Complementary resource use by tree species in a rain forest tree plantation

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Abstract. Mixed-species tree plantations, composed of high-value native rain forest timbers, are potential forestry systems for the subtropics and tropics that can provide ecological and production benefits. Choices of rain forest tree species for mixtures are generally based on the concept that assemblages of fast-growing and light-demanding species are less productive than assemblages of species with different shade tolerances. We examined the hypothesis that mixtures of two fast-growing species compete for resources, while mixtures of shade-tolerant and shade-intolerant species are complementary. Ecophysiological characteristics of young trees were determined and analyzed with a physiology-based canopy model (MAESTRA) to test species interactions. Contrary to predictions, there was evidence for complementary interactions between two fast-growing species with respect to nutrient uptake, nutrient use efficiency, and nutrient cycling. Fast-growing *Elaeocarpus angustifolius* had maximum demand for soil nutrients in summer, the most efficient internal recycling of N, and low P use efficiency at the leaf and whole-plant level and produced a large amount of nutrient-rich litter. In contrast, fast-growing *Grevillea robusta* had maximum demand for soil nutrients in spring and highest leaf nutrient use efficiency for N and P and produced low-nutrient litter. Thus, mixtures of fast-growing *G. robusta* and *E. angustifolius* or *G. robusta* and slow-growing, shade-tolerant *Castanospermum australe* may have similar or even greater productivity than monocultures, as light requirement is just one of several factors affecting performance of mixed-species plantations. We conclude that the knowledge gained here will be useful for designing large-scale experimental mixtures and commercial forestry systems in subtropical Australia and elsewhere.

Key words: Australia; Castanospermum australe; Elaeocarpus angustifolius*; Grevillea robusta; MAESTRA; nutrient cycling; nutrient use efficiency; tree mixtures.*

Introduction

The emerging interest in mixed-species plantations is based on the recognition that systems with greater tree diversity have ecological benefits not provided by monocultures. Benefits of mixed-species plantations include improved soil fertility and nutrient cycling, reduced erosion (Binkley et al. 1992, Montagnini 2002, Russell et al. 2004), greater resilience against pests and diseases (Ewel 1986, Brown and Ewel 1987, Wazihullah et al. 1996), diversity of high-value timber products and reduced market risk (Russell et al. 1993, Lamb and Tomlinson 1994, Harrison et al. 2000), improved landscape aesthetics (Herbohn et al. 2005), provision of wildlife habitats or corridors, and restoration of biodiversity on degraded lands (Lamb et al. 2005*b*). Further, mixed-species plantations can have higher biomass production and carbon (C) sequestration than

monocultures (DeBell et al. 1989, Forrester et al. 2004, Erskine et al. 2006). Thus, mixed-species plantations potentially meet numerous economic, silvicultural, and sustainability objectives (Forrester et al. 2005).

Two processes have been put forward as mechanisms responsible for higher productivity in mixed-species plantations compared with monocultures (Kelty 1992). One mechanism considers complementary resource use, also termed "good ecological combining ability" (Harper 1977), which reduces competition for limiting resources (Vandermeer 1989, Kelty 2006). Complementary resource use can occur in mixtures in which species use different resources or use the same resource at different points in time or space (Vandermeer 1989). Matching of functional traits related to resource use underlies theories considering effects of biodiversity on ecosystem functioning (Hooper et al. 2005). For example, in mixed-species tree plantations canopy stratification between shade-tolerant and intolerant species reduces light competition and increases light interception (Haggar and Ewel 1997, Menalled et al. 1998, Forrester et al. 2005, Amoroso and Turnblom 2006, Manson et al. 2006). Similarly, greater niche exploitation occurs in mixtures with distinct foliar phenology of deciduous and

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evergreen tree species (Kelty 1992) and in mixtures with complementary root structures and nutrient requirements (Ewel 1986, Lamb and Lawrence 1993, Haggar and Ewel 1997, Rothe and Binkley 2001). Rooting niche complementarity for both water and nutrients has been explored extensively in agroforestry systems (Ong and Leakey 1999, Schroth 1999), but is less commonly applied to tree mixtures (Coll et al. 2008). Overall, mechanisms based on complementarity imply that productivity in mixtures can increase only when the proportion of resources captured, such as light or nutrients, increases or when individuals become more efficient at using the available resources (Binkley et al. 2004).

The second mechanism put forward as causing greater productivity of mixtures than monocultures involves facilitation: one species having a positive effect on another species (Vandermeer 1989). Facilitation has been observed in mixtures containing N_2-fixing trees in which increased soil N availability enhances growth of non-fixing trees (Forrester et al. 2006). Positive modification of soil water relations (Vandermeer 1989) or light environment in plantings beneath nurse trees (Ashton et al. 1997) and reduction of pest attack (Brown and Ewel 1987) are other examples of the facilitative principle.

Despite demonstrated ecological and production advantages of tree mixtures over monocultures, studies of mixed-species plantations have been limited to few species combinations. Little information exists that could be used for prescribing plantation designs that maximize productivity, particularly for mixed plantations of rain forest timber species, which are increasingly planted in Australia's subtropics and elsewhere. In subtropical and tropical Australia, ~7000 ha of mixed-species plantations of native high-value rain forest timber species, which were previously logged from native forests, have been planted in the past 20 years to restore forest cover and for timber production (Bristow et al. 2001, Lamb et al. 2005a, Vize et al. 2005). The most common design of these plantations is a mixture of fast- and slow-growing species (Erskine et al. 2005b). Results from a small number of experimental plantings suggest that pairings of fast-growing and light-demanding species are less productive than pairings of species with different shade tolerances (Erskine et al. 2005a, Lamb et al. 2005c, Manson et al. 2006). However, physiological and silvicultural causes of different tree species' interactions in mixtures have not been established (Lamb et al. 2005c).

Our objective was to examine physiological traits of three functionally different and commonly planted rain forest timber trees and to predict outcomes of interactions in mixed-species plantations. Here the term "rain forest timber tree" refers to species found in subtropical notophyll vine forest in accordance with Webb (1959) or subtropical moist forest based on Holdridge (1947). *Elaeocarpus angustifolius* F. Muell. ("blue quandong"),

Grevillea robusta Cunn. Ex. R. Br. ("silky oak"), and *Castanospermum australe* Cunn. & C. Fraser ex Hook ("black bean") are fast-, medium-fast-, and slow-growing trees, respectively. We examined the hypothesis that mixtures of two fast-growing species (*G. robusta* and *E. angustifolius*) compete for resources, while mixtures of shade-tolerant (*C. australe*) and intolerant (*G. robusta* or *E. angustifolius*) species are complementary. Because no field trials exist in which these species are grown in monoculture and binary mixtures, we studied young trees grown at wide spacing in a mixed-species plantation. Canopies were not closed, and it was assumed that trees were not competing for aboveground resources. Leaf physiological measurements were combined with computer modeling to test hypotheses of stand dynamics under different species combinations without the need for expensive long-term field trials.

It should be noted, however, that results presented are site-specific and do not consider belowground nutrient interactions; therefore, caution should be used before applying these findings too widely. On the other hand, we consider this study useful for providing one of the first physiological demonstrations of complementary interactions for nutrients and light in Australian subtropical rain forest tree mixtures. Establishing a scientific basis for the design of future private plantations or large-scale field demonstrations in subtropical Australia could encourage further uptake of mixed rather than monoculture plantings (Nichols et al. 2006) and improve the sustainability of forest industries.

METHODS

Study site and species

The mixed-species tree plantation was located on private land near Maleny in southeast Queensland, Australia (26°45′97″ S, 152°52′44″ E). The 3.5-ha plantation was established on an east-facing slope (~11°), 420 m above sea level in March 2000. The previous land use was a dairy farm dominated by introduced pasture species including *Pennisetum clandestinum* Hochst. ex Chiov. The dairy farm was established on cleared primary rain forest that would have contained many of the rain forest tree species now present in the plantation. Prior to planting tree seedlings, pasture was eradicated with an herbicide in 2 m wide strips along the contour; these strips were chisel ploughed, rocks were removed, and the strips were planted with a cover crop. Nursery-supplied tree seedlings (~0.15 m high) established from local seed, where possible, were planted on 4-m centers with a small application of di-ammonium phosphate fertilizer, and the slashed cover crop was provided as mulch. Each 2 m wide planting strip was separated by a 2 m wide strip of original pasture to prevent erosion. Twenty-seven high-value timber tree species were planted at a density of 629 trees/ha, with 4 × 4 m spacing in diagonal, alternating rows of fast- and slow-growing species. The study trees were located mid-slope in the center of the plantation.

Measurements were made from 2004 to 2006 before canopy closure had occurred and it was assumed that species were not competing for light with neighboring trees.

Mean annual rainfall at the site is 1957 mm (Bureau of Meteorology, Maleny) with most rainfall occurring in summer (December–February). However, during two of the three study years, total annual rainfall was below average (2004, 1943 mm; 2005, 1569 mm; 2006, 1388 mm). The climate is subtropical with a mean maximum temperature of 29°C in summer (December–February) and a mean minimum of 9°C in winter (June–August). Hourly temperature and humidity measurements were recorded at the plantation (CR10X data logger, CS500 temperature and relative humidity sensors; Campbell Scientific, Logan, Utah, USA), while rainfall data were obtained from a weather station 5 km away (Appendix B, Bureau of Meteorology, Maleny). Soil moisture was logged monthly from September 2004 to January 2006 using a portable soil moisture probe (Diviner 2000, Sentek, Stepney, South Australia) (Appendix B). Readings were taken to 0.7 m depth in permanent PVC access tubes located close to and 2 m away from 3–4 replicate trees of each species. Soil moisture content was calculated using the probe's default calibration equation. The plantation soil is Red Ferrosol (Isbell 2002) and initial nutrient tests prior to planting indicated that the soil had minor phosphorus and molybdenum deficiency (D. Haynes, *personal communication*).

