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Mixed-species plantations of *Eucalyptus* with nitrogen fixing trees: a review

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ABSTRACT

Mixed-species plantations of *Eucalyptus* with a nitrogen (N₂) fixing species have the potential to increase productivity while maintaining soil fertility, compared to *Eucalyptus* monocultures.

However, it is difficult to predict combinations of species and sites that will lead to these benefits.

5 We review the processes and interactions occurring in mixed plantations, and the influence of species or site attributes, to aid the selection of successful combinations of species and sites. Successful mixtures, where productivity is increased over that of monocultures, have often developed stratified canopies, such that the less shade-tolerant species overtops the more shade-tolerant species. Successful mixtures also have significantly higher rates of N and P cycling than
10 *Eucalyptus* monocultures. It is therefore important to select N₂-fixing species with readily decomposable litter and high rates of nutrient cycling, as well as high rates of N₂-fixation. While the dynamics of N₂-fixation in tree stands are not well understood, it appears as though eucalypts can benefit from fixed N as early as the first or second year following plantation establishment. A meta-analysis of 18 published studies revealed several trials in which mixtures were significantly
15 (P<0.001) more productive than monocultures, and no instances in which mixtures were less productive than monocultures. Regression analyses of such data were more informative than indices of relative yield, and were more informative in trials that contrasted four or more different species compositions. Thus replacement series examining compositions of 100:0, 67:33, 33:67, and 0:100 were more informative than minimalist 100:0, 50:50 and 0:100 series.

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1. Introduction

Eucalyptus is one of the most widely used genera in global commercial plantation timber industries (James and Del Lungo, 2005). These plantations are generally monospecific and have been managed successfully and sustainably for many years. Nevertheless, concerns have been raised
25 about the costs of fertilisers, reduced biodiversity, and productivity losses from pests and disease

(DeBell et al., 1987; FAO, 1992). Mixed-species plantations containing a eucalypt and a nitrogen (N₂) fixing species have the potential to address some of these concerns and improve nutrient cycling (Binkley et al., 1992; Forrester et al., 2005b), soil fertility (Montagnini, 2000), biomass production (Binkley et al., 2003b; Forrester et al., 2004) and carbon sequestration (Kaye et al., 5 2000; Resh et al., 2002; Forrester et al., 2006a) while providing other benefits through a diversification of products (Montagnini et al., 1995; Khanna, 1997; Montagnini, 2000), improved risk management and protection from pests and diseases (Ewel, 1986; FAO, 1992; Montagnini, 2000). Mixtures can also be used as a silvicultural system for growing high quality timber (Ewel, 1986; Keenan et al., 1995; Montagnini et al., 1995; DeBell et al., 1997; Medhurst et al., 2003).

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The design and silviculture of a mixture depends on the specific objectives. For example, the admixed N₂-fixing species may be used to produce a wood product or simply to increase N availability, and the aim of the admixture may be to maximise biomass, volume, or structural diversity, or to improve tree form and wood quality. The wide range of design and silvicultural options available are beyond the scope of this review (see Haines and DeBell, 1980; FAO, 1992; 15 Kelty and Cameron, 1995), however, the species and site attributes that should be considered when managing the processes and interactions in mixtures will be similar for most of these objectives.

Knowledge about these factors will greatly improve the probability of success. Previous reviews have examined the growth and interactions that occur in agroforestry systems (Rao et al., 1998;

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García-Barrios and Ong, 2004; Jose et al., 2004; Thevathasan and Gordon, 2004), in mixed stands of trees in general (Cannell et al., 1992; FAO, 1992; Kelty, 1992, 2006), mixtures containing a N₂-fixing species (Binkley, 1992; Sanginga et al., 1995; Khanna, 1998) and the nutritional interactions in mixtures (Rothe and Binkley, 2001). However, a considerable amount of recent research has

advanced our understanding of the interactions that occur in mixtures, particularly those containing

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Eucalyptus with a N₂-fixing species. The aim of this review was (1) to examine the processes and interactions that affect the productivity in mixed-species stands containing *Eucalyptus* and a

nitrogen-fixing-species; (2) to identify the growth habits and physiological characteristics of tree species that allow an assessment of the likely interactions between species, and (3) to examine the effect of site factors (nitrogen, phosphorus and water) on these interactions and processes to enable the successful matching of species and sites.

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2. Interactions in mixed stands

To improve the productivity in mixed plantations, there are three main processes that need to be considered: competition, competitive reduction and facilitation (Vandermeer, 1989; Kelty, 1992).

Competition occurs when two or more plants or populations interact such that one exerts a negative effect (growth or mortality) on the other (Vandermeer, 1989). Competitive reduction, also known as complementarity or the competitive production principle, occurs when interspecific competition in the mixture is less than intraspecific competition in the monocultures (Vandermeer, 1989; Kelty and Cameron, 1995). This results from a differentiation in resource (light, water or nutrients) requirements (Kelty and Cameron, 1995) leading to a more complete use of site resources.

Facilitation, also known as the facilitative production principle, occurs when one species has a positive effect on another (Vandermeer, 1989). Mixtures will out-yield monocultures, when the positive interactions of facilitation and competitive reduction dominate the competitive interactions.

3. Competition

3.1 Symmetry of competition in mixed stands

The way in which competition is distributed in a stand of trees depends on the resources for which plants are competing (Weiner, 1985; Hara, 1986; Weiner, 1986, 1990). Competition for light is often asymmetrical because tall plants can shade small plants but not vice versa to the same extent.

Competition for belowground resources, such as water and nutrients, is theoretically more symmetrical as the roots of smaller plants may take up the same amount of resource per unit root

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surface area (Weiner, 1985, 1986; Kikuzawa and Umeki, 1996). Although variations in fine root architecture, growth rates, distribution and mycorrhizal associations may also lead to asymmetrical competition belowground. The degree of asymmetry depends on the resource for which plants are competing most intensely (Weiner, 1985; Hara, 1986; Weiner, 1986, 1990). Asymmetric
5 competition leads to an increase in size inequality with time because small individuals lack the resource and lag behind (Hara, 1986). The degree of asymmetry and resource differentiation is likely to change with time depending on the resources that become most limiting during the different stages of development. Asymmetric competition in a mixed-species plantation may lead eventually to the suppression of one species.

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3.2 Interspecific and intraspecific competition

The occurrence of both interspecific and intraspecific competition leads to more complex interactions in mixtures than monocultures. What is commonly being measured as intra- and interspecific competition is the net effect of all interactions between plants (which may have
15 positive or negative effects). It is theoretically possible that interactions occurring in mixtures can lead to substitution (Figure 1a-b), reduced (Figure 1c) or increased yields (Figure 1d-e).

If intra- and interspecific competition are the same (or the density is too low for plants to interact) then the average plant size and overall size inequality should be the same in mixture and

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monoculture (Figure 1a). In this case it is just as beneficial to plant monocultures of each species. Where the interspecific competition is greater than intraspecific competition for one species (B) and vice versa for the other, the species receiving the greater share of resources (A) will be larger in mixture than in monoculture, while the species receiving a lower supply of resources will be correspondingly smaller (B) (Trenbath, 1974) (Figure 1b). This compensatory effect is often
25 observed in mixtures of herbaceous species (Trenbath, 1974).

