer material. C_R was estimated from aboveground biomass (measured annually) using a regression between coarse-root biomass (>2 mm) and

aboveground biomass (Giardina and Ryan 2002). Live fine-root biomass (<2 mm diameter) was measured using three cores per plot in October 1995 and January 1996 and 15 cores per plot in August 1999 (Giardina and Ryan 2002). Because fine-root biomass changed by <0.02 kg C·m⁻²·yr⁻¹ from 1995 to 1999, and fine-root biomass was $\sim 5\%$ of total root biomass, we assumed zero net annual change in the pool of fine-root C. C_S was measured to a depth of 0.30 m at three permanently located sites per plot in May 1994 and in January 1997 (Binkley and Resh 1999), and again for all plots in January 2000. For annual estimates of TBCA, we assumed that the rate of change in soil C was constant within these two periods. From earlier work at nearby sites with similar soils and land use (Bashkin and Binkley 1998), we expected that soil C below 0.30 m changed little over the course of this four-year study (Giardina and Ryan 2002, Binkley et al. 2004).

Statistical analysis

Relationships between photosynthetic capacity or foliar dark respiration and foliar N were assessed using analysis of covariance, with the treatment \times foliar N term being a test for the equality of slopes among treatments. Linear regressions of these relationships showed that the intercept term was not significant, so regressions were fit with a zero intercept (r^2 estimated as recommended by Kvalseth [1985]).

Measurements began in January 1995 and continued through December 2000 (year 1–year 6). Values of fluxes for each year are the averages over that year. When plotted, values are paired with their age at mid-year: because seedlings were ~ 0.5 years old in January 1995 (from date of planting), the age at mid-year equals the measurement year. Treatment differences in standing crops for woody biomass, canopy N content, and LAI were assessed using year 6 data (maximum biomass, average canopy N, and LAI) with a randomized-block ANOVA. Differences in fluxes with stand age and treatment were assessed with a randomized-block, repeated-measures ANOVA using data from years 2–6, because canopy closure for the LD treatment occurred in year 2 and fluxes for the HD treatment were similar in years 1 and 2. Both sets of ANOVAs were analyzed using only the C and HF treatments. Omitting year 1 and the RF treatment from these analyses was done to simplify interpretation. Inclusion of year 1 and the RF treatment generated strong interactions with stand development that confounded trends with stand development: interactions that were easily explained by the changing fertility in year 4 for the RF treatment or the lack of canopy closure for the LD treatment in year 1. Whether carbon flux for the RF treatment equaled or exceeded that for the HF treatment was assessed with ANOVA by comparing RF means for ANPP_w, GPP, and TBCA from year 6 with HF means from year 2 (peak values at canopy closure).

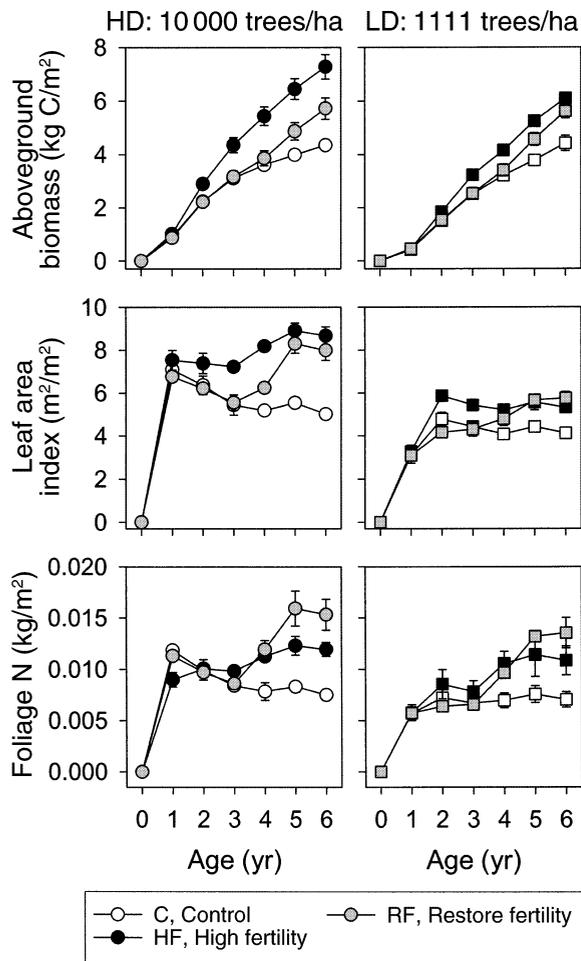


FIG. 3. Aboveground biomass was highest in the High-Fertility (HF) and Restore-Fertility (RF) treatments for high-stem-density (HD) and low-stem-density (LD) treatments. Leaf area and foliage N content of the canopy remained stable as aboveground wood production declined. Values are expressed as means \pm 1 SE.

We harvested one of the LD–HF plots in 1999 for another study (Binkley et al. 2002), and this plot was omitted from the analysis for years 5 and 6. ANOVA was accomplished using SAS Proc Mixed using the “REML” estimation method, which can accommodate missing cells (SAS Institute 1999).

RESULTS

Stocks and structure

Canopy closure occurred by the end of year 1 for the HD treatments and by the end of year 2 for the LD treatments. Leaf area index remained high for all treatments after canopy closure (Fig. 3). Canopy height profiles showed that the canopies changed from thin, uniform layers at canopy closure to more complex, deeper arrangements as trees grew in height (Fig. 4). The canopies moved upward at a rate of 0.5–1 m per month, and fertilization increased leaf area in a uniform pattern

throughout the canopies. In year 6, LAI differed by fertility and tree density ($P < 0.01$), with the HD treatment averaging 2.0 m²/m² more leaf area than the LD treatment, and the HF treatment averaging 2.5 m²/m² more leaf area than the C treatment (Fig. 3). Differences in LAI with tree density were most pronounced for the HF treatment.

In December 2000 at age 6.5 years, tree diameter averaged 18.1 cm for the LD plots (maximum 33.8 cm) and 9.3 cm for the HD plots (maximum 26.8 cm). Tree height averaged 23.2 m for the LD plots (maximum 33.4 m) and 12.3 m for the HD plots (maximum 29.6 m). At the end of year 6, aboveground woody biomass was lower in the C treatment (4.56 kg C/m²) than the HF treatment (6.98 kg C/m², $P < 0.01$), and did not differ with tree density (Fig. 3, $P = 0.23$). Canopy N content was lower in the C treatment (0.0073 kg N/m²) than the HF treatment (0.011 kg N/m², $P < 0.01$), and did not differ with tree density (Fig. 3; $P = 0.37$).

Ecophysiological differences with treatment and stand development

Photosynthetic capacity.— A_{\max} (directly measured or estimated from $V_{c_{\max}}$) varied with foliar N, both N/area (Fig. 5; $r^2 = 0.46$, $P < 0.01$) and N content ($P < 0.01$), but the relationship between A_{\max} and N did not vary with canopy position ($P = 0.17$), sampling date ($P = 0.18$), tree density ($P = 0.19$), or fertility treatment ($P = 0.49$). A_{\max} also varied with foliar P/area ($r^2 = 0.03$, $P = 0.04$), but not with P content ($P = 0.13$). When included in a multiple linear regression with N/area, P/area did significantly increase r^2 by a marginal 3%. A_{\max} and foliar respiration were linearly related ($r^2 = 0.26$, $P < 0.01$). A_{\max} measured in September 1999 (not plotted in Fig. 5 because N and A_{\max} could not be matched for individual samples) was similar to measurements from 1995 to 1998 for a given foliar N concentration (data are from Barnard and Ryan 2003). Results similar to those just described were also found when A_{\max} and foliar N were both expressed on a mass basis. A_{\max} declined from the canopy top to the bottom and from the outer to inner leaves on a shoot.