The three study species were chosen for their contrasting growth rates and functional traits. *Elaeocarpus angustifolius* (Elaeocarpaceae) is a fast-growing, early secondary successional canopy rain forest tree endemic to forests from northern New South Wales to northern Queensland, mostly growing along creek banks in areas of high rainfall (>1000 mm; Boland et al. 2006). *Grevillea robusta* (Proteaceae) is a fast-growing, later secondary successional semi-deciduous tree in rain forests and vine thickets. Although commonly observed growing near creeks, *G. robusta* also occurs on exposed hillsides in subtropical regions of Australia with rainfall >720 mm (Boland et al. 2006). *Castanospermum australe* (Fabaceae) is a slow-growing, late-successional rain forest tree with a wide distribution in eastern Australia from northern New South Wales to Cape York Peninsula in northern Queensland, where it typically occurs as a canopy tree in gallery-type rain forests next to streams and in areas with rainfall >1000 mm (Boland et al. 2006).

Gas exchange measurements

Photosynthetic light response curves (AQ) and CO_2 response curves (AC_i) were conducted in summer (December to February) after rainfall. Youngest, fully expanded mature leaves and older, shaded leaves were chosen for measurements from north-facing branches on four trees of each species. Branches were reached via a moveable platform 1.5 m high. Only lower branches of *G. robusta* and *E. angustifolius* species could be measured. Photosynthesis was measured with a portable photosynthesis system (LI-6400, LI-COR, Lincoln, Nebraska, USA) equipped with a CO_2 control module and a light source of red and blue light-emitting diodes. The AC_i curves were determined by measuring the response of net photosynthesis (A) to varying intercellular CO_2 concentrations (C_i). External CO_2 was supplied in decreasing concentrations from 400 to 50 μmol CO_2/mol, followed by increasing amounts from 600 to 1600 or 2000 μmol CO_2/mol in 11 steps. During AC_i curve measurements irradiance (Q) was maintained at saturating levels: 2000, 1500, and 1000 μmol·m^{-2}·s^{-1} for *E. angustifolius*, *G. robusta*, and *C. australe*, respectively. The AQ curves were determined by measuring the response of A to varying levels of Q at a constant external CO_2 concentration of 400 μmol/mol. Irradiance was reduced from 2500 μmol photons·m^{-2}·s^{-1} to darkness in 12 steps for sun leaves of *E. angustifolius* and *G. robusta* or from 2000 μmol photons·m^{-2}·s^{-1} to darkness in 11 steps for sun leaves of *C. australe*. Photosynthesis values for both curves were recorded once rates had equilibrated and stomatal conductance values were >0.05 μmol CO_2·m^{-2}·s^{-1}. The dark respiration rate (R_d) was taken as the leaf photosynthetic rate at the end of the AQ curve after leaving the leaf in the darkened chamber for 5 min. Ambient leaf temperature was maintained (±1°C) during measurements. Measurements were completed in the morning as trees generally reduced photosynthetic rates at midday. During measurements airflow rate into the chamber was kept constant (400 μmol·m^{-2}·s^{-1}), and leaf-to-air vapor pressure deficit reflected ambient conditions. *Grevillea robusta* has strongly lobed leaves that did not cover the cuvette. Thus, the leaf area inside the cuvette was marked during measurements, measured using scanner and image analysis software (Leaf Area Measurement version 1.3; University of Sheffield, Sheffield, UK), and photosynthetic rates were recalculated with the actual leaf area.

The AC_i curves were analyzed to determine three biochemical parameters: the maximum rate of Rubisco carboxylation (V_{cmax}), the maximum rate of electron transport (J_{max}), and day respiration rate (R_{day}), based on the model of Farquhar et al. (1980) as modified by von Caemmerer and Farquhar (1981). In the model we assume that internal conductance to CO_2 (g_i) is infinite, and therefore C_i is equivalent to the chloroplastic CO_2 concentration. Although there is evidence that this is not the case (Warren 2006), an assessment of g_i was beyond the scope of this study. Values for Michaelis-Menton constants (K_c and K_o) and the intercellular CO_2 photo-compensation point (Γ^*) were taken from von Caemmerer et al. (1994): $K_c = 259$ μbar, $K_o = 179$ mbar, $\Gamma^* = 38.6$ μbar at 25°C. Temperature dependence was modeled using an Arrhenius function and activation energies (H_a) from Bernacchi et al. (2002): $H_a(K_c) =$

80.99 kJ/mol, $H_a(K_o) = 23.72$ kJ/mol, $H_a(\Gamma^*) = 24.46$ kJ/mol. These constants were chosen because they were determined in vivo at chloroplastic CO_2 concentrations, which is an assumption of the Farquhar-von Caemmerer model (Ethier and Livingston 2004). The temperature dependence of V_{cmax} and J_{max} was modeled using a peaked function and mean values for tree species reviewed by Medlyn et al. (2002): $H_a(V_{cmax}) = 69.92$ kJ/mol, $H_a(J_{max}) = 55.69$ kJ/mol, $H_d = 200$ kJ/mol, $\Delta S(V_{cmax}) = 634.54$ J/mol, $\Delta S(J_{max}) = 607.56$ J/mol. The temperature response of R_{day} was modeled with an Arrhenius function described by Bernacchi et al. (2001): $H_a(R_{day}) = 46.39$ kJ/mol. Both V_{cmax} and R_{day} were determined from the substrate-limited section of the AC_i curve by varying the C_i cut-off point from 150 to 500 µmol/mol and selecting values from the best least-squares regression fit. The remaining points in the curve and the calculated R_{day} value were used to estimate J_{max}.

The AQ curves were analyzed to determine the maximum rate of photosynthesis (A_{max}) under saturating light and ambient CO_2 concentrations, the apparent quantum yield of photosynthesis (Φ), and the curvature (Θ) by fitting a nonrectangular hyperbola function to the data (Farquhar and Wong 1984). Data collected at $Q < 50$ µmol·m^{-2}·s^{-1} were excluded from the least-squares fits to avoid overestimation of Φ due to the "Kok effect" (Sharp et al. 1984). Transition to triose-phosphate utilization (TPU)-limited photosynthesis at high irradiance was not observed in our AQ curves.

Instantaneous measurements of maximum photosynthesis at 400 µmol/mol external CO_2, ambient temperature and humidity, and 2000, 1500, or 1000 µmol·m^{-2}·s^{-1} irradiance were recorded along an age sequence of 15 leaves for *E. angustifolius*, *G. robusta*, and *C. australe* trees, respectively. Photosynthetic rates were recorded from the first fully expanded adult leaf and then on subsequent leaves along the branch where branch position correlated to increasing leaf age (branch chronosequence). This method is acceptable if successive leaf production occurs in a species (Kitajima et al. 2002). The species in this study produce leaves throughout the year although there are seasons in which leaf production is more pronounced; because this could bias our results we only describe trends in the data without further analysis. Instantaneous measurements of photosynthesis were recalculated to a common leaf temperature (25°C) and C_i (250 µmol/mol) using simulated values of A and C_i produced from measured V_{cmax}, J_{max}, and R_{day} parameters.

Fifteen youngest fully expanded new leaves on *E. angustifolius* and *G. robusta* trees were tagged in summer (December to February) 2005, and photosynthetic rates were determined on each tagged leaf every month over a six-month period. The results from this experiment were used to determine the approximate leaf ages of the branch chronosequence study. For both species, the first three leaves in the chronosequence were <80 d old and were classed as young leaves, while the remainder were classed as older leaves. For *C. australe* the first three youngest leaves were <120 d old (see *Foliage characteristics*).

Foliage characteristics

Following gas exchange measurements, leaves were collected and leaf area was determined using a scanner connected to image analysis software (Leaf Area Measurement). Leaves were dried at 65°C, and measurements of dry mass were used to calculate leaf mass per area (LMA). The dried samples were ground and analyzed for C and nitrogen (N) content in a combustion furnace (LECO CNS-2000, LECO, St. Joseph, Michigan, USA). A subset of samples was analyzed for phosphorus (P) content using nitric acid digestion and detection by inductively coupled plasma atomic emission spectrometry (Rayment and Higginson 1992).

Recently fallen litter was collected from shade cloth placed beneath six trees of each species. Litter was collected from the cloth in intervals of six days or less and discarded if heavy rainfall occurred between collections. Litter was dried at 65°C and ground before analysis for C, N, and P content. Measured resorption efficiency (MRE) (van Heerwaarden et al. 2003) was calculated as

$$MRE = 100\% \times \left(1 - \frac{N_{abs}}{N_{green}}\right) \qquad (1)$$

where MRE is the amount of N (or P) resorbed from old leaves during leaf abscission and N_{abs} (in grams per square meter) is calculated using the LMA of the last (closest to the stem) three leaves from the photosynthesis age sequence (assuming no change in leaf area between old and abscised leaves, LMA = 98.2, 96.8, and 95.8 g/m^2 for *E. angustifolius*, *G. robusta*, and *C. australe*, respectively) and the N (or P) content (in milligrams per gram) of litter, while N_{green} is the N (or P) content (in grams per square meter) of these same three leaves (2.4, 1.8, 2.4 g N/m^2 and 0.13, 0.06, 0.10 g P/m^2, respectively).