Where interspecific competition is greater than intraspecific competition for both species, the average size of both species in mixture will be smaller than in monoculture (Figure 1c). When interspecific competition is lower than intraspecific competition for both species the average size of both species in a mixture will be greater than in a monoculture and the yield of mixtures will be greater than that of monocultures (Figure 1d). It is important to note that these outcomes depend on the yield-density functions of each species, as well as on the inter- and intra-specific competition (Harper, 1977). A typical yield-density function is shown in Figure 1e (for example, line B for species B), where the yield increases with increasing plant density until a maximum yield is reached. If neither species responds to the other, the yield of each species will follow its yield-density function and mixtures could be more or less productive than monocultures depending on their yield-density functions (Figure 1e). This situation is less likely to occur and requires that the availability of light, water and nutrient are not limited due to competition from the other species.

It is usually not possible to separate the effect of positive or negative interactions occurring in mixtures and it is likely that they are often interrelated. However, it is possible to answer certain research questions by carefully considering the design of the mixed-species experiment. There are several designs used for mixed-species experiments (Harper, 1977; Jolliffe, 2000; Freckleton and Watkinson, 2000; Vanclay, 2006), but the two most common types are the replacement series and additive series designs. In replacement series designs, the density of monospecific and mixed treatments is constant and the proportions of the two component species are varied (deWit, 1960). In additive series, the density of one species remains constant across the monocultures and mixtures while that of the other varies, such that mixtures have a higher density than monocultures (Harper, 1977). This latter design is often used to study the effects of weed species on crops planted at standard densities (Harper, 1977; Kelty, 1992).

Additive designs can be used to quantify interspecific competition, (Sackville Hamilton, 1994) and therefore the number of N₂-fixing trees that could be added to a given density of *Eucalyptus* to increase growth, or to avoid a reduction in growth rates. Replacement series can be used to determine whether inter- and intraspecific competition are equal or unequal (Sackville Hamilton, 5 1994) and therefore, whether the interspecific interactions have net positive or negative effects on the growth of either species in a mixture. Replacement series are often used when the productivity of both species is of interest. Designs that contain both replacement and additive series (such as addition series) can be used to examine the complete range of outcomes (Firbank and Watkinson, 1990; Kelty and Cameron, 1995). Alternatively, neighbourhood designs at the level of individual 10 trees, both interspecific and intraspecific interactions can be examined, and such analyses have shown more complex trends than were evident from stand level analyses in the same trial (see (Boyden et al., 2005).

There are many indices used to describe the growth outcome of mixed-species stands in replacement series and all have advantages and disadvantages (Jolliffe, 2000; Williams and 15 McCarthy, 2001). A frequently used index is the relative yield (RY).

$$\text{RY of species A} = \frac{\text{yield of species A in mixture}}{\text{yield of species A in monoculture}} \quad (\text{Harper, 1977}).$$

20 It is important to note that this indicates the outcome of all interactions occurring in the stand, including both species interactions and the yield-density functions of either species (Harper, 1977). RY equal to the proportion of the given species in mixture indicates that, on average, trees were the same size in mixture as in monoculture. For example, in a 1:1 mixture an RY of 0.5 indicates that plants of that species were of the same average size in mixture and monoculture (Figure 1a). RY of 25 more than 0.5 shows that the plants were bigger in mixture than monoculture (Figure 1d), and an

RY below 0.5 shows that plants were smaller in mixture than in monoculture (Figure 1c). Figure 2 shows the RY of 1:1 mixtures of *Eucalyptus* and N₂-fixing trees in 19 mixtures. In some cases, the relative yield is divided by the proportion of the given species in mixture (Williams and McCarthy, 2001). This facilitates the comparison of treatments with different species proportions. That is, regardless of the species proportion, an $RY_{\text{species proportion}}$ of 1 means the trees were the same size in mixture as they were in monoculture.

4. Competitive reduction

Competitive reduction may occur spatially through the stratification of foliage or roots or temporally due to phenological differences. Generally competitive interactions between tree species are divided into two groups; aboveground competition for light and belowground competition for soil resources (Kelty, 1992). Above- and belowground interactions are unlikely to be independent of each other (Kelty, 1992). However, to simplify the discussion, both interactions are considered separately.

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4.1 Canopy stratification – competition for light

Successful mixed-species plantations often have stratified canopies with a fast-growing and less shade-tolerant species forming the upper canopy and a more shade-tolerant species forming the lower canopy (Assmann, 1970; see studies 1, 7, 8-10 in Table 1 and Figure 3). This canopy stratification can lead to higher stand-level light capture and more efficient use of light in the upper canopy.

Shade-intolerant species such as many of the *Eucalyptus* genus (Bell and Williams, 1997) are capable of higher maximum rates of photosynthesis than more shade-tolerant species. Therefore more efficient use will be made of the higher light intensities in the upper canopy of a mixture than

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in the upper canopy of a more shade-tolerant species monoculture. In contrast, shade-tolerant species are capable of maintaining foliage at lower light intensities than less shade-tolerant species because they have lower light compensation points (Kelty, 1992). Light compensation occurs at the irradiance level where the net carbon exchange by a leaf is zero and rates of photosynthesis and respiration balance (Lambers et al., 1998). Below this point there is insufficient light to compensate for respiratory CO₂ release (Lambers et al., 1998). Shade-tolerant species therefore make more efficient use of light at low levels (Vandermeer, 1989; Kelty, 1992) and increase the amount of light intercepted compared to monocultures of the shade-intolerant species. For example, total light interception (photosynthetically active radiation; PAR) was measured in mixtures of *Eucalyptus saligna* with *Falcataria molucanna* and *E. globulus* with *Acacia mearnsii* (Trials 1 and 7 in Table 1; Binkley, 1992; Bauhus et al., 2004). In both studies, monocultures of the relatively shade-intolerant *Eucalyptus* spp. intercepted less light (66% of PAR) than mixtures with, or monocultures of the more shade-tolerant *F. molucanna* (87-92% of PAR) and *A. mearnsii* (73-78% of PAR). Furthermore, Bauhus et al. (2004) suggested that the interception of diffuse and direct light might be optimised in mixtures over the course of a day because mature foliage of *E. globulus* is vertically oriented (James and Bell, 2000) while that of *A. mearnsii* is more horizontally oriented. This was also shown in mixed stands of *E. nitens* and *A. dealbata* (Hunt, 1998; Hunt et al. 2006), which are very closely related to *E. globulus* and *A. mearnsii*, respectively, and have similar crown architecture and leaf morphologies. The light extinction coefficient, which measures the fraction of incident photons absorbed per unit leaf area (Beadle, 1997), was significantly higher in mixtures (0.65) than that normally occurring in eucalyptus monocultures (0.5) (Hunt, 1998; Hunt et al. 2006). Therefore, the combination of a shade-tolerant and a taller and less shade-tolerant species will increase light capture (compared to monocultures of less shade-tolerant species) and the efficiency of the upper canopy (compared to monocultures of the more shade-tolerant species).