Foliar respiration.—Foliar respiration varied with foliar N content (Fig. 6; $P < 0.01$), and much of the difference in rates between treatments, sample periods, and position within the canopy was related to differences in foliar N content. Average rates, by treatment, were 0.50, 0.55, 0.39, and 0.58 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for the C–HD, C–LD, HF–HD, and HF–LD treatments, respectively. In an initial analysis, the relationship between respiration and foliar N differed between expanding and fully expanded foliage ($P < 0.01$). At the same level of foliar N, respiration for expanding foliage was nearly twice as great as that for fully expanded foliage in the upper canopy (1.41 vs. 0.80 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Because expanding foliage represents <5% of the canopy biomass, and because we estimated R_F for growing foliage using construction respiration,

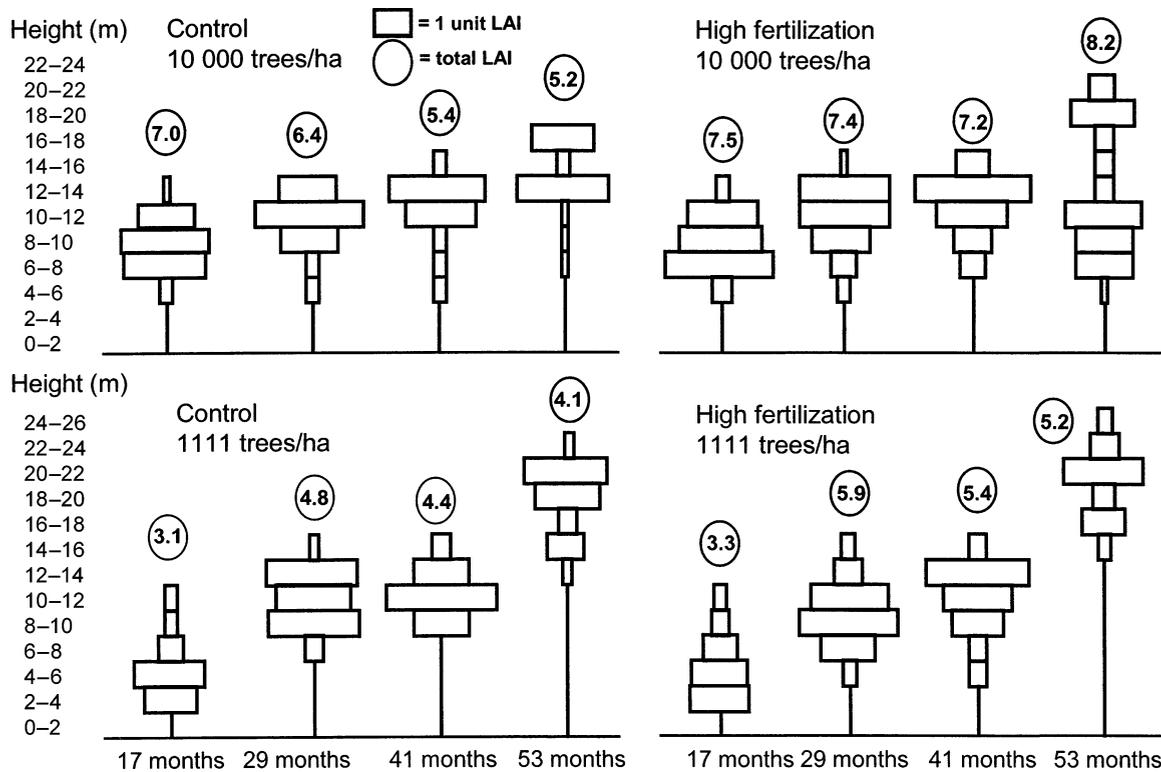


FIG. 4. Canopy height profiles showed that tree growth changes the canopy from a thin, uniform layer to a more complex, deeper arrangement. Fertilization increased leaf area in a fairly uniform pattern throughout the canopies. The canopies moved upward at a rate of 0.5–1 m per month.

we omitted expanding foliage from the analysis for maintenance respiration. For fully expanded foliage (maintenance respiration only), respiration per unit foliar N varied with fertility treatment (Fig. 6; $P < 0.01$), but not with tree density ($P = 0.96$), position within

canopy ($P = 0.52$), or year ($P = 0.18$). Respiration per N was greater for the control treatment than for the high-fertility treatment. We estimated foliar dark respiration maintenance coefficients for the control and high-fertility treatments (5.16 and 4.21 mmol C (mol foliar N)⁻¹·s⁻¹ at 20°C, respectively) using linear regression with a zero intercept, because the intercepts were not significantly different from zero ($P = 0.62$ for the C treatment and 0.31 for the HF treatment; $r^2 = 0.37$ for the C treatment and $r^2 = 0.21$ for the HF treatment).

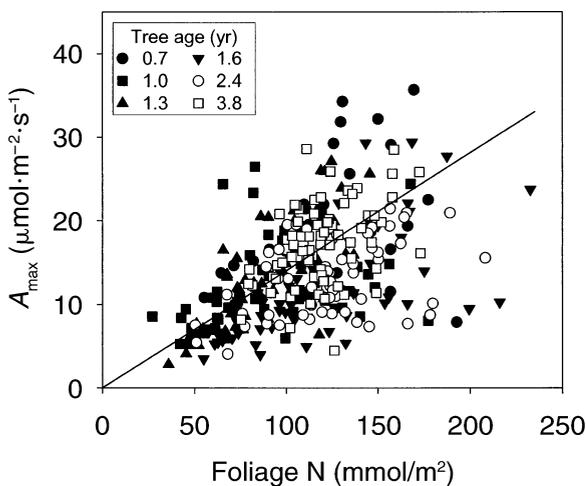


FIG. 5. Photosynthetic capacity, estimated as A_{max} (photosynthesis under saturating light, low vapor pressure deficit, and ambient CO₂) is related to foliar N content ($A_{max} = 0.141$ foliage N; $R^2 = 0.46$, $P < 0.01$), and the relationship does not vary with tree age ($P = 0.18$).

Foliar nutrients.—For the bulk canopy, N concentration was greater in the HF than the C treatments (19.6 mg N/g vs. 16.8 mg N/g, $P < 0.01$) and greater in the HD than the LD treatments (19.5 mg N/g vs. 16.9 mg N/g, $P < 0.01$). Differences between the HF and C treatments were less pronounced in the LD treatment ($P = 0.03$ for the tree density × fertility interaction). Bulk canopy foliar N concentration did not vary with time (Fig. 7B; $P = 0.40$). Patterns in the means of the “diagnostic” foliage, taken from scaffold towers in one block, were similar to those seen in the bulk canopy (Fig. 7A). Foliar N concentration for the RF treatments quickly reached HF concentrations after the application of the HF fertilizer regime. Foliar N declined from the canopy top to the bottom and from the outer to inner leaves on a shoot, similar to patterns reported in Barnard and Ryan (2003).