A sequence of 10 leaves removed sequentially from the branch tip to the tree stem from both lower- and upper-canopy north-facing branches were collected from four replicate trees of *E. angustifolius* and *C. australe*. Leaves were immediately stored cold and transferred to the laboratory where leaf light absorption, transmission, and reflection (λ, 400–1100 nm) was measured by a spectroradiometer (Unispec, PP systems, Amesbury, Massachusetts, USA) connected to an integrating sphere and light source (LI 1800-12, LI-COR), within 24 h. Only lower-canopy leaves were measured for *G. robusta* because the leaf area of upper-canopy leaves was insufficient to cover the detector.

Leaf production and mortality was recorded monthly on lower branches from three trees per species over an average of 462 d. Leaf cohorts were tracked with colored wire tied around leaf petioles. A total of eight branches were measured for *G. robusta*, six branches for *E. angustifolius*, and three branches for *C. australe*. Leaf

life span was calculated as the mean time a leaf remained on a branch (±15 d), that is, the average of the maximum possible leaf age (assuming the leaf was produced one day after the previous month's census) and the minimum possible leaf age (assuming the leaf was produced one day before the current census). Many leaves of *C. australe* remained on the tree longer than the measurement period so values reported represent the minimum leaf life span. Near the end of the experiment several branches on *E. angustifolius* study trees died because these lower branches were shaded by higher branches; therefore, only leaf life span calculations from leaves produced at the start of the study were used from these branches. The proportion of leaves in two age classes (young and older) at each time point or season was calculated using age cutoff points determined from the photosynthesis measurements described previously, except for *C. australe*, for which tagged branches were the same branches as the chronosequence study and leaf age was determined directly. Therefore, young leaves were classed as <80, <80, or <120 d old for *E. angustifolius*, *G. robusta*, and *C. australe*, respectively.

Tree growth and architecture

Tree heights of 14 *C. australe* trees and 20–21 trees of *G. robusta* and *E. angustifolius* were measured at the start and end of the experiment using a clinometer. The difference between the height of the lowest branch and total tree height was used to determine mean crown height for four trees of each species. Trees measured for height were also measured for diameter at breast height (at 1.3 m above the ground surface), which was recorded every three months over 21 months for *G. robusta* and *E. angustifolius* using stainless steel dendrometer bands (Cattelino et al. 1986). Due to rapid tree growth, band slack was negligible one month after installation and no measurement corrections were necessary (Auchmoody 1976). *Castanospermum australe* stems were too small to permit band fitting so diameter at breast height was only recorded at the start and end of the experiment on 17 trees using digital callipers and a spirit level. Stem basal areas were summed before back-calculating total tree diameter for *C. australe* with multiple stems.

Total stem biomass was estimated using volume equations determined from rain forest trees harvested from native forests (Eamus et al. 2000): *E. angustifolius* and *G. robusta*, $V = (-0.4098 + 0.7756 \times L - 0.01027 \times L^2) \times (BA + 0.023)$; *C. australe*, $V = (0.03692 + 0.6379 \times L - 0.005208 \times L^2) \times (BA + 0.023)$, where V is stem volume (in cubic meters), L is length (in meters) of the main stem, and BA is stem basal area (in square meters) at 1.3 m. These equations were also used to calculate the volume of any branches >4 cm diameter on each species. Stem and branch biomass was calculated from wood density values of 390 and 448 kg/m^3 determined on 8-yr-old trees of *E. angustifolius* and *G. robusta*, respectively (Glencross and Nichols 2005). The lowest

reported wood density value of 565 kg/m^3 was used for *C. australe* stem and branch biomass calculations (Boland et al. 2006).

Relationships between leaf number and branch diameter were determined for each species in autumn 2006 when trees were pruned. Lower branches were counted from four trees for each species producing a total of 63, 51, and 68 branches for *E. angustifolius*, *G. robusta*, and *C. australe*, respectively. Branch diameter was measured 5 cm from the base. Extrapolations of these relationships to trunk diameter were performed to estimate total leaf area of each tree at the start of the leaf phenology study. It was assumed that the relationship between leaf number and branch diameter determined in autumn 2006 on lower branches did not vary with season or canopy position. Leaf areas of pinnate *C. australe* leaves were estimated by multiplying the mean leaflet area by the mean number of leaflets per leaf (15 ± 2, $n = 68$). Whole leaf areas of young, intermediate, and old pinnate *G. robusta* leaves were recorded separately to LMA measurements with a leaf area meter (LI 3100, LI-COR).

Tree crown nutrient calculations

Tree crown nutrient content and nutrient demand were calculated using the following steps and assumptions: (1) The percentage of young and older leaves and the fraction of new leaves produced or leaves lost per month on a branch were assumed to be representative of the entire crown at each census date. (2) Total tree leaf area at the start of the leaf phenology study was determined from the relationship between tree diameter and leaf number multiplied by the mean leaf area. This area was modified each month by the fraction of leaves produced and lost from the studied branches. (3) Leaf N and P contents for each leaf class (young and old) were used to calculate total N and P content in the crown leaf biomass of each tree:

$$N_t = \left(n \times \frac{y}{L} \times N_y \times a_y \right) + \left(n \times \frac{o}{L} \times N_o \times a_o \right) \qquad (2)$$

where N_t is the total biomass of N in the crown at the census time, n is the total number of leaves in the crown at the census time, y is the total number of young leaves on the census branch, o is the total number of old leaves on the census branch, L is the total number of leaves on the census branch, $N_{y,o}$ is the N content (in grams per square meter) of young and old leaves, respectively; and $a_{y,o}$ is the area (in square meters) of young and old leaves, respectively. This calculation assumes that N and P contents of young and old leaves do not vary at different depths in the crown. (4) The amount of N needed to maintain crown nutrient biomass between census periods was calculated as

$$N_{dem} = N_t - N_{t-1} - (N_{green} - N_{abs}) \qquad (3)$$

where N_{dem} at time t (census date) is positive if more N is required for new leaf growth than that resorbed from

senescing leaves or negative if more N is resorbed from senescing leaves in excess of foliage requirements. A similar calculation was made for tree P demand. It was assumed that the proportion of N or P resorbed did not vary at different times of the year or at different points in the canopy and that losses of leaf N and P from leaching were minimal.

Total tree nutrient use efficiency was calculated by adding stem and branch biomass to total leaf biomass to produce an estimate of aboveground biomass for each species at each census date. The change in aboveground tree biomass over a year was divided by the mean crown N and P content of each species and termed canopy N and P use efficiency (CNUE and CPUE) after Harrington et al. (1995).

Model description and parameterization

The MAESTRA model (Medlyn 2004; *available online*),[4] an updated version of MAESTRO (Wang and Jarvis 1990), is a three-dimensional model of forest canopy radiation absorption, photosynthesis, and transpiration. We used MAESTRA to test the effects of different light environments on canopy photosynthesis of each study species under five different scenarios: growing as a single tree (single), growing in a monoculture of the target tree (monoculture), growing in a monoculture of another tree species, growing in a plantation of trees 50% shorter than the target tree (short) or 50% taller (tall). For the "short" tree scenario, tree dimensions of *C. australe* were used for *E. angustifolius* and *G. robusta* simulations, and for the "tall" tree scenario *E. angustifolius* dimensions were used for *C. australe* simulations. The plantation was represented as a three-dimensional array of tree crowns, with each crown given an *x* and *y* coordinate in a 4 × 4 m grid pattern with a 4-m gap between the edge of the plantation and the first tree. Each tree in the plantation was given a mean value for height, stem diameter, trunk space, canopy radius, and leaf area (Appendices A and B), except for the target tree, for which measured values for that specific tree were used. Daily meteorological data (air temperature, humidity, precipitation) were used as model inputs and incident photosynthetically active radiation was calculated from the mean daily temperature amplitude (Bristow and Campbell 1984). Leaf angle, leaf area distribution, and canopy shape of each tree species was not measured and values were chosen from general tree observations (Appendix A). The MAESTRA physiology sub-model included parameters for an empirical model of stomatal conductance (Ball et al. 1987), which were fitted to data used to derive photosynthetic parameters according to Medlyn et al. (2005) (Table 1). Leaf N and specific leaf area (Table 2), photosynthetic parameters, foliage respiration rates, leaf reflectance,

and leaf light transmittance data were also included (Table 1). Default values were used for any parameters not listed in Table 1 or Appendix A. We report values for both gross (P_g) and net canopy photosynthesis (P_n), however, because stem and root respiration parameters such as Q_{10} were not measured for the study species, the net photosynthesis rates are estimates only. An accurate validation of the MAESTRA model was not possible because MAESTRA simulates a single-species stand. Rather, we used the model to analyze hypotheses of the effects of light on species' photosynthetic rates, while future testing of these concepts in experimental plots would complete this study.

RESULTS

Tree growth

Tree height increased over the study period at a rate of 1.6 m/yr for *E. angustifolius* and *G. robusta* and 1.4 m/yr for *C. australe*. At the end of the study in March 2006, *E. angustifolius* had a mean height of 13 m, while *G. robusta* and *C. australe* were 10 m and 6 m high, respectively. Mean diameter growth rates for *E. angustifolius* and *G. robusta* ranged from 0.06 and 0.12 cm/month in winter (June to August) 2004 to 0.53 and 0.56 cm/month in summer (December to February) 2005, respectively (Appendix B). Both species had the same mean annual diameter increment of 3.6 cm/yr. Measured only at the start and completion of the study, *C. australe* had a lower annual increment of 2.5 cm/yr and an average stem diameter of 9.6 cm in March 2006. Seedlings of all species were planted as similar-sized tube stock, and annual stem diameter increment calculated over the six years since plantation establishment differed significantly ($P < 0.05$) between species, ranging from 1.6 ± 0.3 cm/yr (mean ± SD) for *C. australe* to 3.5 ± 0.5 cm/yr for *G. robusta* and 4.1 ± 0.4 cm/yr for *E. angustifolius*.