To survive in a mixed stand, shade-intolerant species need a competitive advantage to overtop the more shade tolerant species (Yoshida and Kamitani, 2000). In studies 5 and 11 in Table 1 and Figure 3, the shade-intolerant *Eucalyptus* species was not able to overtop the associated N₂-fixing species and grew smaller in mixtures than in monocultures. In contrast the *Eucalyptus* spp. in studies 1, 7, 8-10 in Table 1 and Figure 3 overtopped the associated species (although not always initially) and the productivity of mixtures was greater than that of monocultures. It is important to note that canopy stratification alone is probably not the only factor responsible for the success or failure of these mixed stands, but it is a key factor to ensure the coexistence of the species until the end of the rotation. Furthermore the relative influence of different interactions on stand growth (such as competitive reduction due to canopy stratification or facilitation due to N₂-fixation) can change with time as the stands develop (Forrester et al., 2004).

Desired differences in tree height and the avoidance of crown competition between species can result from more rapid early height growth of the shade-intolerant species, the advanced planting of the less shade-tolerant species (Harrington and Deal, 1981) or by modifying the planting pattern to create patches, where trees of one species are only subject to intraspecific competition (Kelty and Cameron, 1995). These differences in height growth can also be used to improve the form and wood quality of either species in the mixture. It has been argued that *Eucalyptus* trees require pruning of live branches to produce clear, solid wood products or that self-pruning must be promoted through high stand densities (Montagu et al., 2003). The shading of the *Eucalyptus* stems by the N₂-fixing trees may be more intense than the shade provided from other eucalypts, when mixtures are planted at the same density as monocultures (Bauhus et al., 2004). Thus self-pruning of eucalypts may be accelerated in mixtures without increasing stand density and thus planting costs. Where pruning of live branches is required, improvements in nitrogen nutrition (from N₂-fixation) may improve the ability of the *Eucalyptus* trees to rebuild their crowns after pruning. In other plantation systems, shading from *Eucalyptus* trees has been used to improve the form of

Acacia melanoxylon, which can grow large branches and develop a poor form in pure stands (Medhurst et al., 2003; Medhurst et al., 2006). However, in these mixtures the eucalypts are regarded as a temporary component that serve as a trainer species for the acacias to produce high-value timber.

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Owing to the paucity of studies which have examined the growth dynamics of mixed plantations it is difficult to predict how a species will grow in a mixture (Forrester et al., 2004). Nevertheless, height-age curves of each species in monocultures (Fisher and Binkley, 2000) and information about each species' relative shade tolerance should aid with species selection (Forrester et al., 2005a).

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4.2 Root stratification – competition for nutrients and water

The potential reduction of below ground competition occurs through the physical or chemical stratification of roots. Chemical stratification can occur when co-occurring species employ different acquisition strategies to obtain nutrients. Such stratification may occur when different plant species are associated with different types of mycorrhizae (Ewel, 1986; Schulze et al., 1994). Detailed studies of mycorrhizal associations and soil N sources have not been carried out in mixtures containing *Eucalyptus* with N₂-fixing species. However, while *Eucalyptus* spp. (Gardina and Malajczuk, 1988; Bellei et al., 1992; Adjoud-Sadadou and Halli-Hargas, 2000) and *Acacia* spp. (McGee, 1986; Bellgard, 1991; Brundrett and Abbott, 1991; Reddell and Milnes, 1992) can both form symbioses with arbuscular mycorrhizal fungi, *Eucalyptus* also form ectomycorrhizal associations as they age (Gardina and Malajczuk, 1988; Bellei et al., 1992). Therefore chemical stratification may occur in mixed plantations of *Eucalyptus* and N₂-fixing species at certain stages of stand development when different mycorrhizal associations are formed.

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Physical stratification occurs through differences in fine-root distribution that affect exploitation strategies. For example, vertical differentiation of fine roots was observed in a regrowth forest stand containing *Eucalyptus maculata*, *E. pilularis* and *Acacia mabellae* (Neave and Florence, 1994). *Eucalyptus maculata* had a greater fine-root biomass in the deeper soil layers than the associated species, leading to more effective nutrient acquisition in the lower soil layers and a greater competitive ability during times when surface soils dry out (Neave and Florence, 1994). Similarly Khanna (1997) found evidence of root stratification in a three-year-old *A. mearnsii*/*E. globulus* mixture such that *A. mearnsii* roots were mostly confined to the surface 10 cm while *E. globulus* roots generally occupied the deeper soil layers. However, a later study in the same trial by Bauhus et al. (2000) found that fine-root architecture and vertical distribution were similar for *A. mearnsii* and *E. globulus* in the top 0-30 cm when the stand was six years old. This suggests similar soil exploitation strategies and potentially strong competition for soil resources. On the basis of these two studies it cannot be ascertained whether these contrasting results are due to differences in methodology or represent a real disappearance of early root stratification when trees aged and both species explored the soil more fully.

However, while root stratification has been linked to increased production in several mixtures of herbaceous species (Trenbath, 1974), it has not been linked to increased productivity in tree stands. The studies above indicate that root stratification may enable the coexistence of different species on sites, where belowground resources are limiting.

5. Facilitation

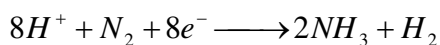
Facilitation may occur directly, by the amelioration of harsh environmental conditions or through increased resource availability, or indirectly, via the elimination of potential competitors, the introduction of beneficial organisms (mycorrhizae and other soil microbes) or protection from

herbivores (Callaway, 1995). This section focuses on direct facilitation through improved nitrogen availability.

Often the primary objective of using N₂-fixing species in mixed systems is to increase the N
 5 available to the main crop or companion species. Total N in the plant-soil system can be increased
 by atmospheric N₂-fixation (Kelty, 1992; Kelty and Cameron, 1995). In addition, N availability can
 be increased by accelerating the rate of N cycling without an increase in total N levels in the plant-
 soil system (Kelty, 1992; Kelty and Cameron, 1995). Either way, N can be transferred between the
 N₂-fixing species to the non-N₂-fixing species via the decomposition of litter (such as foliage and
 10 fine-roots) and the subsequent mineralisation of organic N (including root exudates).

5.1 Nitrogen fixation

Nitrogen fixation can only be performed by certain strains of prokaryotic microbes (Fisher and
 Binkley, 2000). These microbes use the nitrogen fixing enzyme, nitrogenase, to reduce atmospheric
 15 N₂ to ammonia (NH₃), which is a form that plants can utilise (Walker et al., 1983; Sprent, 1987).



Many plants form symbiotic, mutualistic relationships with these prokaryotes, which receive
 20 carbohydrates and microaerobic environments and supply reduced N for use in amino acids,
 proteins and other biochemicals (Binkley and Giardina, 1997). Plants capable of forming such
 symbioses, such as legumes or actinorhizal plants, are sometimes used in agroforestry and forestry
 systems. Legumes such as *Acacia*, *Falcataria*, *Leucaena*, *Lupinus* and *Robinia* have symbiotic,
 mutualistic relationships with the bacteria genera *Rhizobium* and *Bradyrhizobium* (Binkley and
 25 Giardina, 1997; Fisher and Binkley, 2000). Actinorhizal species from genera such as *Alnus*,

Casuarina and *Ceanothus* are associated with the *Frankia* genus of actinomycetes (Benson and Silvester, 1993).