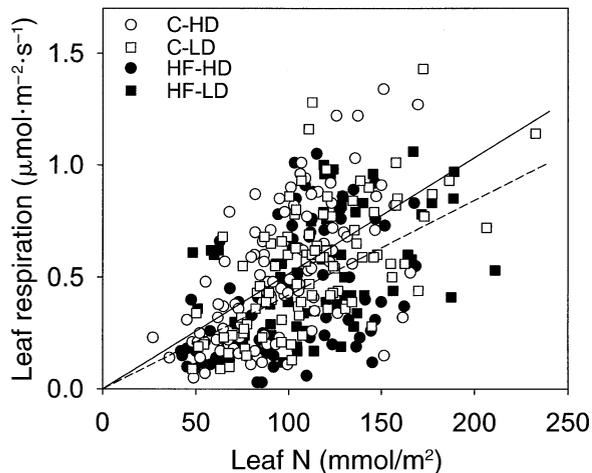


FIG. 6. Foliage respiration rates (at 20°C) for fully expanded foliage vary with foliar N content and fertility treatment, but do not vary with tree density (high density, HD = 10 000 trees/ha; low density, LD = 1111 trees/ha) or year. Coefficients for the Control (C) and High-Fertility (HF) treatments were 5.16 and 4.21 $\text{mmol C} \cdot (\text{mol foliar N})^{-1} \cdot \text{s}^{-1}$ at 20°C, respectively.

Woody respiration.—Respiration rate per unit biomass differed with tree density and fertility and declined with time (Fig. 8; $P < 0.01$ for all tests). Respiration per unit of sapwood biomass (Ryan 1990) also declined with time (M. G. Ryan and R. S. Senock, unpublished data; $P < 0.01$). Differences in respiration rates among treatments were related largely to differences in growth rate: using growth as a covariate eliminated treatment effects or the effect of position on tree (most measurements were taken at 1.4 m, but some measurements were taken at 3, 6, 10, or 20 m). Partitioning R_w into the components of growth and maintenance respiration showed that both growth and maintenance coefficients, as estimated from a regression of respiration/biomass with growth/biomass, declined with time (M. G. Ryan and R. S. Senock, unpublished data). We used treatment-specific biomass rates for each year to estimate R_w , because it was the simplest method of extrapolation. However, the method of calculation had little effect on estimates of R_w , and no impact on the pattern of R_w through time. Estimates for R_w calculated using growth and maintenance coefficients and annual growth and woody biomass were highly correlated with R_w estimated using treatment-specific biomass rates ($r = 0.92$), and differed by an average of only 0.1 $\text{kg C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$.

Carbon fluxes by treatment and stand age

Aboveground NPP.—ANPP_w showed the expected pattern of declining after canopy closure, from 1.39 $\text{kg C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at age 2 to 0.60 $\text{kg C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at age 6, averaged over the C and HF treatments (Fig. 9; $P < 0.01$). The decline was steeper for the C than for the HF treatment ($P < 0.01$): ANPP_w in year 6 was 39%

of that in year 2 for the C treatment vs. 45% for the HF treatment. The decline was also steeper for the HD than for the LD treatment ($P = 0.01$): ANPP_w in year 6 was 37% of that in year 2 for the HD treatment vs. 50% for the LD treatment. ANPP_w for the RF treatment never equaled or exceeded that at peak growth ($P < 0.01$). ANPP_w was greater in the HF than the C treatment ($P < 0.01$, average 1.13 vs. 0.68 $\text{kg C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$), and did not differ with tree density ($P = 0.98$). ANPP_w in the HF treatments for the 1998 plantation at age 2 was similar to that in the primary plantation at age 2 (Fig. 9), demonstrating that the decline in ANPP_w in the primary plantation was not caused by environmental change.

NPP_F also declined with stand age after canopy closure from 0.40 $\text{kg C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at age 2 to 0.27 $\text{kg C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ at age 6 ($P < 0.01$). The rate of decline in NPP_F did not differ between fertility treatments ($P = 0.66$), but was slightly more rapid for the LD treatment ($P = 0.01$). NPP_F for the RF treatment recovered to

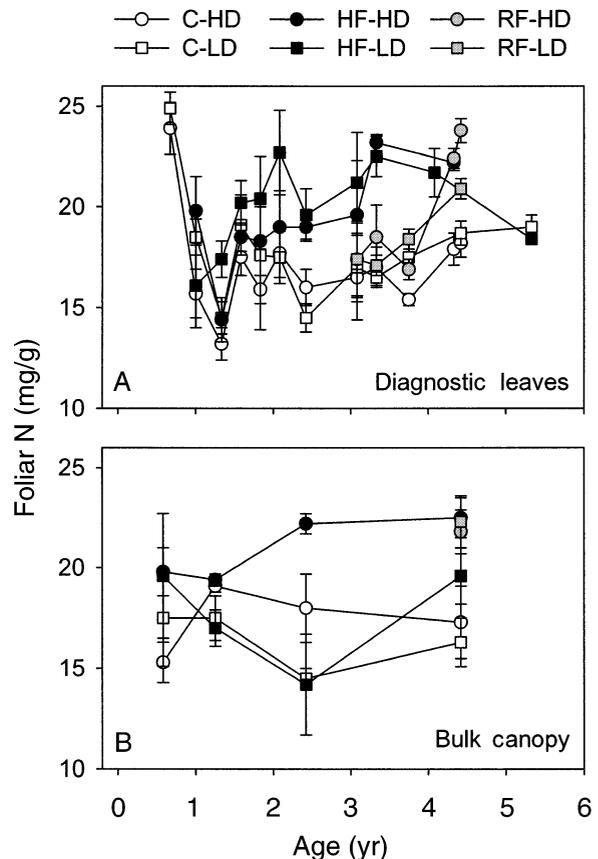


FIG. 7. Foliar N concentrations differed by treatment but were fairly uniform through time within a treatment (C, Control; HF, High-Fertility; RF, Restore-Fertility; HD = 10 000 trees/ha, LD = 1111 trees/ha). (A) Patterns from the "diagnostic" leaves taken from scaffolding towers on one block matched those of the (B) bulk canopy of harvested trees. For diagnostic leaves, values are means of all five positions; error bars are ± 1 SE.

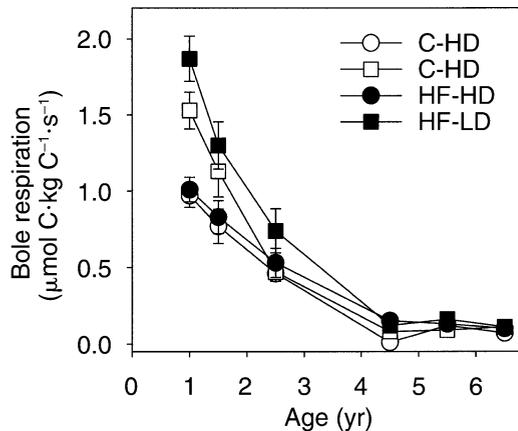


FIG. 8. Bole respiration rates (at an average temperature of 22.5°C) differ among treatments and decline with stand development and tree size (C, Control; HF, High-Fertility; HD = 10 000 trees/ha, LD = 1111 trees/ha). Values are expressed as mean \pm 1 SE.

HF levels during the year when the RF treatment was implemented. NPP_F was greater in the HF than in the C treatment (Fig. 9; $P < 0.01$, average 0.38 vs. 0.27 kg C·m⁻²·yr⁻¹), and was greater in the HD than the LD treatment ($P < 0.01$, average 0.34 vs. 0.31 kg C·m⁻²·yr⁻¹).