Foliage characteristics

Foliage of *E. angustifolius* had highest P and intermediate N contents, *C. australe* had highest N and intermediate P contents, while *G. robusta* had lowest N and P contents (Tables 2 and 3). Expressed on a mass basis, leaf N and P contents mostly ranked young > old > litter. The C:N ratios were highest in *G. robusta* leaves and litter compared to the other species, while young leaves within species had the lowest, and litter the highest, C:N ratios. The N:P ratios were generally similar across ages and species, although older leaves of *G. robusta* had higher N:P ratios than *E. angustifolius* leaves. There was no difference between N contents of young and old leaves in each species when expressed on an area basis due to differences in LMA between species (Tables 2 and 3). *Elaeocarpus angustifolius* and *C. australe* had significantly lower LMA than *G. robusta*. In contrast to N contents, P (per unit leaf area and leaf

TABLE 1. MAESTRA model parameters for *Elaeocarpus angustifolius*, *Grevillea robusta*, and *Castanospermum australe* (means with SE in parentheses).

Parameters	E. angustifolius	G. robusta	C. australe
Photosynthesis model			
V_{cmax} (μmol CO_2·m^{-2}·s^{-1})	52.1 (7.7)	47.8 (2.9)	39.1 (1.7)
J_{max} (μmol e$^-$·m^{-2}·s^{-1})	100.2 (12.8)	106.4 (6.3)	83.6 (5.6)
R_{day} (μmol CO_2·m^{-2}·s^{-1})	1.25 (0.22)	1.69 (0.23)	1.41 (0.13)
J_{max}:V_{cmax}	1.98	2.25	2.14
V_{cmax} (μmol CO_2·g^{-1} N·s^{-1})	17.9 (1.9)	18.3 (3.6)	14.9 (1.0)
J_{max} (μmol e$^-$·g^{-1} N·s^{-1})	34.7 (4.2)	41.6 (10.3)	31.8 (2.6)
A_{max} (μmol CO_2·m^{-2}·s^{-1})	11.4 (1.4)	15.3 (1.8)	8.7 (1.4)
Φ (mol CO_2/mol quanta)	0.04 (0.01)[b]	0.08 (0.01)[a]	0.04 (0.00)[b]
Θ	0.21 (0.05)	0.22 (0.18)	5×10^{-6}
Respiration parameters			
R_d (μmol CO_2·m^{-2}·s^{-1}) (°C)	1.78 (25.4)	1.45 (26.2)	0.94 (23.8)
Q_{10}†	2	2	2
Stomatal conductance model			
g_0 (mol H_2O·m^{-2}·s^{-1})	0.022	0.001	0.033
g_1	5.89	7.47	2.09
Γ (μmol/mol)	55.5 (1.0)	53.6 (0.7)	55.7 (1.8)
Leaf width (m)	0.046 (0.001)	0.008 (0.000)	0.035 (0.001)
Leaf properties			
Transmittance at 400–700 nm (%)	5[b]	8[ab]	8[a]
Reflectance at 400–700 nm (%)	27[b]	26[b]	34[a]
Transmittance at 700–3000 nm (%)‡	38	40	40
Reflectance at 700–3000 nm (%)‡	47	45	45
Thermal transmittance (%)	1	1	1
Thermal reflectance (%)	5	5	5

Notes: Respiration parameters include R_d, the rate of dark respiration (with measurement temperature reported in parentheses), and Q_{10}, the temperature response coefficient. Parameters for the Ball-Woodrow-Berry model of stomatal conductance include: g_0, stomatal conductance at $Q = 0$; g_1, model coefficient; and Γ, the light compensation point ($n = 4$–8). Different lowercase letters indicate significant differences between species ($P < 0.05$, Tukey's honestly significant difference test for unequal N). Other abbreviations are: V_{cmax}, maximum Rubisco carboxylation rate; J_{max}, maximum electron transport rate; R_{day}, day respiration rates; A_{max}, maximum rate of net photosynthesis; Φ, apparent quantum yield; Θ, curvature factor. The study was conducted at a mixed-species tree plantation located on private land near Maleny in southeast Queensland, Australia.

† Mean value from Meir et al. (2001).

‡ Westrup (1993).

mass) was highest in young leaves of *E. angustifolius* and lowest in old leaves of *G. robusta*.

Resorption efficiency of N from old leaves prior to abscission was significantly higher in *E. angustifolius*, followed by *G. robusta* and *C. australe* (Table 4). Similarly, resorption efficiency of P was lowest in *C. australe* leaves, although it was highly variable and not significantly lower than *E. angustifolius*. Leaves of *C.*

TABLE 2. Foliar nutrient content and leaf mass per area (LMA; mean with SE in parentheses) of different-aged leaves and litter of *Elaeocarpus angustifolius*, *Grevillea robusta*, and *Castanospermum australe* trees ($n = 4$ trees per species).

Leaf age	N (mg/g)	N (g/m^2)	C:N	P (mg/g)	P (g/m^2)	N:P	LMA (g/m^2)
E. angustifolius							
<80 d	25.6 (0.7)[bc]	2.08 (0.10)[ab]	18[e]	2.10 (0.17)[a]	0.16 (0.00)[a]	12[b]	82.3 (2.7)[b]
>80 d	23.3 (0.4)[cd]	2.16 (0.41)[a]	20[de]	1.44 (0.06)[b]	0.14 (0.00)[ab]	16[b]	94.0 (1.1)[b]
Litter	11.0 (0.2)[f]	1.05 (0.02)[cd]	42[b]	0.61 (0.07)[de]	0.06 (0.01)[ef]	18[ab]	ND
G. robusta							
<80 d	20.4 (0.9)[d]	2.15 (0.13)[ab]	24[d]	0.79 (0.00)[cde]	0.08 (0.00)[cde]	26[ab]	108.3 (4.5)[a]
>80 d	16.5 (0.4)[e]	1.88 (0.06)[b]	30[c]	0.61 (0.01)[de]	0.07 (0.00)[ef]	25[a]	110.9 (2.5)[a]
Litter	10.2 (0.3)[f]	0.94 (0.03)[d]	49[a]	0.43 (0.02)[e]	0.04 (0.00)[e]	24[a]	ND
C. australe							
<120 d	30.0 (1.0)[a]	2.52 (0.12)[a]	16[e]	1.37 (0.03)[b]	0.11 (0.00)[bc]	22[ab]	83.3 (2.8)[b]
>120 d	25.5 (0.7)[b]	2.32 (0.06)[a]	20[de]	1.18 (0.10)[bc]	0.11 (0.01)[bd]	21[ab]	92.0 (1.8)[b]
Litter	15.7 (0.5)[e]	1.46 (0.04)[c]	32[c]	0.78 (0.12)[d]	0.07 (0.01)[cf]	20[a]	ND

Notes: Different lowercase letters denote significant differences between measurements ($P < 0.05$, Tukey's honestly significant difference test for unequal N). "ND" indicates measurements that were not determined.

TABLE 3. Two-way ANOVA F statistics and significance values for the effects of species and leaf age on foliar nutrient content and leaf mass per area (LMA) of different-aged leaves and litter of *Elaeocarpus angustifolius*, *Grevillea robusta*, and *Castanospermum australe* trees.

Variable	df†	N (mg/g)	N (g/m^2)	C:N	P (mg/g)	P (g/m^2)	N:P	LMA (g/m^2)‡
Whole model	8	91.4***	35.6***	141.3***	35.3***	32.1***	6.7***	20.4***
Species	2	100.8***	21.5***	133.56***	61.7***	50.7***	18.8***	38.9***
Leaf age	2	216.1***	120.7***	400.8***	65.2***	64.0***	5.7**	10.1**
Species × leaf age	4	5.4***	NS	11.6***	11.5***	8.1***	NS	NS

** $P < 0.01$; *** $P < 0.001$; NS, not significant.

† Degrees of freedom for the error term are 386 for N and C/N, 36 for P and N/P, and 336 for LMA.

‡ Numerator degrees of freedom for LMA are 5, 2, 1, and 2 for the whole model, species, leaf age, and species × leaf age, respectively.

australe had the longest mean leaf life span of the studied species (Table 4), while *E. angustifolius* and *G. robusta* had similar mean and maximum leaf life spans.

Leaf phenology and nutrient budgets

Total leaf area of each tree was calculated from the relationship between leaf number (y) and branch diameter (x) for each species: *E. angustifolius*, $y = 0.505x^2 + 36.140x$ ($r^2 = 0.89$, $P < 0.001$, $n = 63$ branches); *G. robusta*, $y = 0.500x^2 - 3.784x$ ($r^2 = 0.86$, $P < 0.001$, $n = 51$ branches); *C. australe*, $y = 0.169x^2 - 1.212x$ ($r^2 = 0.87$, $P < 0.001$, $n = 68$ branches). From these equations the mean leaf area and leaf biomass per tree were calculated at different times of the year. Maximum leaf area and leaf mass per tree occurred in *E. angustifolius* in February and early March (134 m^2 and 9 kg in February 2006), when young leaves accounted for 74% of leaves in the tree crown. The lowest leaf biomass (5.3 kg) on *E. angustifolius* occurred in late October and corresponded to the period of maximum leaf fall. During this time, an average of 4–5 kg of leaves was lost from *E. angustifolius*, producing a flux of N and P to the litter layer (Fig. 1). From December to February, *E. angustifolius* regrew young foliage and produced a peak biomass of 6 kg/tree of young leaves (<80 d old) in early 2006 (Fig. 2). Only in summer did *E. angustifolius* have a net production of leaves, and leaves produced in this season had a longer mean leaf life span (241 d) compared to leaves produced in winter (97 d; data not shown).