There are several methods for estimating rates of N₂-fixation in the field, depending on the type or location of the experiment and available resources (Shearer and Kohl, 1986). Common methods are N accretion, chronosequences, acetylene reduction assays and ¹⁵N methods (natural abundance or labelling) (these are described in detail in Silvester, 1983; Caldwell and Virginia, 1989; Fisher and Binkley, 2000).

5.1.1 Rates of N₂-fixation

Nitrogen input rates from symbiotic N₂-fixation in plant symbioses have been estimated to be less than 1 to more than 200 kg N ha⁻¹ year⁻¹, which may be about 10% to nearly 100% of the total N used by the host plant (Binkley, 1992; Binkley and Giardina, 1997; Khanna, 1998; Fisher and Binkley, 2000; May and Attiwill, 2003). Rates of N₂-fixation depend on the density, age and growth of the host plants, the degree of nodulation, the genetics of the host, mycorrhizae and N₂-fixing bacteria, and environmental factors that affect plant growth (see reviews by Danso et al., 1992; Sanginga et al., 1995; Binkley and Giardina, 1997; Fisher and Binkley, 2000; Brockwell et al., 2005).

The effect of soil P availability on N₂-fixation does not appear to have been measured in forests or plantations. In pot trials rates of N₂-fixation and nitrogenase activity of *Acacia* or *Falcataria* seedlings increased with increasing amounts of P fertiliser (Dixon and Wheeler, 1983; Sun et al., 1992; Binkley et al., 2003a), whereas there was little to no effect of P fertiliser on *L. leucocephala* seedlings (Sanginga et al., 1991) or *Casuarina equisetifolia* seedlings (Sanginga et al., 1989b).

Sanginga et al. (1991) suggested that P affected N₂-fixation through its effect on plant growth rather than its effect on the N₂-fixation process directly.

Nitrogen-fixing trees themselves can influence soil P availability, however, the effects vary with species and sites. For example, in mixtures of *F. moluccana* and *E. saligna* soil P availability declined with increasing proportions of *F. moluccana* (Study 7 in Table 1) (Binkley et al., 2000; Kaye et al., 2000). However, aboveground biomass, P in aboveground biomass, and P cycling through litterfall increased with increasing proportions of *F. moluccana* (Binkley et al., 1992; Kaye et al., 2000). The higher P uptake by *F. moluccana* may have been due to associations with mycorrhizae (Binkley and Ryan, 1998; Binkley et al., 2000) and the use of P that was unavailable to *E. saligna* (Binkley et al. 2000). Similarly, P in foliage biomass and litterfall was significantly higher in stands containing *A. mearnsii* than in *E. globulus* monocultures (Forrester et al., 2005b), although soil P was not significantly different in mixtures or monocultures of *E. globulus* and *A. mearnsii* (Pares, 2002).

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There is no clear trend to describe the effect of N availability on N₂-fixation or the proportion of N derived from the atmosphere (N_{dfa}) by trees (Sprent, 1994; Binkley and Giardina, 1997). Several studies have observed declines in the total N₂ fixed or N_{dfa} with increasing N availability (Sanginga et al., 1989a; Baker et al., 1994; Dommergues, 1995; Binkley et al., 2003a). However, in other studies it appeared that N fertiliser increased N₂-fixation by *Alnus* species (Ingestad, 1980; Binkley et al., 1994).

The effect of soil moisture, pH and other soil physical and chemical properties on N₂-fixation are complex and are beyond the scope of this review. The factors that affect N₂-fixation and the effect of N₂-fixing plants on soil chemical and physical properties are discussed by Danso et al. (1992) and Binkley and Giardina (1997).

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5.1.2 Dynamics of N_2 -fixation

Little work has been done on the effects of tree age and N accretion over time on N_2 -fixation and N_{dfa} . The ^{15}N labelling method was used to measure the total N_2 fixed and N_{dfa} by the N-fixing
 5 *Leucaena leucocephala* and *Casuarina equisetifolia* (Parrotta et al., 1996). At year one the N_{dfa} by
L. leucocephala was 98% and this declined to 38% by year 3.5. The N_{dfa} by *C. equisetifolia*
 fluctuated between 43 to 62% between years 1 and 3.5. The N_2 fixed, however, did not decline with
 age, such that the N_2 fixed over 3.5 years was similar for both species, at 73 and 74 kg ha⁻¹ yr⁻¹ for
C. equisetifolia and *L. leucocephala* respectively. The reduction in N_{dfa} by *L. leucocephala* may
 10 have resulted from the cycling of N through litterfall (more than double that of *C. equisetifolia*) and
 decomposition (Parrotta et al., 1996) since increasing N availability has been found to reduce N_{dfa} in
 some studies as explained above.

Using the natural abundance method and several understorey species as non- N_2 -fixing reference
 15 plants, Van Kessel et al. (1994) found that *L. leucocephala* fixed about 74% of its N after the first
 year. However, by years four and six the $\delta^{15}N$ values of the *L. leucocephala* and understorey were
 similar and N_{dfa} could not be determined (Van Kessel et al., 1994), which may result from a
 reduction in N_2 -fixation in response to increased N availability (Dommergues, 1995).

20 5.1.3 Use of fixed N by non- N_2 -fixing species

Nitrogen availability may be increased for non- N_2 -fixing species growing in mixture with a N_2 -
 fixing species in several ways: 1) fixed N may become available to non- N_2 -fixing species after plant
 and microbe tissues die and decompose, releasing N that cycles through the ecosystem (Van Kessel
 et al., 1994; Stock et al., 1995; Fisher and Binkley, 2000; May and Attiwill, 2003); 2) via root

exudation or mycorrhizal connections between root systems when both species form symbioses with the same mycorrhizae (He et al., 2003); and 3) N₂-fixing plants can rely heavily on fixed N, which may be 10% to nearly 100% of the N used by the N₂-fixing plant (Binkley, 1992; Binkley and Giardina, 1997; Khanna, 1998; Fisher and Binkley, 2000; May and Attiwill, 2003) so more soil N may be available to non-N₂-fixing plants before the fixed N is cycled and transferred to the non-N₂-fixing plants.

Studies in agricultural or agroforestry systems have shown that a higher proportion of this symbiotically fixed N₂ may be used than when synthetic N fertilizer is applied (see reviews by Peoples et al., 1995; Crews and Peoples, 2005). Furthermore, less fixed N₂ may be lost from the plant and soil pool (via leaching or volatilization) because it is immobilized in microbial biomass and semi stable soil organic materials during decomposition (Peoples et al., 1995; Crews and Peoples, 2005). However, opposing trends have also been observed, and maximising benefits of symbiotically fixed N₂ also depends on synchronising the timing of N₂-fixation (and enhanced N availability) to when the non-N₂-fixing species require the N (Peoples et al., 1995; Sanginga et al., 1995; Crews and Peoples, 2005).