TBCA.—Belowground carbon allocation also declined with stand age, from 1.92 kg C·m⁻²·yr⁻¹ at age 2 to 1.45 kg C·m⁻²·yr⁻¹ at age 6 ($P < 0.01$). TBCA did not differ between fertility ($P = 0.61$) and tree density ($P = 0.23$) treatments (Fig. 9); a near-significant ($P = 0.07$) interaction between age and fertility showed that much of the decline in TBCA with stand age was in the C treatment.

Respiration.—From stand age 2 to 6 years, R_W declined from 0.66 to 0.22 kg C·m⁻²·yr⁻¹ ($P < 0.01$), and the decline was sharper for the HF than for the C treatment. Fertility increased R_W over the C treatment (Fig. 10; $P < 0.01$, average 0.53 vs. 0.29 kg C·m⁻²·yr⁻¹), but R_W did not vary with tree density. R_F differed among years ($P < 0.01$), with R_F for the HF treatment tending to increase with stand age and R_F for the C treatment tending to decrease ($P < 0.01$). Fertility increased foliage respiration over the C treatment (Fig. 10; $P = 0.05$, average 0.65 vs. 0.57 kg C·m⁻²·yr⁻¹), and R_F was greater for the HD than the LD treatment ($P = 0.05$, average 0.65 vs. 0.57 kg C·m⁻²·yr⁻¹).

GPP.—GPP declined with stand age from an average of 5.00 kg C·m⁻²·yr⁻¹ at age 2 to 3.17 kg C·m⁻²·yr⁻¹ at age 6 for the combined HF and C treatments (Fig. 10; $P < 0.01$). There was a tendency for a sharper decline in the C than the HF treatment ($P = 0.11$) and in the HD than the LD treatment ($P = 0.16$). GPP in the RF treatment never equaled or exceeded GPP in the HF treatment ($P < 0.01$). Fertility increased GPP (averaged across all years) from 3.55 in the C treatment to 4.34 kg C·m⁻²·yr⁻¹ in the HF treatment ($P < 0.01$).

Partitioning of GPP.—The fraction of GPP allocated to $ANPP_W$ ($ANPP_W : GPP$) decreased with stand age from 0.28 in year 2 to 0.19 in year 6 (Fig. 11, $P = 0.01$). $ANPP_W : GPP$ was lower in the C treatment than the HF (Fig. 11; 0.19 vs. 0.26, $P < 0.01$), but did not differ with tree density ($P = 0.15$). The fraction of GPP allocated to NPP_F ($NPP_F : GPP$) increased slightly with stand age from 0.075 in years 2 and 3 to 0.091 in years 5 and 6 ($P < 0.01$). $NPP_F : GPP$ differed slightly with fertility ($P = 0.03$), but not with tree density ($P = 0.31$). Belowground allocation as a fraction of GPP ($TBCA : GPP$) increased from 0.38 in year 2 to 0.46 in year 6 ($P < 0.01$), with no interactions between stand age and fertility or tree density ($P > 0.23$). Fertility dramatically changed $TBCA : GPP$ to 0.38 for the HF treatment from 0.48 in the C treatment (Fig. 11, $P < 0.01$), but $TBCA : GPP$ did not vary with tree density (Fig. 11, $P = 0.57$).

The fraction of GPP allocated to R_W declined with stand age from 0.13 at age 2 to 0.07 at age 6 ($P < 0.01$). Fertility changed $R_W : GPP$ from 0.08 in the C treatment to 0.12 in the HF treatment (Fig. 12, $P < 0.01$). $R_W : GPP$ did not vary with tree density ($P = 0.24$). The fraction of GPP allocated to R_F increased

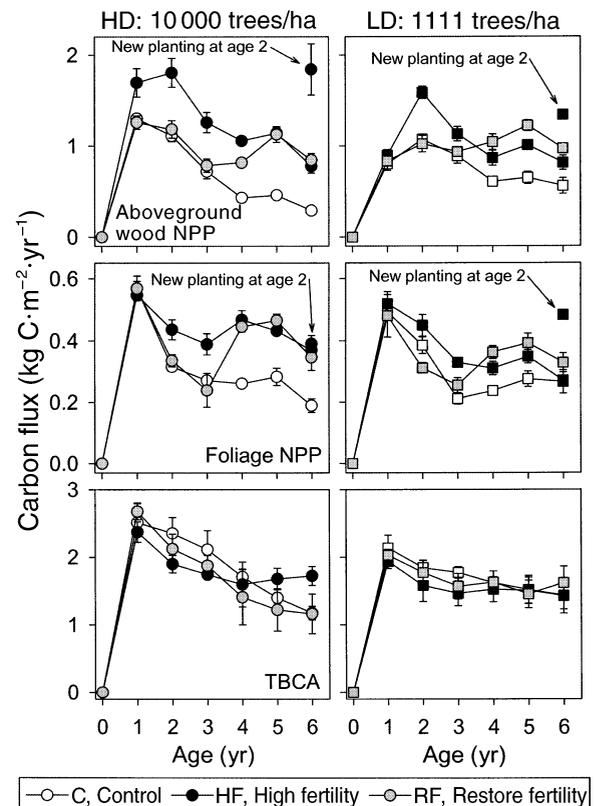


FIG. 9. Wood and foliage NPP and TBCA generally decline with tree age. The restore-fertility treatment increased wood and foliage NPP, but not to levels equal to or greater than those for the high-fertility treatment at peak. Values are expressed as mean \pm 1 SE.

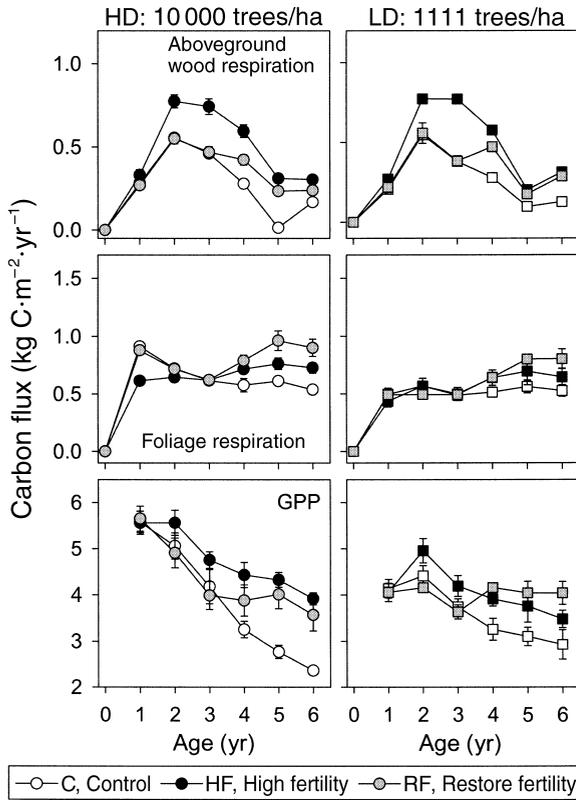


FIG. 10. Wood respiration and GPP decline after year 2 in the control and high-fertility treatments. The restore-fertility treatment increased GPP, but not to a level equal to or greater than that for the high-fertility treatment at peak. Values are expressed as mean \pm 1 SE.

with stand age ($P < 0.01$) from 0.13 at age 2 to 0.19 at age 6, but did not vary with tree density ($P = 0.15$) or fertility ($P = 0.10$). The fraction of GPP used for autotrophic respiration (estimated as $[R_w + R_f + 0.5(TBCA)]/GPP$) averaged 0.48, and increased slightly with stand age from 0.45 at age 2 to 0.49 at age 6 (Fig. 12; $P < 0.01$).