Maximum leaf area and leaf mass in semi-deciduous *G. robusta* occurred in November 2005 (187 m^2 and 20 kg/tree), following replacement of all foliage in September (Fig. 2). During *G. robusta* leaf drop there was a flux of N to the litter layer, producing a total of 49 g N/tree returned in litter during August and September 2005, compared to 87 g N/tree in litterfall of *E. angustifolius* in October and November 2005 (Fig. 1). Input of P to the litter layer in *G. robusta* litterfall during maximum leaf drop in 2005 was 2 g P/tree, while it was more than double (5 g P/tree) for *E. angustifolius* during maximum leaf drop (Fig. 1). Leaves produced during winter and spring (June to November), when *G. robusta* foliage replacement was highest, had a mean leaf life span of 286 and 245 d, respectively, while leaves produced in autumn (March to May) had a mean life span of 157 d (data not shown).

Castanospermum australe produced a low amount of litter, with a maximum of 1.1 kg of leaves dropped in October 2005, corresponding to a flux of 14 g N·tree^{-1}·month^{-1} and 0.7 g P·tree^{-1}·month^{-1} to the litter layer (Fig. 1). Time of maximum leaf area (52 m^2/tree) and biomass (4.5 kg/tree) on *C. australe* was in mid-summer (January), similar to *E. angustifolius*, when 67% of the crown consisted of young leaves (<120 d old). Production of new leaves on *C. australe* peaked in October 2005 at a rate of 1.4 kg/tree, in the period between *E. angustifolius* and *G. robusta* leaf flush, although total new foliage biomass was much lower in *C. australe* than these two species (Fig. 2).

Total rainfall for the six months prior to December 2004 (354 mm) was ~50% of rainfall during the same period in 2005 (631 mm). The higher amount of rainfall in winter and the earlier start of summer rainfall in 2005 (Appendix B) correlates to the earlier loss of foliage and growth of new leaves in *E. angustifolius* in 2005 (Figs. 1

TABLE 4. Mean resorption efficiency and leaf life span (mean with SE in parentheses) of *Elaeocarpus angustifolius*, *Grevillea robusta*, and *Castanospermum australe*.

Species	N resorption (%)	P resorption (%)	Mean leaf life span (d)	Maximum leaf life span (d)
E. angustifolius	56.1 (0.8)[a]	54.1 (5.1)[ab]	228 (14)[b]	458
G. robusta	48.4 (1.4)[b]	68.7 (1.5)[a]	235 (13)[b]	441
C. australe	38.7 (1.9)[c]	34.8 (9.3)[b]	368 (22)[a]	ND

Notes: For resorption efficiency, $n = 5$–6 trees per species; for mean and maximum leaf lifespan, $n = 3$ trees per species. Different lowercase letters within columns denote significant differences between species ($P < 0.05$, Tukey's honestly significant difference test for unequal N); ND, not determined.
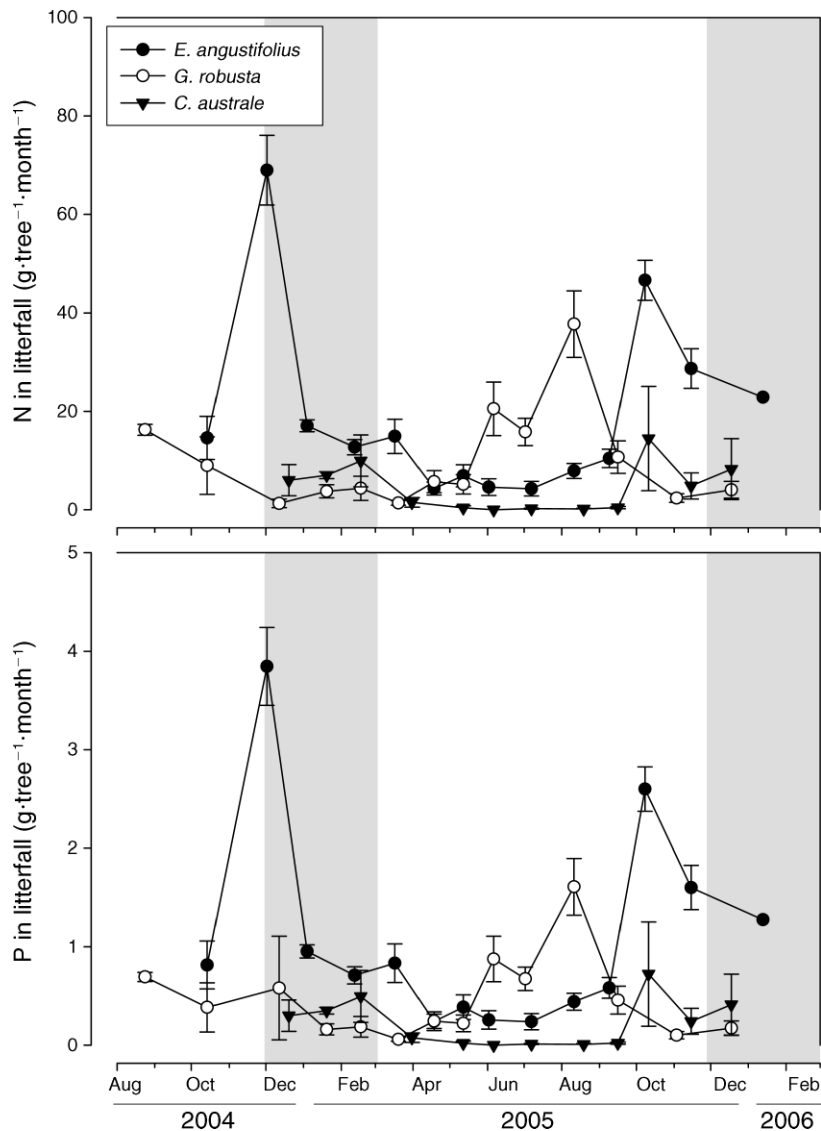
FIG. 1. Amount of N and P returned in litterfall per month (mean ± SE) for each studied tree species (*Elaeocarpus angustifolius*, *Grevillea robusta*, and *Castanospermum australe*), plotted at the midpoint between sampling times, from August 2004 to February 2006 (*n* = 3 trees per species). Shading indicates summer months. The study was conducted at a mixed-species tree plantation located on private land near Maleny in southeast Queensland, Australia.

and 2). Timing of leaf drop in *G. robusta* did not change between years, although amounts of litter production differed, with 43% less litter biomass produced in August 2004 compared to 2005. Litterfall of *C. australe* was measured throughout one year only.

From leaf and litter production, differences in demand and storage of nutrients in each species were calculated (Fig. 3). In *E. angustifolius* maximum N (284 g/tree) and P (20 g/tree) content in the crown occurred in February after leaf flush. During this time, demand of *E. angustifolius* could not be met by resorption of N or P from senescing leaves, resulting in a requirement for an additional 79 g N/tree and 7 g P/tree (Fig. 3). In contrast to *E. angustifolius*, *G. robusta* crown N (442 g/tree) and

P (16 g/tree) content peaked when the majority of foliage consisted of young leaves in November 2005. The time of maximum crown N and P content also corresponded to maximum nutrient demand in *G. robusta* (239 g N/tree and 9 g P/tree; Fig. 3).

There was only a slight change in crown nutrient content of *C. australe* over the course of a year, with N content increasing by 50 g/tree and P content by 2 g/tree (Fig. 3). There was no obvious peak in canopy nutrient content during times of high leaf turnover, although values varied considerably between individual *C. australe*. There was a small increase in demand for N (16 g/tree) and P (0.8 g/tree) by *C. australe* in late spring 2005, coinciding with maximum leaf drop.
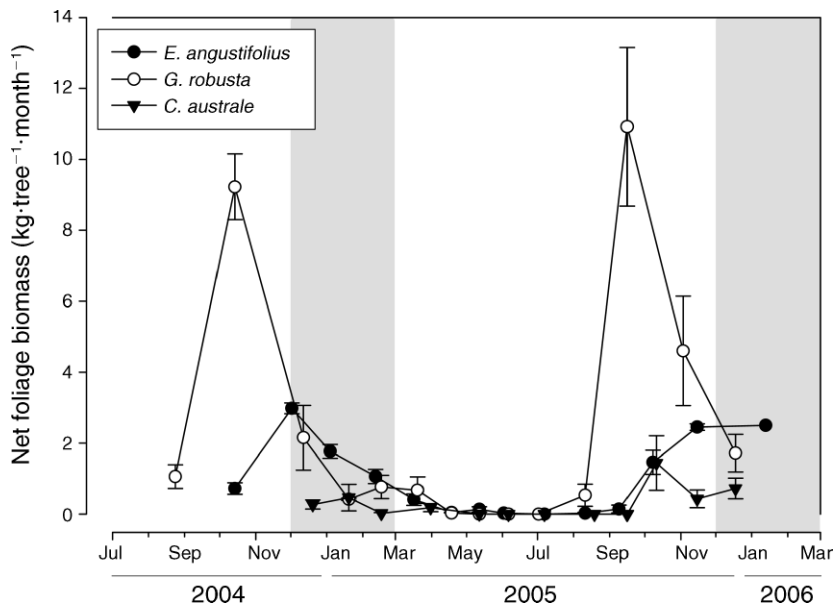
FIG. 2. Biomass of new foliage (dry mass basis) produced per month (mean ± SE) for each studied tree species (*Elaeocarpus angustifolius*, *Grevillea robusta*, and *Castanospermum australe*), plotted at the midpoint between sampling times, from August 2004 to February 2006 ($n = 3$ trees per species). Shading indicates summer months.