Few studies have examined the time it takes for the N fixed by the N₂-fixing species to benefit the associated species. In mixtures of *Eucalyptus x robusta* with *C. equisetifolia* or *L. leucocephala*, Parrotta et al. (1996) found that the *E x robusta* was taking up the fixed N by both N₂-fixing species after two years. This was demonstrated using the ¹⁵N labelling method. Similarly, using the natural abundance method Van Kessel et al. (1994) found that after one year, the δ¹⁵N of the non-leguminous understorey of a *L. leucocephala* plantation was about 7.3‰ compared to less than 4‰ for *L. leucocephala*, but by years four and six, δ¹⁵N of the understorey and *L. leucocephala* were about 1‰ and Van Kessel et al. (1994) concluded that the understorey relied as much on previously fixed N as the *L. leucocephala*.

Khanna (1997) showed that *E. globulus* in mixture with *A. mearnsii* (Study 1 in Table 1) were larger in terms of height growth from as early as 25 months, and *E. globulus* in mixture had higher N concentrations in fine-roots and senescent foliage when compared to monocultures at 31 and 25 months respectively. Since leaf litterfall had not commenced at this stage, increased growth and N-concentrations must have resulted from nutrient cycling through fine-roots (including nodules) (Khanna, 1997). In the same trial, average rates of N₂-fixation up to age 10 years were found to be about 140 and 188 kg ha⁻¹ yr⁻¹ in 1:1 mixtures and *A. mearnsii* monocultures respectively (Forrester, unpublished).

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5.1.4 Effect of competition on N₂-fixation

Few studies have examined the effect of competition from a non-N₂-fixing species on rates of N₂-fixation or N_{dfa} by a N₂-fixer. In an 18 month old pot trial, where N₂-fixing *C. cunninghamiana* were planted in 1:1 mixtures with *E. globulus*, N₂-fixation and N_{dfa} increased from 125.48 g N plant⁻¹ and 86.68% in monocultures to 152.69 g N plant⁻¹ and 94.75% in mixture (same total plant density as monocultures) (Study 16 in Table 1; Baker et al., 1994). This was probably the result of competition for soil N from *E. globulus* (Baker et al., 1994). Also, both species grew larger in mixture than monoculture. While *E. globulus* may have competed for N, the net effect of competition for all resources from *E. globulus* on *C. cunninghamiana* must have been less than the competition from other *C. cunninghamiana* (Baker et al., 1994). In contrast, competition from *E. x robusta* planted with *C. equisetifolia* did not have any significant effect on the quantity of N fixed or N_{dfa} by *C. equisetifolia* between 6-24 months of age (Parrotta et al., 1994). However, this may be due to less intense competition in the plantation when compared to the pots (Baker et al., 1994).

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5.2 Litter fall and nutrient cycling

Litterfall includes all plant organs and tissues that fall to the ground, and together with decomposing roots, litterfall constitutes the principal source of organic matter for the biochemical cycling of nutrients in terrestrial ecosystems (Meentemeyer et al., 1982). Both the quantity and
5 quality of litter have a strong influence on the nutrient flow in forests.

Reviews on litter decomposition of single-species litter have been carried out by Swift et al. (1979), Aerts (1997) and Paul et al. (2004). Rates of litter decomposition are influenced by temperature, humidity, moisture content (Meentemeyer, 1978; Nagy and Macauley, 1982; Guo and Sims, 1999),
10 and litter quality, which may be described by lignin, C and nutrient concentrations or ratios of these (Nagy and Macauley, 1982; Taylor et al., 1991; Attiwill and Adams, 1993; Berg and McLaugherty, 2003). Slow rates of decomposition and N release can slow tree growth, even when total ecosystem nitrogen is adequate (Kelty, 1992; Kelty and Cameron, 1995). Litter production may then exceed
15 decomposition so that high quantities of nitrogen and other nutrients are stored in an organic form in the litter where they are unavailable for plant growth (Polglase and Attiwill, 1992; O'Connell and Grove, 1996).

Eucalyptus species often produce litter with low nutrient concentrations and which decomposes slowly during the early stages of decomposition (Guo and Sims, 2001; Paul et al., 2004). As a result
20 high proportions of nutrients may be held in undecomposed litter (Adams and Attiwill, 1986). In contrast, N₂-fixing species often have higher N concentrations and decompose more rapidly (e.g. Toky and Singh, 1993; Parrotta, 1999), at least initially. Mixing eucalypt litter with more readily decomposable and more nutrient rich litter may enhance the decomposition of eucalypt litter
(Briones and Ineson 1996). Gartner and Cardon (2004) found that in terms of mass loss, synergistic
25 effects occurred in the majority of mixed-litter decomposition studies (47.5%), whereas additive

(33.3) or antagonistic effects (19.1%) were less frequently observed. However, longer-term rates of decomposition may be slower for litter with high N concentrations because N can retard the later stages of lignin decay (Berg and Ekbohm, 1991; Berg, 2000). The consequences of mixing litter from different species on the long-term dynamics and quality of soil organic matter, which is more
5 important for nutrient supply to trees, have not been sufficiently researched (Prescott 2005), and there are no long-term data on litter decomposition for combinations of eucalypts and N-fixing species.

Soil fauna and microbes play important roles in litter decomposition (Brussaard, 1998). Microbes
10 require N and other nutrients to break down the various components of litter (lignin, tannins, cellulose). Microbial activity can increase when a species with a higher foliar N content (such as a N₂-fixing species) is included in the early stages of stand development to decrease the C: N ratio of the litter (Ewel, 1986; Kelty, 1992). Thus the cycling of N and other nutrients held in soil organic matter may be accelerated (Kelty and Cameron, 1995).

15

Quantities of N and P cycled through litterfall are often higher in mixtures of N₂-fixing trees and non-N₂-fixing trees, than monocultures of the non-N₂-fixing species (Binkley, 1992; Binkley et al., 1992; Parrotta, 1999). However, trends in the initial rates of decomposition and nutrient loss from mixed-species litter (compared to monoculture litter) are complex and inconsistent, and litter in
20 mixtures with N₂-fixing species does not necessarily decay faster than that of non-N₂-fixing species in monocultures (see reviews by Binkley, 1992; Rothe and Binkley, 2001; Gartner and Cardon, 2004).

Two examples, where productivity and rates of nutrient cycling through litterfall have increased in
25 mixtures of N₂-fixing species compared to monocultures of the *Eucalyptus* spp., include *Falcataria moluccana* with *Eucalyptus saligna* (Study 7 in Table 1) (Binkley et al., 1992; DeBell et al., 1997;

Binkley et al., 2003b), and *Acacia mearnsii* with *Eucalyptus globulus* (Study 1 in Table 1) (Forrester et al., 2004; Forrester et al., 2005b). In both studies, the N and P contents of annual litterfall were significantly higher in plots containing the N₂-fixing species than monocultures of the *Eucalyptus* species. Rates of litter decomposition were also significantly higher in mixtures than in the *Eucalyptus* monocultures (Forrester et al., 2005b). Similar increases in N and P cycling or availability have been observed in other mixed-species systems containing *Eucalyptus* species (Turvey et al., 1984; Parrotta et al., 1996; Parrotta, 1999; May and Attiwill, 2003). It is important to note that even species with low rates of N₂-fixation (< 10 kg N ha⁻¹ yr⁻¹) but high leaf nutrient contents and rates of nutrient cycling may significantly enhance nutrient cycling in mixed stands (Forrester et al., 2005a).