Hypothesis tests for causes of age-related stand decline

Fig. 13 summarizes the differences in the annual carbon budget from canopy closure at age 2 to age 6. We averaged the tree density treatments because the interaction between fertility and tree density was rarely significant, and because fertility was more central to our tests of hypotheses than was tree density.

Hypothesis 1: GPP remains high after canopy closure, but increased allocation to (1a) R_w , (1b) TBCA, or (1c) other sink or some combination causes a decline in $ANPP_w$.—The data strongly refuted this hypothesis. $ANPP_w$ did decline with stand age, but GPP, R_w , and TBCA also declined. Additionally, $R_w : GPP$ declined with stand age. The decline in $ANPP_w$ was steeper for the treatment with higher tree density, but there were

no differences in either $R_w : GPP$ with tree density, and only a very slight difference in $R_f : GPP$ with tree density.

Hypothesis 2: GPP declines with stand age, and the decline in $ANPP_w$ is proportional to the decline in GPP.—The data also refuted this hypothesis. By year 6, GPP had declined to 56% of the rate at canopy closure in the C treatment and to 73% of the rate at canopy closure in the HF treatment. However, partitioning of annual GPP to $ANPP_w$ also declined from 36% in year 2 to 27% in year 6.

Hypothesis 3: GPP declines with stand age, but the decline in $ANPP_w$ is disproportionately larger because partitioning shifts as well.—The data supported this hypothesis. GPP in year 6 had declined to 64% of its peak rate, but $ANPP_w$ had declined more: to 43% of its peak rate (both are the average of C and HF treatments). Partitioning of GPP to TBCA and R_f increased slightly with stand age, from 38% to 46% for TBCA, and from 13% to 19% for R_f . The decline in GPP was exacerbated by reduced nutrient supply (in the C treatment), but high nutrient supply (HF and DF treatments) did not prevent a GPP decline or a decline in $ANPP_w$. GPP declined after canopy closure, despite sustained

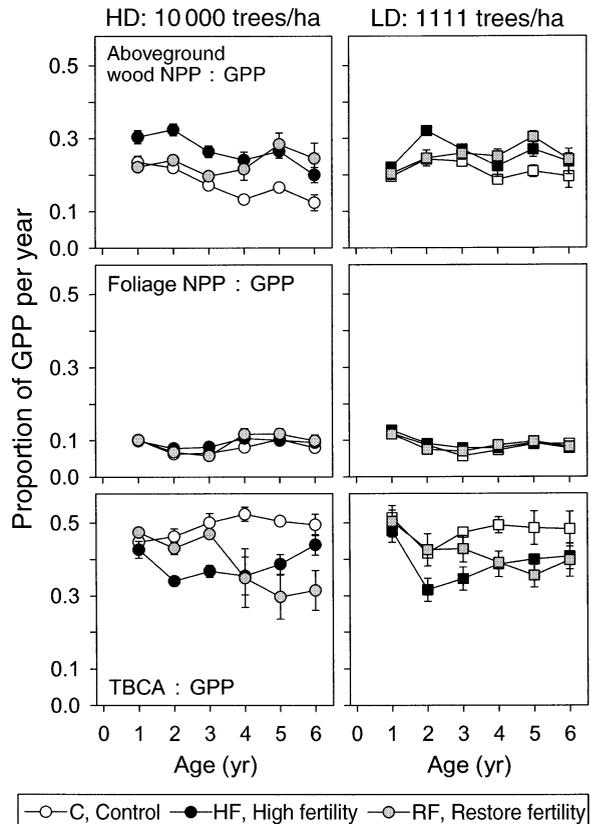


FIG. 11. The proportion of GPP used for aboveground wood NPP decreased and that used for TBCA increased with tree age within a given fertility regime. Error bars are \pm 1 SE.

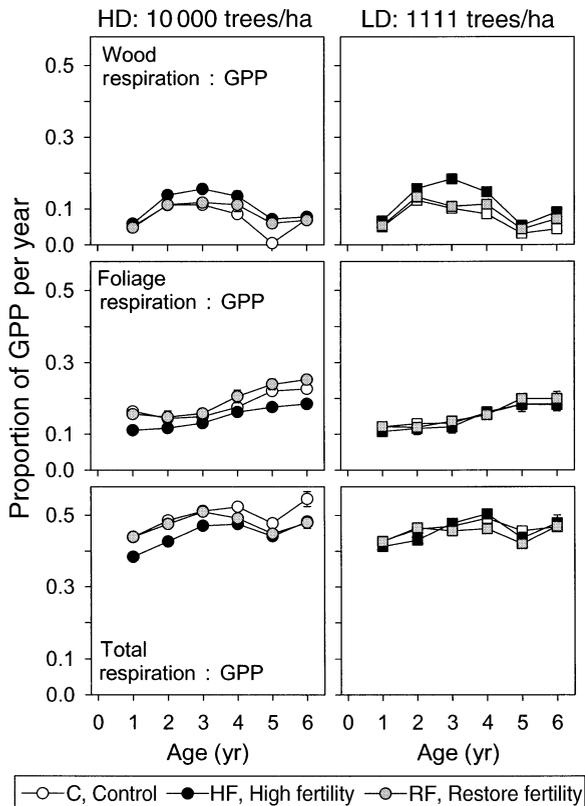


FIG. 12. The proportion of GPP used for aboveground woody respiration was low and declined slightly with stand age. The foliage respiration : GPP ratio increased with stand age. Total respiration, estimated as $0.5 \text{ TBCA} + R_F + R_W$, averaged 0.48 of GPP and increased slightly with stand age. Error bars show ± 1 SE.

high leaf area, canopy N content, and photosynthetic capacity.

DISCUSSION

Our experimental forest of rapidly growing eucalypts proved to be an excellent model system for measuring forest growth and its components, and the decline in wood production after canopy closure. Similar to results from chronosequence studies (Ryan et al. 1997a), ANPP_W peaked at canopy closure (about one year after planting for the HD treatment and about two years after planting for the LD treatment). Peak ANPP_W ($1.4 \text{ kg C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, $\sim 35 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) was greater than that reached in other chronosequence studies, and standing biomass at age 6.5 yr was similar to that in temperate forests that are decades to centuries older (DeAngelis et al. 1980). Measurements of stand development over time in our model system ensured that changes were caused by physiological or structural changes in the stands, avoiding assumptions that underlie chronosequences about similarities in sites, conditions of stand establishment, and genetics.

We tested three hypotheses about the proximate causes of the decline of ANPP_W after canopy closure, and

rejected two of them. The use of experimental manipulation of nutrition, repeated measurements on the same developing forest, and a carbon budget approach strongly supported the conclusion that GPP (net photosynthetic C uptake during the day) declines after canopy closure. However, ANPP_W declined more than the decline in GPP, because of ontogenetic shifts in annual partitioning of GPP. Sustained high nutrient availability did not prevent a decline in GPP and ANPP_W , and leaf area, canopy N content, and photosynthetic capacity remained constant (within a treatment) while GPP declined. Another study on the same site (Barnard and Ryan 2003) indicated that hydraulic limitation of canopy conductance (as outlined by Ryan and Yoder 1997) was not responsible for the decline in canopy photosynthesis after canopy closure, but we have not yet demonstrated an alternative mechanism (see *Discussion*).