The three tree species resorbed nutrients in excess of requirements at various times of the year (Fig. 3). However, the sum of the resorbed nutrients was on average insufficient to cover the demand for N and P in most branches of *C. australe* and at least half the measured branches of *G. robusta* over the course of a year, but was sufficient for all measured *E. angustifolius* branches.

Photosynthetic traits

Instantaneous photosynthetic nitrogen and phosphorus use efficiencies (PNUE and PPUE, respectively) were calculated for a leaf age sequence (Fig. 4) and expressed at a common temperature (25°C) and C_i (250 µmol CO_2/mol) using photosynthetic parameters of young leaves (Table 1). The third fully expanded leaf of *E. angustifolius* had a maximum PNUE of 4.9 µmol $CO_2 \cdot g^{-1}$ $N \cdot s^{-1}$, which was significantly ($P < 0.05$) lower than maximum PNUE of *G. robusta* (7.0 µmol $CO_2 \cdot g^{-1}$ $N \cdot s^{-1}$; Fig. 4). However, it was significantly ($P < 0.05$) higher than the maximum PNUE of *C. australe* leaves (2.5 µmol $CO_2 \cdot g^{-1}$ $N \cdot s^{-1}$; Fig. 4). The same pattern was observed for PPUE in each species with maximum values of 70, 194, and 51 µmol $CO_2 \cdot g^{-1}$ $P \cdot s^{-1}$ in *E. angustifolius*, *G. robusta*, and *C. australe*, respectively. However, while most PNUE values for *E. angustifolius* leaves were significantly ($P < 0.05$) higher than *C. australe* foliage, there were almost no significant differences between PPUE values for either species (Fig. 4). In contrast, *G. robusta* had significantly ($P < 0.01$) higher PPUE values for all leaf ages compared to the other two species and significantly ($P < 0.01$) higher PNUE values than *C. australe* leaves.

These differences in leaf level nutrient use efficiency did not extend to the canopy since canopy nitrogen use efficiency (CNUE) was similar for all three species (Fig. 5). However, *E. angustifolius* had significantly lower CPUE than *G. robusta* and *C. australe*. In contrast, estimated aboveground biomass measured at the end of the study (December 2005) was significantly higher in *E. angustifolius* than *C. australe*.

Table 1 lists the photosynthetic characteristics of each species used in the MAESTRA model. These values were quite variable and did not differ between species, except for *G. robusta*, which had a significantly higher Φ than the other two species. In general, *C. australe* had lower A_{max}, J_{max}, and V_{cmax} than the other two species. The ratio of J_{max} to V_{cmax} was similar between species and ranged from 2.0 to 2.4. However, leaf transmittance of radiation in the 400–700 nm wavelengths was significantly lower in *E. angustifolius* than *C. australe*, and leaf reflectance was significantly higher in *C. australe* leaves than the other two species (Table 1).

Model outputs

The different photosynthetic characteristics of each species (Table 1) were reflected in the MAESTRA modeled responses of P_g and P_n and absorbed radiation (Q_a) under the five different plantation scenarios (Table 5). The highest rates of P_g (29 µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) and P_n (17 µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) were simulated for a single *G. robusta* tree, although isolated *E. angustifolius* trees absorbed the greatest amount of incident radiation (389 MJ·tree^{-1}·d^{-1}). *Elaeocarpus angustifolius* showed the largest reduction (60%) in P_g, Q_a, and P_n of all three species when grown as a monoculture compared to a
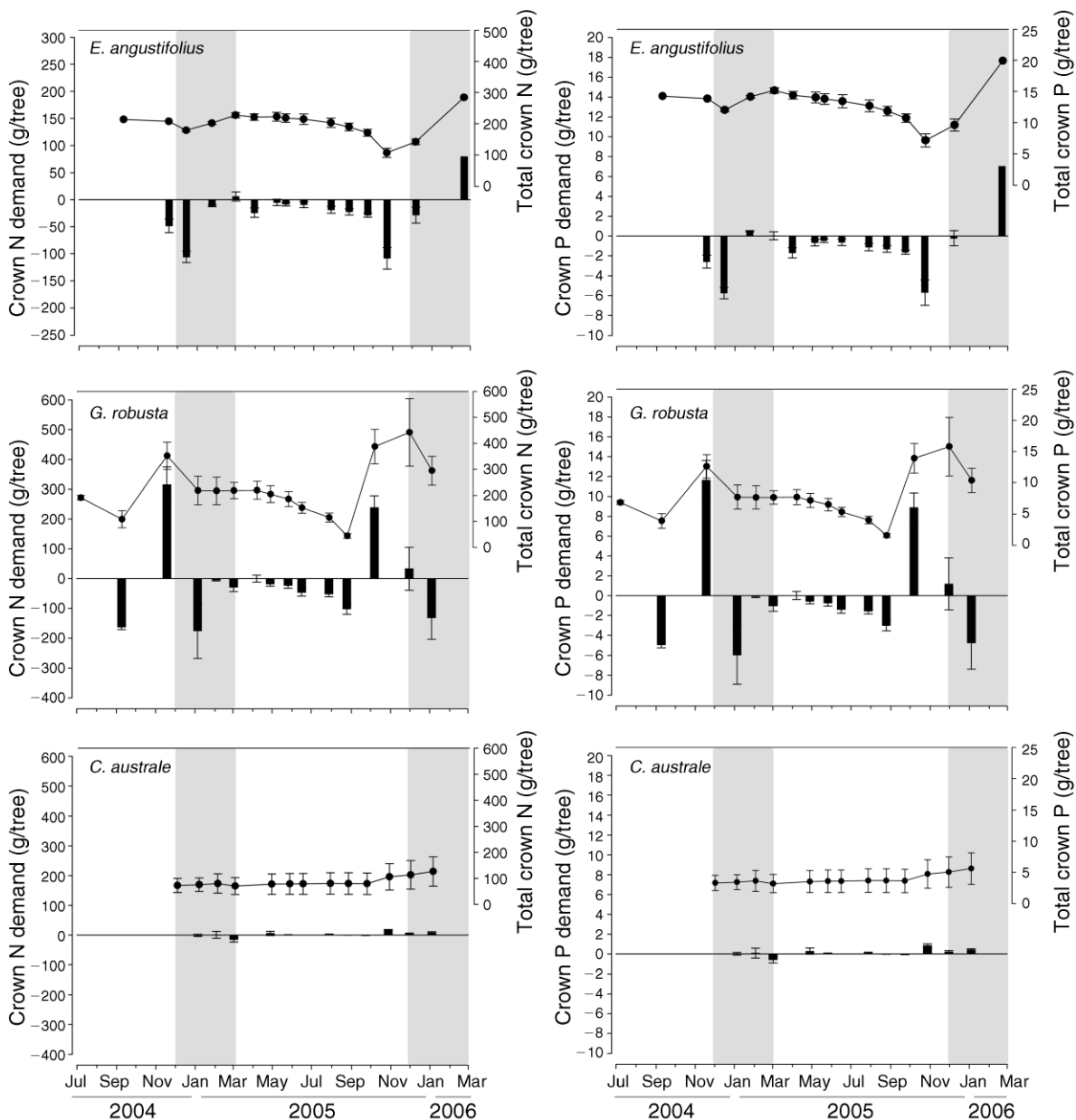
FIG. 3. Mass (mean ± SE) of N and P in crown foliage and foliage nutrient demand (positive) or nutrients in excess of requirements (negative) for the whole measurement period plotted at the end of each census for each of three tree species: *Elaeocarpus angustifolius*, *Grevillea robusta*, and *Castanospermum australe* (*n* = 3 trees per species). Shading indicates summer months.

single tree. *Castanospermum australe* showed the lowest decrease (14%) in photosynthetic rates under a monoculture scenario. *Elaeocarpus angustifolius* surrounded by trees similar to *C. australe* or *G. robusta* had higher rates of P_g compared to a monoculture of *E. angustifolius*. Simulations of *G. robusta* surrounded by trees similar to *C. australe* also resulted in higher rates of P_g, compared to other scenarios, while P_g was reduced by a further 15% under *E. angustifolius* compared to a monoculture scenario. When a *C. australe* target tree

was surrounded by *E. angustifolius*, MAESTRA simulated no P_n over the entire year. In contrast, a *C. australe* target tree surrounded by *G. robusta* maintained photosynthetic rates at 2.1 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, 23% lower than a *C. australe* monoculture scenario.