These results from mixed plantations are consistent with those from native *Eucalyptus* forests, where *Acacia* species and other N₂-fixers can be an important component owing to the quantity of the N they fix (Hamilton et al., 1993; May and Attiwill, 2003) and the amount of N they cycle through litterfall (McColl, 1966; Hingston et al., 1979; Grove and Malajczuk, 1985; O'Connell, 1986).

5.3 Resource use efficiency and biomass allocation

Plantation growth can be described as a function of resource supply, the proportion of resources captured and the efficiency with which they are used to fix CO₂ (Binkley et al., 2004). The previous sections have discussed increases in resource capture, through canopy and root stratification, and increased supply, through N₂-fixation and accelerated rates of nutrient cycling. In addition and complementary to these processes, growth may be influenced by changes in the efficiency of resource use.

Binkley et al. (2004) found that *Eucalyptus* plantations on more productive sites tend to have higher resource use efficiencies than those on less productive sites, and hence that silvicultural treatments may not only increase resource supplies but also the efficiency of resource use. Thus the increased N availability from N₂-fixation and the accelerated rates of N and P cycling may also increase the
 5 nutrient, light and water use efficiency of mixed-species stands.

For example several studies have found that increased N and P availability increased instantaneous water use efficiency in a number of species (Sheriff et al., 1986, *Pinus radiata*; Green and Mitchell, 1992, *Pinus taeda*; Bruck et al., 2000, *Pennisetum glaucum*; Bruck et al., 2001, *Canna edulis*;
 10 Hobbie and Colpaert, 2004, *Pinus sylvestris*). However, Hubbard et al. (2004) found that following fertilization in an *E. saligna* plantation, stand water use increased because leaf area increased, and water use efficiency was similar in fertilized and unfertilized stands. Similarly Hatton et al. (1998) found linear relationships between tree leaf area and mean daily water use for several *Eucalyptus* species and sites. Therefore mixtures, which are more productive and have higher leaf areas than
 15 *Eucalyptus* monocultures, may use more water.

Light saturated rates of photosynthesis in *Eucalyptus* species often increase with increasing leaf N concentrations as a result of N fertilisation, foliage N-concentration gradients within the canopy or species differences (Mooney et al., 1978; Clearwater and Meinzer, 2001; Grassi et al., 2002;
 20 Warren and Adams, 2004), although this is not always the case (Close et al., 2004). Leaf N concentrations have increased in *E. globulus* (Bauhus et al., 2004) and *E. saligna* (Forrester, 2004) growing with *A. mearnsii* in plantations and in *E. delegatensis* growing with *A. dealbata* in a native forest (Küppers, 1996). However, despite the increased N concentrations of *E. globulus* in 1:1 mixtures (1.24%) compared to monocultures (1.09%) light saturated rates of photosynthesis in the
 25 mid canopy were lower in mixtures ($11.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than monocultures ($14.6 \mu\text{mol CO}_2 \text{ m}^{-2}$)

s^{-1}) (Bauhus et al., 2004). In addition the efficiency of *E. globulus* crowns, estimated as aboveground tree biomass per unit crown volume, was similar in mixture to monoculture.

Nevertheless Binkley et al. (2004) showed that trends occurring at the scale of leaves and seconds
5 may not represent those occurring at the scale of stands and years, as a result of more complete biomass accounting (including respiration), interactions among resources and adaptation of biomass partitioning to optimize resource capture and use. On the scale of trees and stands, Binkley et al. (1992) and Forrester et al. (2005b) found that *E. saligna* and *E. globulus* were more efficient in their N and P use than *F. moluccana* and *A. mearnsii*, respectively (where efficiency was estimated as
10 aboveground biomass increment per unit nutrient in annual litterfall). Thus monocultures of the *Eucalyptus* species were most efficient and those of *F. moluccana* and *A. mearnsii* were least efficient. The same trend was found in a pot trial containing mixtures of *E. globulus* and *A. mearnsii* (Forrester et al., 2006b). However, it did not appear as though the nutrient use efficiencies of any species were changed by growing in mixtures. In contrast, possible changes in efficiency were
15 observed by Binkley (1983) in mixtures of *Pseudotsuga menziesii* and *Alnus rubra*. In this study, foliar N concentrations of *P. menziesii* increased from 9.3 mg g⁻¹ in monoculture to 14.1 mg g⁻¹ in mixture with *Alnus rubra*, and *P. menziesii* annual stem biomass growth was about 20% higher in mixture with only 35% of the leaf biomass of the *P. menziesii* growing in monocultures (Binkley, 1983). This may have resulted from a greater net photosynthetic rate per unit leaf area or a change
20 in biomass allocation (Binkley, 1983).

Increased N availability may also increase leaf area, which increases light capture and canopy photosynthesis, and hence gross primary production (see Landsberg, 1997). For example Cromer et al. (1993) and Smethurst et al. (2003) found that N and P fertiliser increased leaf area and biomass
25 production in plantations of *E. grandis* and *E. nitens*, respectively. However, increases in leaf area

in response to fertiliser may also be associated with changes in the allocation of C from belowground to aboveground growth (Cannell, 1985).

Increases in nutrient availability can shift allocation of C from roots and mycorrhizae (for nutrient uptake) to aboveground plant parts, to increase the capture of light and CO₂ (Cannell, 1985; Raich, 1998; McConnaughay and Coleman, 1999). However, few studies have examined whether increases in aboveground growth associated with a higher nutrient availability result from an increase in total productivity (both above- and belowground), a shift in biomass partitioning, or both (Ryan et al., 1996; Keith et al., 1997). Furthermore, the results of such studies have been variable, documenting increases, decreases and no change in belowground C fluxes with increasing nutrient supply (Haynes and Gower, 1995; Ryan et al., 1996; Keith et al., 1997; Raich, 1998; Zak and Pregitzer, 1998; Pongracic, 2001; Giardina and Ryan, 2002; Giardina et al., 2003). These contrasting findings may result from species-specific strategies for acquiring belowground resources, and therefore general trends in belowground C allocation with changing nutrient availability may exist only for groups of plants and not all species as a whole (Zak and Pregitzer, 1998).

Only one study has investigated the C allocation in mixtures of *Eucalyptus* and N₂-fixing species. In an 11 year old mixed-species plantation where 1:1 mixtures of *E. globulus* and *A. mearnsii* produced twice the aboveground biomass of *E. globulus* monocultures (Study 1 in Table 1), the total annual belowground C allocation (TBCA; 14.6 to 16.3 Mg ha⁻¹ yr⁻¹) was not significantly different between the mixture and the monocultures (Forrester et al., 2006a). Higher ratios of aboveground net primary production to TBCA in the mixtures (0.41) than in either monoculture (100%A: 0.28, 100%E: 0.31) indicated that trees in mixture partitioned a lower proportion of their C belowground than those in monocultures. Since the mixture was as productive as monocultures belowground but more productive aboveground, it was also more productive overall. Therefore

mixed-species plantations may have the potential to increase C sequestration above that of monocultures.

6. Effects of site quality on species interactions

5 As discussed above, differing characteristics can allow component species of a mixture to coexist in an environment with high productivity (Harper, 1977). However, in addition to this matching of species, successful mixed-species plantations require the matching of the species combination with the site so that the competitive interactions are minimised while the competitive reduction and facilitative interactions are maximised.