Respiration

The decline in rates of woody respiration with stand development (Fig. 8) and the constant fraction of canopy photosynthesis used for woody respiration clearly refute the respiration hypothesis of Kira and Shidei (1967), and support the conclusions of Möller et al. (1954) and Ryan and Waring (1992). The decline in woody respiration rate with stand development paralleled the decline in wood growth, and the ratio of woody respiration to wood growth *plus* wood respiration remained constant through time (~ 0.25), suggesting that the decline in wood growth promoted the decline in respiration rates. Similar declines in woody respiration rates with tree age have also been reported for jack pine by Lavigne and Ryan (1997). However, some modeling studies still suggest that woody respiration can cause NPP decline (Hunt et al. 1999, Makela and Valentine 2001), perhaps because such studies assign a fixed maintenance cost for sapwood respiration instead of having sapwood respiration decline as growth declines (Lavigne and Ryan 1997). Such studies also ignore the growing evidence that respiration is roughly a constant fraction of canopy photosynthesis, and independent of biomass, temperature, or stand age (Gifford 1994, Ryan et al. 1994, 1997b, Waring et al. 1998).

Belowground allocation

The annual flux of carbon used for TBCA declined with stand age for both the fertility and the tree density treatments, demonstrating that increased belowground allocation to nonwoody components did not cause the decline in ANPP_W . The carbon balance approach for estimating TBCA confirmed that a large fraction of canopy photosynthesis (32–51%) supported belowground allocation, and that high fertility dramatically reduced partitioning of GPP to TBCA (see also Giardina et al. 2003). ANPP_W did decrease more rapidly with stand age than did TBCA (about two times faster),

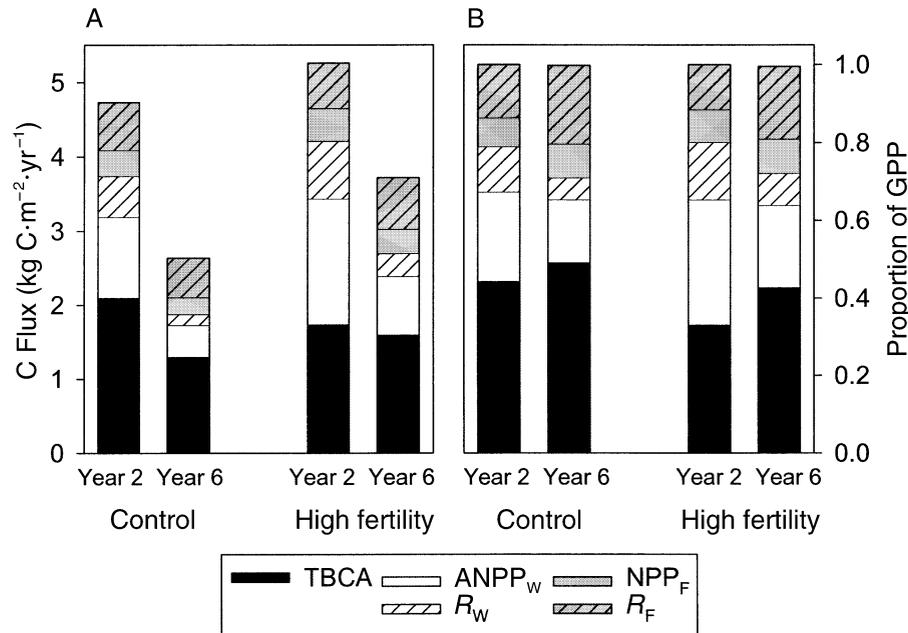


FIG. 13. (A) GPP, ANPP_w, R_w, and TBCA decline from year 2 to year 6, even for the High-Fertility treatment (values are averaged over tree density treatments). (B) The proportion of gross primary productivity used for each of the five components of carbon flux was relatively uniform from year 2 to year 6, but partitioning to aboveground wood production decreased, while partitioning to total belowground carbon allocation (TBCA) and foliage dark respiration increased.

suggesting that shifts in allocation exacerbate, but do not cause, the decline in ANPP_w. Smith and Resh (1999) found similar results for a replicated chronosequence of lodgepole pine. Our results are counter to those found in a modeling study by Magnani et al. (2000, and references therein). A potential explanation for the discrepancy is that Magnani et al. (2000) relied on studies that measured changes in fine-root standing crop with stand development, whereas our method measured the total flux of carbon that plants send belowground (including root respiration, root turnover, and carbon used by mycorrhizae and root exudates in addition to that used for biomass).

Reduced GPP and changes in partitioning of GPP

Estimates of GPP using a plot-level, carbon balance approach supported the hypothesis that GPP declined after canopy closure, and that this decline was largely responsible for the decline in ANPP_w. A reduction in GPP was also supported by declines in four of the five components used to estimate it (only R_F increased, and only slightly). This study also supports the connection between the timing of ANPP_w decline and closure of the canopy (Ryan et al. 1997a), because both ANPP_w and GPP peaked at canopy closure (during year 1 for the HD treatment and year 2 for the LD treatment) and then declined. Many chronosequence studies have shown that reduced ANPP_w after canopy closure is accompanied by a reduction in LAI (Ryan et al. 1997a). In our study, the reduction in GPP occurred without

changes in LAI, and without changes in photosynthetic capacity.

The fraction of GPP used for both TBCA and R_F did increase with stand development for both the fertility and density treatments, suggesting an age-related shift in partitioning. Ryan and Waring (1992) found a similar shift in partitioning for TBCA in lodgepole pine. Interestingly, the ratio of (ANPP_w + TBCA) : GPP was nearly constant across all age classes and density and fertility treatments (0.64–0.67), indicating the potential constraints on the plasticity of allocation.

An appealing mechanism for reducing GPP without reducing LAI or photosynthetic capacity is the hydraulic limitation hypothesis (Yoder et al. 1994, Ryan and Yoder 1997), which states that path length and gravitational potential increase with tree height, and these changes force stomata to close at higher relative humidity (to protect the water conducting system) and reduce photosynthesis. Hydraulic limitation has been shown to reduce canopy average stomatal conductance with tree height in ponderosa pine *Pinus ponderosa* (Hubbard et al. 1999, Ryan et al. 2000), Oregon white oak, *Quercus garryana* (Phillips et al. 2003), European beech, *Fagus sylvatica* (Schäfer et al. 2000), and perhaps Douglas-fir, *Pseudotsuga menziesii* (McDowell et al. 2002b), but not in some tropical angiosperms (Phillips et al. 2001). Additionally, hydraulic limitation is suggested as the mechanism causing ANPP_w decline in Scots pine (Mencuccini and Grace 1996a).

We examined this mechanism at our site by comparing the average stomatal conductance of the canopy

for 6-year trees in this study (LD, HF treatment) with 1-year trees receiving the same treatment in an adjacent, new plantation (Barnard and Ryan 2003). Average stomatal conductance did not differ between the trees of different heights, because increased sapwood area : leaf area and decreased minimum midday leaf water potential compensated for the increased height. Greater discrimination against ^{13}C in the taller trees, coupled with similar average stomatal conductance, supported estimates of reduced GPP by the carbon balance method, but a mechanism has yet to be demonstrated (Barnard and Ryan 2003).

To our knowledge, the Barnard and Ryan (2003) study is the first to directly test the hydraulic limitation hypothesis in connection with direct measurements of a decline in stand ANPP_w (this study). Other studies of the hypothesis have focused strictly on physiological differences between short and tall individuals. The evidence that hydraulic limitation can lower canopy average stomatal conductance and photosynthesis in tall trees is strong, and hydraulic limitation might further depress ANPP_w as the stand grows taller. However, hydraulic limitation (as conceived by Yoder et al. [1994] and Ryan and Yoder [1997]) was not responsible for the sharp decline in ANPP_w immediately after canopy closure in this case.