DISCUSSION

Complementary use of resources by component species is considered one of the underlying reasons for greater stability and productivity of biodiverse commu-
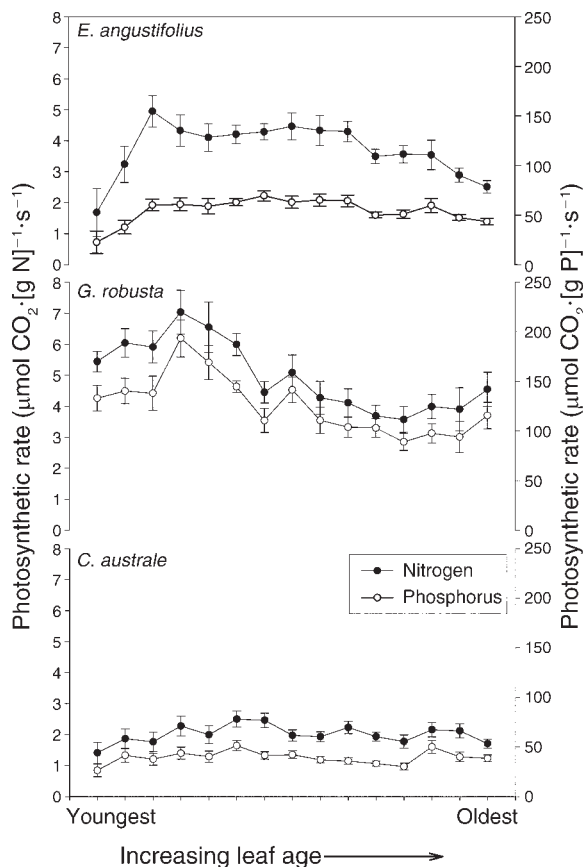
FIG. 4. Maximum instantaneous photosynthetic N and P use efficiency (mean ± SE) along a leaf-age branch chronosequence recalculated at 25°C and an intercellular CO_2 concentration, C_i, of 250 μmol/mol using photosynthetic parameters from young leaves of *Elaeocarpus angustifolius*, *Grevillea robusta*, and *Castanospermum australe* ($n = 3$–4 trees and 7–8 branches per species).

nities compared with less diverse systems (Hooper et al. 2005). We examined how resource use can be assessed in mixed-species tree plantations and present evidence for temporal and quantitative complementarity in nutrient and light use associated with functional attributes in three Australian rain forest tree species. Contrary to initial hypotheses, the two fast-growing tree species exhibited complementary nutrient interactions, leading to the possibility for improved nutrient cycling and reduction of nutrient losses within a mixed plantation compared to a monoculture. Model simulations also indicated that careful design could result in greater canopy light interception in mixtures than in monocultures. However, our findings are based on aboveground light and nutrient interactions and further work is needed to ensure that belowground nutrient cycling follows the observed patterns. In addition, while we discuss our results within the broader context of mixture design, the applicability of our data to other sites and regions has not been tested, and further studies in other

plantations are needed to confirm the generality of our findings.

Nitrogen and phosphorus were examined as representative nutrients most commonly limiting the productivity of plant communities (Güsewell 2004). From measurements of leaf turnover and nutrient content of leaf cohorts, including abscised leaves, we predict that *G. robusta* has the highest nutrient demand (239 and 8.9 g/tree for N and P) during early spring, when most foliage is replaced with new leaves. In contrast, *E. angustifolius* has the highest nutrient demand (79 and 7.0 g/tree for N and P) in mid-summer to support growth of new foliage. Maximum foliage production and nutrient demand of *C. australe* coincides with *G. robusta* in spring. However, slow growth rates and low foliage biomass of *C. australe* create a comparatively low N and P demand, 15- and 13-fold lower respectively, than demand of *G. robusta*. The observed temporal separation of highest nutrient demand in *E. angustifolius* and *G. robusta* and low nutrient demand of *C. australe* forms the basis for nutritional complementarity and provides a testable hypothesis that can be applied to an experimental system of replicated mixture and monoculture plots for each species. Similar separation of nutrient demand or seasonal complementarity has been observed in experimental grassland biodiversity plots, leading to higher total resource use (Hooper and Vitousek 1998) and greater input and retention of N in biodiverse systems (Fargione et al. 2007). Temporal complementarity has also been observed in agroforestry systems, where seasonal and spatial separation of soil N uptake between crops and trees has led to higher productivity (Schroth 1999, Rowe et al. 2005).

We calculated that nutrient demand of *E. angustifolius* was 60% (N) and 22% (P) lower than demand of *G. robusta*. However, because only lower branches of *E. angustifolius* were measured here, this is likely to be an underestimate. *Elaeocarpus angustifolius* exhibits characteristics of fast-growing pioneer species, in which increases in whole-plant leaf area are primarily associated with height growth (Ackerly 1999). As observed in other tropical species with short leaf life spans (Ackerly and Bazzaz 1995), self-shaded lower leaves are abscised in *E. angustifolius*, and N is retranslocated from abscised leaves to upper branches to provide a source of N, complementing N uptake by roots. The high rate of N resorption observed in *E. angustifolius* allows high N retention within the plant and optimizes C gain by allocating N from older, shaded leaves to more efficient young leaves (Field 1983, Aerts and Chapin 2000).

While shaded lower branches of *E. angustifolius* resorb more N from senescing older leaves than required for new foliage, thus providing a source of N for the upper canopy, this was not observed in *G. robusta*. In *G. robusta*, most of the studied branches had a higher demand for N and P than amounts provided by senescing foliage, indicating that during periods of high demand, N and P are likely to be derived from the soil.
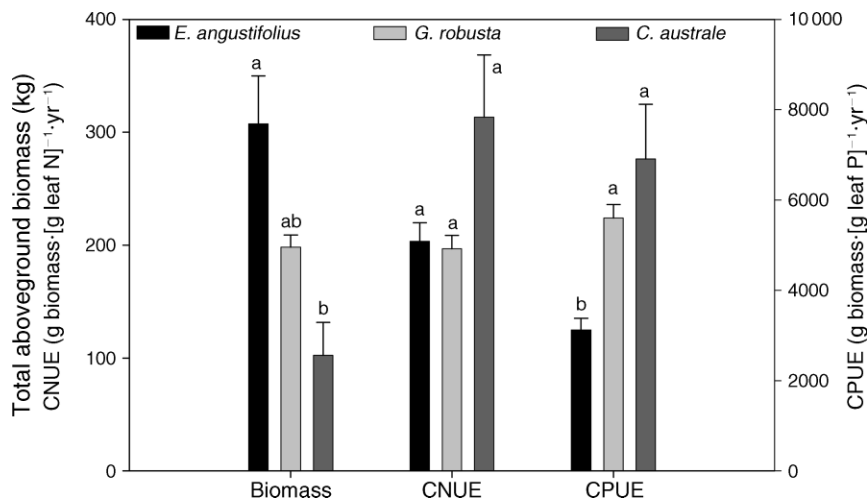
Fig. 5. Total aboveground biomass (kg; left axis) calculated from stem diameter and height in December 2005 and mean canopy N and P use efficiency (CNUE and CPUE; left and right axis, respectively) for each of three tree species (*Elaeocarpus angustifolius*, *Grevillea robusta*, and *Castanospermum australe*; mean + SE). Different letters within a group indicate significant differences ($P < 0.05$, Scheffé's S test) between species.

Further, species in the Proteaceae are most common in nutrient-limited habitats and have a good ability to access soil nutrients via cluster roots (Lambers et al. 2008). A superior ability to take up soil nutrients combined with high foliage resorption efficiency allows *G. robusta* to replace its canopy annually and to persist in more nutrient-limited soils as its natural range indicates (Boland et al. 2006). Our results show that irrespective of absolute N and P demands of the studied species, temporal separation of nutrient demand by the two fast-growing tree species, *E. angustifolius* and *G.*

robusta, will reduce competition for soil nutrients and facilitate greater nutrient capture and retention compared to a monoculture.

Nutrient cycling in tree plantations is not only affected by timing and efficiency of nutrient uptake by trees but also by the return of nutrients to the soil via litter. Of the three studied species, *G. robusta* had the highest nutrient resorption proficiency: the ability to withdraw nutrients from senescing leaves (Killingbeck 1996), a trait common to species adapted to oligotrophic sites (Wright and Westoby 2003). Low-nutrient litter

TABLE 5. MAESTRA model outputs of gross photosynthesis (P_g), absorbed photosynthetically active radiation (Q_a), net photosynthesis (P_n), and percentage reduction in P_g from a single tree scenario for each species (*Elaeocarpus angustifolius*, *Grevillea robusta*, and *Castanospermum australe*).

Scenario	P_g (mol·tree^{-1}·d^{-1})	Q_a (MJ·tree^{-1}·d^{-1})	P_n (mol·tree^{-1}·d^{-1})	P_g reduction (%)
E. angustifolius				
Single	24.7 (9.03)	389 (145)	14.3 (4.27)	
Monoculture	9.46 (2.78)	130 (52.1)	2.51 (1.69)	60
G. robusta	11.5 (3.01)	147 (49.7)	3.00 (1.62)	52
C. australe	11.6 (3.08)	144 (45.5)	3.42 (1.74)	51
Tall	1.89 (0.89)	21.2 (12.8)	−8.00 (4.98)	92
G. robusta				
Single	29.0 (13.4)	222 (89.2)	16.9 (6.45)	
Monoculture	16.6 (6.73)	130 (52.3)	5.29 (2.04)	40
E. angustifolius	14.3 (9.83)	104 (77.2)	3.41 (3.31)	55
C. australe	21.1 (8.58)	151 (54.5)	8.63 (2.66)	25
Tall	6.01 (2.22)	40.0 (19.3)	1.86 (1.15)	77
C. australe				
Single	3.20 (0.97)	55.3 (19.9)	2.08 (0.62)	
Monoculture	2.75 (0.84)	46.0 (17.1)	1.66 (0.49)	14
E. angustifolius	0.56 (0.25)	6.91 (4.05)	−0.58 (0.22)	83
G. robusta	2.06 (0.74)	32.1 (14.9)	0.98 (0.40)	37
Short	2.25 (0.69)	33.5 (11.8)	1.18 (0.34)	30

Notes: Values (with SD in parentheses) are averaged over an entire year excluding days when P_g or P_n was negative (except when all values were negative). Scenarios include a single tree (single), a monoculture of the target species (monoculture), a monoculture of another tree species, and the target species surrounded by a monoculture of trees 50% shorter (short) or 50% taller (tall).

with high C:N ratio decomposes slowly and leads to lower nutrient turnover and availability (Hobbie 1992, Gartner and Cardon 2004). In support of this notion, it has been observed elsewhere that *G. robusta* litter has a high lignin content and low rate of decomposition and N release compared to other species (Mugendi and Nair 1997).