10

Facilitation often occurs simultaneously with competition, and the complex interactions between these mechanisms determine the overall productivity (Callaway, 1995; Holmgren et al., 1997).

Facilitation or competitive reduction interactions generally predominate where resources are in low supply, under high physical stress or high consumer pressure (Bertness and Callaway, 1994;

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Holmgren et al., 1997). The dominance of competition increases on more productive sites, where physical stress or consumer pressures are low (Bertness and Callaway, 1994; Holmgren et al., 1997). Facilitation or competitive reduction in mixed stands may only increase yields, if there is a limited supply of the resource for which acquisition was facilitated or competition was reduced, such that the effect of these positive interactions outweigh the negative, competitive effects.

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The influence of soil N and P availability on the growth of mixtures have been examined directly in a field trial with *E. saligna* and *F. moluccana* (Boyden et al., 2005) and in a pot trial with *E.*

globulus and *A. mearnsii* (Forrester et al., 2006b). Forrester et al. (2006b) compared the growth of *E. globulus* and *A. mearnsii* in mixed pots, which contained one of each species, to monospecific

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pots, which contained two *E. globulus* or two *A. mearnsii* plants. These were fertilised with high

and low rates of N and P. *Eucalyptus globulus* grew larger in mixture than monocultures and this effect was greater at high levels of N or P than at low levels (Figure 4). *Acacia mearnsii* also grew larger in mixture than monoculture at low levels of N. However, growth was not significantly different at high or low levels of P, and at high N, *E. globulus* suppressed *A. mearnsii* growth, and mixtures were less productive than *E. globulus* monocultures. This experiment indicated that a very fast growing and efficient user of site resources, such as many *Eucalyptus* spp., planted on a site with high resource availability may not produce higher yields when grown in mixture.

Boyden et al. (2005) examined the inter- and intraspecific interactions between *E. saligna* and *F. moluccana* neighbours along gradients of N and P availability, and found similar trends to that of Forrester et al. (2006). The growth of *E. saligna* trees increased with *F. moluccana* at high P but declined at low P. Growth of *F. moluccana* was higher with *E. saligna* neighbours at low N, but lower at high N, where the competitive influence of *E. saligna* was higher. These interactions measured for individual trees were more complex than indicated by stand level analyses, which showed that *E. saligna* trees had higher growth rates in mixtures than monocultures and *F. moluccana* trees were neither positively or negatively affected by growing in mixture (Binkley et al., 2003b).

7. Meta-analysis of published mixed-species trials

Table 1 presents a large collection of data which individually is often inconclusive, but which collectively may shed light on the benefits of mixed-species plantings. Relative Yields (RY) are often used for such comparisons, but a thorough analysis requires data from both monocultures as well as one or more species mixtures. The computation of RY relies heavily on the estimate of the monoculture yield, and any error or bias in the estimated monoculture yield propagates through the calculation and may have an undue influence on the analysis.

We have used an alternative regression approach (and the statistical software ARC, Cook and Weisberg 1999) which allowed greater use of the available data (Figure 5). Our null hypothesis assumed no interaction between species (cf. Figure 1a), implying a straight line regression between the logarithm of total yield and the percentage of eucalypts in the treatment ($\text{Log}_{10}Y = \beta_0 + \beta_1 P_e$). The logarithm transform was indicated by the Box-Cox test ($\lambda\text{-hat} = 0.23$), and stabilized the variance. Notice that the fitted regressions need not pass through any of the points, but represent the best (least squares) fit to all of the data points within a study (e.g., solid line for Study 15 in Figure 5), reducing the possible risk of bias from misleading monoculture data. If the null hypothesis (that there is no species interaction) is correct, the residuals about these regression lines should not exhibit a pattern, but should approach randomness.

Figure 6 illustrates the pattern of residuals arising from fitting these regressions. In most of the studies reported in Table 1, there is evidence of a trend in these residuals. In most cases, this trend is 'n-shaped', indicating that mixtures have higher production than monocultures (as in Figure 1d). In the case of the filled symbols (Studies 2 & 14 shown as ▲, and studies 1, 4, 7, 9Ent, 11L, 16 & 18 [except 18.LoP] shown as ●), this trend is quite pronounced. Three studies (9L, 12ret and 17) exhibit a 'u-shaped' trend indicating that a mixture has a lower production than monocultures. Study 4, which appeared to have a lower production when examined using RY in Figure 2, is seen here to have a slight 'n-shaped' trend indicative of a slightly increased production in a mixture (and Table 1 indicates 5.9 Mg ha⁻¹ from eucalypts, 26.4 from acacias = 16.15 Mg ha⁻¹ average for monocultures; cf. 16.4 Mg ha⁻¹ from the mixture).

Figure 6 illustrates that the null hypothesis (no species interactions) may be inadequate, and this impression is confirmed by formal testing using a quadratic equation of the form

$\text{Log}_{10}Y_i = \beta_{0i} + \beta_{1i}P_e + \beta_{2i}P_e^2$ (where the i is specific to each study). An ANOVA (Table 2) reveals that

the regression is adequate (Regression $P < 0.0001$), sufficient (Lack of fit $P = 0.06$), and that a quadratic trend is warranted ($P = 0.0001$). The significant quadratic term ($P = 0.0001$) refutes the null hypothesis: this meta-analysis provides strong evidence that species interactions are evident in the data reported in Table 1.

5

Parameter estimates from the regression suggest that it may be useful to group the studies from Table 1 into three groups according to the magnitude of the yield increase evident in mixtures (Table 3). Studies 1, 2, 7, 11L, 16 and 18HiP have β_2 's that are significantly different from zero ($P \leq 0.05$). The estimated β_2 for Study 2 is large (in magnitude; < -0.0002), and significantly different from most of the other studies, so was grouped with Study 14 for which a similar estimate of β_2 was obtained (Group 1). Studies 1, 4, 7, 9Ent, 11L, 16 and 18 (except 18LoP) have estimates that are similar (between -0.00010 and -0.00025) and which do not differ significantly ($P > 0.05$), so these were assigned to Group 2. Studies 3, 5, 6, 9F, 10, 11C, 12rem, 13, 15 & 18LoP have estimates of β_2 that are negative (thus implying an 'n-shaped' trend), but not significantly different from zero ($P > 0.3$; call this Group 3). Studies 9L, 12ret & 17 have parameter estimates that are positive ('u-shaped' trend), but not significantly different from any of the members of Group 3, and Study 8 has insufficient data to allow an estimate to be quantified, so all were included in Group 3.

Refitting this equation ($\text{Log}_{10} Y_i = \beta_{0i} + \beta_{1i} P_e + \beta_{2j} P_e^2$, where j represents the group) offered parameter estimates for β_2 of -0.000352 (s.e.= 0.000043 , $P < 0.0001$), -0.000161 (s.e.= 0.000019 , $P < 0.0001$) and -0.000027 (s.e.= 0.000015 , $P = 0.0798$) for Groups 1, 2 & 3 respectively. The estimates for groups 2 & 3 differ from zero, and from each other ($P = 0.0001$), supporting the contention that three groups are necessary and adequate. It is important to note that this grouping is not based on prior knowledge of the studies involved, and there are no a priori reasons for this grouping based on the nature of the mixtures (stand structure, experimental design, species composition).