Nutrient supply

Nutrition had a powerful role in shaping the carbon uptake, retention, and allocation in our study, but a balanced (excess) supply of nutrients failed to prevent a decline in GPP or ANPP_w . Better nutrition increased leaf area, GPP, ANPP_w , and standing biomass, and strongly reduced the fraction of GPP used belowground (see Giardina et al. [2003] for further details on the nutrition response). However, the decline of GPP and ANPP_w in the HF treatment and the failure of GPP and ANPP_w to equal or exceed the peak at canopy closure in the RF treatment argue strongly against nutrition as a cause of GPP and ANPP_w decline.

ANPP_w declined more rapidly in the C than in the HF treatment, suggesting that nutrient availability declined with stand development, and that this decline amplified the decline in ANPP_w caused by other mechanisms. The difference in the rate of decline in ANPP_w with fertility suggests that declines in nutrition and ANPP_w may have been confounded in past studies (reviewed in Gower et al. 1996, Murty and McMurtrie 2000). Nutrition does not appear to follow a single, general pattern with stand development (Ryan et al. 1997a), and future studies on nutrition and ANPP_w decline should include a treatment with high nutrient availability to avoid any confounding effects.

Analysis of errors and assumptions

Testing hypotheses about the mechanisms responsible for a decline in ANPP_w relies on the soundness of the estimates for each component, and on estimating

GPP as the sum of annual flows to dry matter production, respiration, and belowground allocation. Next, we examine the potential effect of measurement precision and assumptions on estimates of carbon flux and on our conclusions.

Precision of estimates and cumulative error.—Two statistical problems are perceived to occur when subsamples (e.g., diameters of individual trees) are scaled to plot estimates and when parameters are linear combinations of other measurements (TBCA and GPP): (1) subsample variance must be measured and used in estimating the variance of replicate plots, and (2) special estimates of variance are required to estimate the “cumulative error” associated with linear combinations of measurements. Giardina and Ryan (2002) demonstrated that when the experimental unit is a plot, and measurements for scaling variables (e.g., diameter and soil respiration) are measured on every plot, the variance associated with estimates of a parameter for replicate plots contains all available information on subsample variance and cumulative error. Therefore, error estimates in Fig. 3 and Figs. 9–12 include subsample variance and cumulative error (if it applies). A larger and less tractable issue is the possibility that scaling equations (e.g., biomass allometry, tissue respiration rates) might be biased. Any bias would largely affect the means, not variances; we discuss any potential biases below by component.

TBCA.—A thorough description of the assumptions and potential biases in TBCA for this experiment is given in Giardina and Ryan (2002). That study concluded that the carbon balance method for estimating TBCA is unbiased and accurate, with a coefficient of variation for replicate plots averaging 17%. Measurements of soil respiration are the largest potential source of bias and can vary $\pm 20\%$ for different techniques (Norman et al. 1997). However, because the soils, measurement conditions, and equipment were the same for all treatments and for the 6.5-year measurement period, we expect that any bias among treatments would be unlikely.

R_w .—Potential problems associated with estimates of R_w include the following: (1) measurements in years 1–3 were only from plots in one of the three blocks; (2) flux was estimated using biomass, not sapwood and growth; (3) sampling of the respiration of upper stems, branches, and twigs was limited; and (4) measurements outside the stem may underestimate true flux (Teskey and McGuire 2002). Woody respiration rates varied strongly with growth rate among treatments, so flux estimated for an individual treatment plot probably represented all plots for the treatment in all blocks. When all plots were measured, there were no differences among replicate plots, using tree as the experimental unit. A comparison of scaling methods for R_w (described under *Methods*) showed only a minor effect of scaling on R_w and GPP, and no effect on the conclusions.

Recent work with CO₂ probes in sapwood suggests that measurements of CO₂ efflux outside the stem may underestimate actual rates of woody respiration (Teskey and McGuire 2002). If so, and if CO₂ produced in the stem is used for foliar photosynthesis or exits in the upper stem, branches, or twigs, we may have underestimated R_w . Measurements taken at our experimental site suggest that any underestimate is likely to be small and would not alter our conclusions. We used the techniques outlined in Levy et al. (1999) to estimate the fraction of photosynthesis likely to be derived from CO₂ in the xylem stream (measurements of $p\text{CO}_2$, pH, temperature, and flux of xylem water). We estimated that 3% of photosynthesis in 1-year trees and 1.5% in 5-year trees might be derived from xylem CO₂, if it were not refixed in the branches or twigs before it reached the leaves (M. G. Ryan, N. Phillips, and H. R. Barnard, *unpublished data*). These measurements suggest that R_w might have been at most 6–21% of canopy photosynthesis, compared to the 3–18% actually measured—too slight to account for the decline in ANPP_w. We also measured branch, twig, and stem respiration every 2–3 m along the stem for three 3-year and three 7-year trees in May 2001 (M. G. Ryan and R. S. Senock, *unpublished data*). R_w values estimated from the branch, twig, and stem rates were similar to those estimated for the same trees from rates for stem respiration only (the method used in this paper), and total R_w did not differ for the 3-year and 7-year trees.

R_f .—Potential problems associated with estimates of R_f are that measurements were made on plots in only one block and estimates of whole-canopy N content were sparse. Foliar respiration rates were strongly related to foliar N content, and the fact that the rate per unit N did not vary among tree density treatments indicated that plot-to-plot variability in measurements within a treatment would be small. Additionally, our more frequent samples of foliar N from the “diagnostic” leaves suggest that the whole-canopy samples largely reflect foliar N content through time. A complete sample of all of the trees on a HF-LD plot at age 6 (Binkley et al. 2002) gave a canopy N content of 19.3 mg/g, similar to the mean for that treatment at age 4.5.

Aboveground NPP.—NPP_F and ANPP_w estimates are the most straightforward of all the components of the carbon budget to measure, and our estimates are probably unbiased. The allometric equation was developed using trees periodically harvested from the experiment, and residuals plots for the allometric equation for biomass showed that the equation was unbiased for trees of all sizes. Because the equation was constructed using tree mass rather than volume, it also incorporates any increase in wood density with time. For our annual estimates of NPP_F, changes in canopy biomass were minor and NPP_F ≈ litterfall, so any bias in NPP_F would reside in measurements of litterfall, not LAI.

GPP.—Mass balance dictates that the carbon balance approach will produce an unbiased estimate of GPP if estimates of the components are unbiased and all potential sinks or losses of C are measured. Potential losses of C not included in our budget include foliar herbivory, emission of volatile organic compounds, any CO₂ in the xylem stream escaping through the stomata during the day (xylem CO₂ refixed in photosynthesis would be measured where it was used), and losses of soil C to erosion or to groundwater as organic and inorganic C. We observed no foliar herbivory during the study. Isoprene losses measured at our site (Funk et al. 2003) were probably the largest component of volatile organic C emissions. J. L. Funk, C. P. Giardina, and M. T. Lerdau (*unpublished manuscript*) estimated these losses to be ~1% of photosynthesis. Estimates of xylem CO₂ used for photosynthesis at our site ranged from 1.5% to 3% of photosynthesis, but losses through stomata (xylem CO₂ produced by respiration but not fixed in photosynthesis) are likely to be very small, given a strong counter gradient for diffusion. Giardina and Ryan (2002) discussed C loss from soil and concluded that it is <1% of TBCA (<0.5% of GPP). Our mass balance approach for estimating components of the carbon budget would not reveal an internal cycle in which CO₂ generated by woody respiration was exactly matched by canopy photosynthesis used for woody respiration. However, such a cycle (if it exists) would entail offsetting fluxes and would not change our conclusions.