Compared with *G. robusta*, *E. angustifolius* and *C. australe* had lower resorption proficiencies, higher N and P contents and lower C:N ratios in litter, which would result in faster decomposition and nutrient release. Therefore, the large and nutrient-rich litter biomass of *E. angustifolius* could improve nutrient cycling and availability in a mixture compared to a monoculture of *G. robusta*. There is evidence that *G. robusta* does not grow in monoculture, and inhibited nutrient cycling, as well as release of allelopathic compounds, could be contributing factors (Webb et al. 1967). An alternative view is that litter input does not impact greatly on nutrient cycling and availability in soils, but that fine-root turnover, soil microbial activity, and a plant's ability to compete with microbes for nutrients are more important (Knops et al. 2002). While these factors are significant, net input of N and P via litter is considerable at the studied site, and there is evidence that litter derived from mixed-species communities decomposes faster than litter from a single species (Gartner and Cardon 2004). Further, the considerable amount of anti-herbivory compounds in litter of *C. australe* (Hohenschutz et al. 1981, Abu-Zeyad et al. 1999) and the low nutritional quality of *G. robusta* litter could inhibit decomposition in monocultures. While studies on litter decomposition and soil nutrient relations will further this argument, we conclude that in the studied plantation, litter with different nutritional and chemical properties in combination with discrete times of litter fall contributes to soil cover, continuous substrate supply to microbes, and enhanced nutrient cycling.

The observed differences in nutrient demand and phenology of the studied trees can be explained by categorizing each species by their functional traits. Fast-growing *E. angustifolius* has a high acquisition capacity for light due to a large leaf area, but lower tissue density, lower leaf life span, and concomitant lower nutrient retention than species with long leaf life spans (Aerts and Chapin 2000). Short leaf life spans such those observed in *E. angustifolius* are correlated with high maximum rates of photosynthesis, low LMA, high leaf N, and rapid decrease in photosynthetic rates with leaf age (Westoby et al. 2002, Wright et al. 2004). The decline in leaf PNUE with age in *E. angustifolius* leaves was caused by decreasing photosynthetic rates, rather than reallocation of N to younger leaves, as has been suggested previously (Hikosaka 2005), and this may be a result of leaf shading and/or declining mesophyll conductance and water use efficiency (Kitajima et al. 1997). While PNUE of *E. angustifolius* leaves was higher than *C. australe*, both species had similar and low leaf

PPUE. Up-scaled to a whole-plant level, biomass production per gram P invested in foliage (CPUE) was significantly lower in *E. angustifolius* than the other two species. This finding has implications for monocultures of *E. angustifolius*, where high P demand could limit productivity of the plantation.

Grevillea robusta combines characteristics typical of fast-growing species and of nutrient-conserving species adapted to nutrient-poor environments, such as high PNUE and PPUE, which correspond to observed high growth rates. Up-scaled to the whole-plant level, CNUE was similar in *G. robusta* and *E. angustifolius*. The similar CNUE may be due to a larger allocation of resources to belowground root biomass in *G. robusta*, which was not measured here. The cost of different root/shoot allocation in *G. robusta* and *E. angustifolius* could determine how the two species compete under nutrient-poor and -rich conditions. The hypothesis that *E. angustifolius* is a good competitor in mesic and nutrient-rich sites while *G. robusta* may be competitively superior in drier or nutrient-poor sites could be tested in future field trials.

Castanospermum australe had the lowest PNUE and PPUE and long leaf life span characteristic of slow-growing and shaded species that have a low resource acquisition strategy and low tissue turnover rates that result in high nutrient retention within the plant (Aerts and Chapin 2000). High leaf N contents in *C. australe* did not correlate with high rates of leaf photosynthesis, implying that N is invested in anti-herbivory compounds to maximize leaf life span and lifetime C gain. The low LMA observed in *C. australe* also supports the notion that N toxins, rather than tougher leaves, contribute to the long leaf life span in this species. The reliance on N-based defense compounds indicates a good ability to acquire N, and there is evidence that *C. australe* can potentially fix N_2 (Abu-Zeyad et al. 1999), although reports are conflicting (Sprent 2001) and no evidence for nodulation was found here. Interestingly, at the whole-tree level CNUE and CPUE in *C. australe* was similar to *G. robusta* and CNUE was similar to *E. angustifolius*. This is the result of a considerably higher wood density in *C. australe* than the other two species and demonstrates that different strategies at the leaf level can result in overall comparable nutrient use efficiencies. Similarly, other studies have demonstrated a convergence in N, but not P, use efficiencies at the whole-plant level in tropical tree species (Hiremath et al. 2002).

Simulations from the MAESTRA model allowed us to test the hypothesis that different shade tolerances of each species affect light interactions in a mixed-species plantation. Photosynthetic properties of *C. australe*, including low A_{max} and low rates of R_d, are indicative of shade tolerance and allow this species to survive in the shaded rain forest understory before reaching the canopy. The photosynthesis variables measured here are similar to previous studies of *C. australe* (Drane 1995, Swanborough et al. 1998), lending confidence to

our results. As expected, *C. australe* suffered only 14% reduction in simulated gross photosynthetic rates under a *C. australe* monoculture scenario and 37% reduction under a *G. robusta* monoculture, suggesting it could be grown in combination with other species that are less shade tolerant.

Elaeocarpus angustifolius exhibited a high decline in photosynthetic rates of 60–92% under both monoculture scenarios, and this is supported by low stem volumes of *E. angustifolius* observed in field monocultures (Manson et al. 2006). However, *E. angustifolius* had higher photosynthetic rates compared to monocultures when surrounded by trees similar to *G. robusta* and *C. australe*, providing further support for including this species in mixed plantings, as long as the upper canopy remains in full sun. *Grevillea robusta* had the highest simulated rates of gross photosynthesis under all monoculture and mixed scenarios, also indicating the potential for this species to be productive when grown in mixtures with other fast-growing and light-demanding species. Surprisingly, the only species' combination that showed a large reduction in P_g was *C. australe* surrounded by trees similar to *E. angustifolius*, despite the shade tolerance of *C. australe*. Mixtures of shade-tolerant *C. australe* and light-demanding *E. angustifolius* are common in plantations; however, model results suggest that more productive combinations may be *C. australe* and *G. robusta* or *E. angustifolius* and *G. robusta*. While these combinations should be studied further in experimental plantings, the model results provide a framework to test the hypothesis that pairings of species with different shade tolerances may not be the best design for mixed-species plantations. This finding is in contrast to studies from natural and managed forests that have observed greater productivity in stratified mixtures where component species have strongly contrasting light use traits (Kelty 1989, Donoso and Lusk 2007).

The relatively lower inhibition of photosynthetic rates under lower light levels for *G. robusta* may be due to its high rates of carboxylation and electron transport, which are maintained in older, shaded foliage (V_{cmax}, 58 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$; J_{max}, 137 μmol $e^- \cdot m^{-2} \cdot s^{-1}$; A. E. Richards, *unpublished data*). In addition, the lower leaf area and deeply lobed foliage of *G. robusta* would reduce light interception under a monoculture scenario. In support of this, simulated incident radiation on lower branches of *G. robusta* monocultures was 13 μmol $\cdot m^{-2} \cdot s^{-1}$ higher than an *E. angustifolius* monoculture.

Model simulations indicate that certain combinations of *G. robusta*, *C. australe*, and *E. angustifolius* may interact in a complementary fashion for light if *E. angustifolius* can maintain high growth rates such that its crown is kept above the plantation canopy. However, MAESTRA only simulates canopy photosynthetic rates that may not necessarily correlate to overall tree growth as this depends on carbon allocation patterns of each

species (Medlyn 2004). In addition, the current model simulation reflects the wide (4 × 4 m) spacing of the studied plantation, and rates of photosynthesis for all species under the different model scenarios may be reduced if stocking densities were increased to the 2 × 2 m or 2 × 3 m spacing of many recently established mixed-species plantations (Grant et al. 2006).

Taken together our results indicate that the combination of different functional traits of each species has implications for nutrient cycling and retention in mixed plantings. At the level of the whole plant, all species had a similar CNUE, which was achieved through low tissue nutrient contents (*G. robusta*), low tissue turnover rates and high tissue density (*C. australe*) and high nutrient resorption prior to abscission (*E. angustifolius*). A mixed-species plantation made up of species that are efficient at using soil nutrients or internally recycling nutrients for growth should have tighter within-system nutrient cycling and reduced loss of nutrients from soil (Vitousek 1984, Hiremath and Ewel 2001). Our model simulations also demonstrated the potential for complementary light interactions between *G. robusta* and *C. australe* or between *G. robusta* and *E. angustifolius*, while combinations of *E. angustifolius* and *C. australe* may not be productive. These conclusions, along with the hypothesis that *G. robusta* may be competitively superior to *E. angustifolius* on infertile soils as well as drier conditions, need to be further tested in larger-scale tree mixture experiments. The responses studied here reflect short-term, site-specific measurements made at an early stage of development, and caution should be used before applying these findings more generally. We suggest that tree growth, interactions for nutrients (both above- and belowground), and light should be studied in other established plantations of different ages, growing under different environmental conditions, in order to determine the broader applicability of these initial findings.

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APPENDIX A

Structural and mean tree parameters for each species used in the MAESTRA model (*Ecological Archives* A020-043-A1).

APPENDIX B

Mean monthly minimum and maximum air temperatures, mean soil moisture content, daily rainfall, and stem diameter of *Elaeocarpus angustifolius* and *Grevillea robusta* trees at the study site (*Ecological Archives* A020-043-A2).