Mechanism and generality

We have isolated the proximate cause of ANPP_w decline for this study as a decline in GPP accompanied by a shift in annual partitioning in TBCA and R_f . However, we have not identified a mechanism that would lower GPP when LAI and photosynthetic capacity remain high. None of the proposed processes in hypothesis 2 was supported by this study. We suggest two possibilities: (1) a broader interpretation of the hydraulic limitation hypothesis (Barnard and Ryan 2003) that would account for the carbon costs of moving water higher when trees compensate for height by changing the ratio of sapwood to leaf area (McDowell et al. 2002a), leaf water potential (Yoder et al. 1994, Barnard and Ryan 2003), or sapwood conductivity (Pothier et al. 1989); or (2) changes in light capture or light capture relative to foliar N distribution as canopy structure changes with stand development (from a monolayer to a complex surface [Parker et al. 2002]). For this study, the respiration cost of a higher sapwood : leaf area in taller trees was negligible, but lower leaf water potential may have disrupted translocation and reduced photosynthesis (Barnard and Ryan 2003). The effect of structural changes in the canopy with stand development on GPP remains to be explored.

NPP_w decline also coincided with the differentiation of the canopy into dominant, intermediate, and over-

topped trees, and dominant individuals had higher ANPP_w per unit of light, water, or N used (Binkley et al. 2002). If ANPP_w decline is promoted by this differentiation and the emergence of "inefficient" subordinate trees, the inefficiency is likely to be caused by differences in crown photosynthesis among trees, not belowground allocation, because belowground allocation was a relatively constant fraction of GPP throughout stand development, whereas GPP declined.

The decline in ANPP_w appears to be almost universal, but would the decline in GPP that we found apply to the development of even-aged forests elsewhere? We suggest a tentative "yes." We think that other processes might reduce ANPP_w as forests increase in size and age, such as a reduction in leaf area resulting from nutrient deficiencies or canopy abrasion, or a hydraulic limitation with increasing tree height and path length. However, we hypothesize that these processes might increase the rate of age-related (or size-related) decline in wood growth, but that the decline in GPP might be a driver that would apply even when other potential drivers do not apply. We are continuing this line of research with irrigated and fertilized stands of clonal *Eucalyptus* in Brazil to test some of the possible mechanisms that drive the decline in both ANPP_w and GPP with stand age.

Respiration is an unlikely candidate to explain a decline in ANPP_w elsewhere, because angiosperms in this study (in a tropical climate where respiration costs are expected to be the highest) confirmed results from a study on subalpine conifers (Ryan and Waring 1992). Additionally, various studies indicate that autotrophic respiration is a nearly constant fraction of GPP (Gifford 1994, Ryan et al. 1994, 1996, 1997b, Waring et al. 1998, Tjoelker et al. 1999). Model analyses (Hunt et al. 1999, Makela and Valentine 2001) that indicate respiration as the cause should consider modeling respiration as driven by substrate availability (Dewar et al. 1999), not as a fixed "tax."

This study and one with a subalpine conifer (Smith and Resh 1999) show that the flux of fixed carbon to TBCA varies in concert with ANPP_w. The vastly different climate and physiology of the trees in these two studies suggest that increased belowground allocation is unlikely to be a general driver of ANPP_w decline elsewhere. However, increased partitioning to TBCA did compound the decline in ANPP_w initiated by a decline in GPP in this study, and belowground allocation remains the least understood component of a forest's carbon cycle.

Declining nutrient availability with stand development may accelerate the decline in GPP and ANPP_w, as in this study. However, the decline of GPP and ANPP_w in our study under high fertility, with high leaf area and photosynthetic capacity, strongly suggests that nutrition alone will not offset a decline in GPP or ANPP_w. A decline in GPP might be general, but a variety of factors could lower GPP: stomatal closure

promoted by tree height (Yoder et al. 1994) or more complex branching patterns, other limits to photosynthesis (Barnard and Ryan 2003), a decline in LAI (Ryan et al. 1997a), a change in structure (Binkley 2004), limits to the plasticity of allocation, or changes in leaf demography to an older average population.

A single experiment with one species may not capture the suite of processes and rates that would be important in other forests. Ryan et al. (1997a) noted that the decline in stem growth appeared to begin universally near the time of full canopy expansion, but it is possible that further information on different sites or species could find different patterns. Some studies on *Pinus radiata* (Garcia 1990) suggest that age-related decline in stem growth may be less dramatic (or non-existent) near the age when full canopy has been reached. The experimental approach used here should be very useful for examining any differences among species (and genera) in the overall patterns of growth with forest age.

CONCLUSION

ANPP_w peaked at canopy closure, and then declined by half, and the decline was primarily caused by a decline in canopy carbon gain (GPP) and secondarily caused by a shift in the annual partitioning of GPP to belowground allocation and foliage respiration. Our study firmly rejected the traditional hypothesis that increased respiration of woody tissues forces a decline in ANPP_w. GPP declined even under high nutrient availability, when leaf area, canopy N content and photosynthetic capacity remained high. A decline in GPP may be the general proximate cause of a decline in ANPP_w, but several mechanisms may contribute to a decline in GPP with stand development. A hydraulic limitation to canopy conductance was not responsible for the decline in GPP, but we did not identify the mechanism that was.

Although the *Eucalyptus* forest experienced rapid growth, patterns of stand development were similar to those found in temperate forest chronosequences: ANPP_w peaked at canopy closure, ANPP_w declined after canopy closure, and the standing biomass at canopy closure was similar to that of other forests. Future studies of forest development using chronosequences or developing stands should include a treatment with high nutrient availability to avoid confounding any structural or physiological changes with changes in nutrient availability caused by stand development or site-to-site differences.

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APPENDIX: Symbols and abbreviations.

Symbol	Term and definition
GPP	gross primary productivity: annual net canopy photosynthesis during daylight
NPP	net primary production: annual dry matter production
ANPP _w	aboveground net primary production of wood, bark, and branches
NPP _F	net primary production of foliage
R _A	autotrophic respiration
R _F	respiration of foliage
R _w	respiration of aboveground woody components
TBCA	total belowground carbon allocation (including root and mycorrhizae production and respiration and root exudation)
A _{max}	maximum photosynthesis rate per unit leaf area; photosynthesis measured under conditions of saturating light (photosynthetically active radiation > 1300 μmol photons·m ⁻² ·s ⁻¹), high humidity (vapor pressure deficit < 0.05 kPa) and ambient CO ₂ concentration (360 μmol/mol)
V _{cmax}	maximum carboxylation velocity: maximum rate at which the photosynthetic enzyme, RUBISCO, can process CO ₂
LAI	leaf area index: the area that foliage from a column would cover if all leaves were laid flat on ground
F _S	CO ₂ efflux from the soil-litter surface (soil respiration)
F _A	litterfall
ΔC _S	annual change in carbon stored in mineral soil
ΔC _L	annual change in carbon stored in the soil organic layers (litter layer)
ΔC _R	annual change in carbon stored in live roots

Note: All units are kg C·m⁻²·yr⁻¹ except for A_{max} and V_{cmax} (in μmol·m⁻²·s⁻¹) and LAI (dimensionless, m²/m²).