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In Table 3, many of the parameter estimates are not significant, but pooling these data in a meta-analysis provides sufficient data to contribute to a statistically significant ($P < 0.0001$) conclusion that about half of the studies reported in Table 1 can be expected to contribute higher yields when grown in mixtures rather than monocultures. The remaining studies are not considered different from the null hypothesis at conventional significance levels, but there is some evidence of a growth stimulus ($P = 0.08$), and a similar analysis with additional data may be more revealing. Some of the studies were split across groups, and it is noteworthy that a weedy understorey (Study 12) and low phosphorus (Study 18) detracted from an otherwise beneficial mixture. Note that there are insufficient degrees of freedom to comment on the shape of the response (or to detect the optimum composition); the analysis merely reveals the magnitude of the yield stimulus provided by a mixture. Caution is needed in extrapolating these findings to other situations. It is possible that the overall significant finding arose because journals prefer to publish papers which report yield increases in mixtures, rather than reports of indifferent or diminished yields. Also, researchers may be more inclined to investigate species mixtures where synergistic effects between the species occurred, rather than mixtures where antagonistic effects prevailed. Nonetheless, Table 3 offers clear evidence that in some situations, mixed plantings of eucalypts and nitrogen-fixing species can contribute to yields that are higher than could be attained with comparable monocultures.

8. Implications and future research needs

Mixing N_2 -fixing species with *Eucalyptus* species can lead to increases in total stand productivity and in some cases the productivity of the *Eucalyptus* component alone (Binkley et al., 2003b), when compared to *Eucalyptus* monocultures. However, there are also examples of reduced productivity with the N_2 -fixing species suppressing the growth of the *Eucalyptus*. To maximise the probability of success, it is important to understand the processes and interactions that occur in these stands. Based on our current understanding, it is important to select species with compatible height growth rates to

ensure that the less shade-tolerant species are not overtopped by the more shade-tolerant species.

This requires knowledge of height-age curves of each species in monoculture and the relative shade tolerances of each species (Fisher and Binkley, 2000; Forrester et al., 2005a). Competition for light can also be managed using variations of planting designs and the relative timing of planting each species. Following the consideration of height growth dynamics, the selection of N₂-fixing species should be based on their ability to cycle nutrients and on their ability to fix N₂.

Appropriate site selection is also critical to the success of mixed stands. Mixtures will only improve productivity if the processes and interactions between species reduce the competition or increase the availability of a growth limiting resource for that site. This is probably the most difficult information to obtain, particularly when the species have not been grown previously on comparable sites.

While interest and research into mixed-species systems is growing, there are too few observations of the interactions between species, and the influence of site factors on these interactions, to accurately predict successful combinations or sites on which to grow them (Forrester et al., 2005a). For example Table 1 shows all the mixtures containing *Eucalyptus* with a N₂-fixing species that could be found in the literature. This is clearly an incomplete picture. In their review on nutritional interactions in mixtures, Rothe and Binkley (2001) recommended two components to future research. One was a statistical approach to increase the degrees of freedom when analysing processes in mixtures. For example the establishment of the same species combination on different sites or similar species combinations on comparable sites would enable the development of frequency distributions on the occurrence of various effects in mixtures. When using this statistical approach it is useful to consider the hierarchy of different designs in terms of the confidence or degree of certainty to which the results can be applied to other sites or populations. For example, confidence can increase from case studies (with no replication) at a single site, to experiments with

replication at a single site, to replication at several sites, to a meta-analysis of similar experiments that show consistent effects (Binkley and Menyailo, 2005). The degree of confidence will depend on the population within the experiment compared to the population to which the results are to be extrapolated. In the past meta-analyses have not been possible in mixtures of *Eucalyptus* and N₂-
5 fixing trees, however, the recent establishment of trials in South America, Congo (Bouillet et al., 2004), Australia (Forrester, 2004) and China (Zhang, 2003; Xiao et al., 1999), will enable such analyses.

Secondly Rothe and Binkley (2001) recommended a mechanistic approach. This would involve an
10 examination of the processes and interactions between species and their interactions with sites. This information could then be used to develop mechanistic models for predicting the growth of various species combinations, across a range of sites. Existing mechanistic models such as CABALA (Battaglia et al., 2004), which has already been parameterised for *E. nitens* and *E. globulus*, would provide a useful basis for this work. This will require the examination of processes
15 that have received little or no attention in the past such as the dynamics of N₂-fixation in tree stands, fine root nutrient uptake and use efficiencies, belowground C allocation, water use and water use efficiencies.

This mechanistic approach would improve our understanding of what controls the balance between
20 a competitive or facilitative relationship for a given set of species, which is essential when managing mixtures (Boyden et al., 2005). Studies that examine the inter- and intraspecific interactions between *Eucalyptus* and N₂-fixing neighbours along gradients of N and P availability, such as that in *E. saligna* and *F. moluccana* mixtures by Boyden et al. (2005) would also be very useful.

Finally acceptance of mixtures will generally depend on social and economic considerations, both of which are complex and will vary with each location. Several economic analyses on mixtures have shown that mixtures can give more favourable economic outcomes than monocultures (FAO, 1992; Montagnini et al., 1995; DeBell et al., 1997; Xiao et al., 1999).

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10. References

- Adams, M. A., Attiwill, P. M., 1986. Nutrient cycling and nitrogen mineralization in eucalypt
 15 forests of south-eastern Australia. *Plant Soil* 92, 319-339.
- Adjoud-Sadadou, D., Halli-Hargas, R., 2000. Occurrence of arbuscular mycorrhiza on aged
Eucalyptus. *Mycorrhiza* 9, 287-290.
- Aerts, R., 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems:
 A triangular relationship. *Oikos* 79, 439-449.
- 20 Assmann, E., 1970. *The principles of forest yield study*. Pergamon Press. Oxford.
- Attiwill, P., M., Adams, M. A., 1993. Nutrient cycling in forests. *New Phytol.* 124, 561-582.
- Austin, M. T., Brewbaker, J. L., Wheeler, R., Fownes, J. H., 1997. Short-rotation biomass trial of
 mixed and pure stands of nitrogen-fixing trees and *Eucalyptus grandis*. *Aust. For.* 60, 161-
 168.

- Baker, D. D., Du, D., Fried, M., 1994. Influence of combined nitrogen level and *Eucalyptus* competition on dinitrogen fixation in nodulated *Casuarina*. *Protoplasma* 183, 24-28.
- Battaglia, M., Sands, P., White, D., Mummery, D., 2004. CABALA: a linked carbon, water and nitrogen model of forest growth for silvicultural decision support. *For. Ecol. Manage.* 193, 251-282.
- 5
- Bauhus, J., Khanna, P. K., Menden, N., 2000. Aboveground and belowground interactions in mixed plantations of *Eucalyptus globulus* and *Acacia mearnsii*. *Can. J. For. Res.* 30, 1886-1894.
- Bauhus, J., van Winden, A. P., Nicotra, A. B., 2004. Above-ground interactions and productivity in mixed-species plantations of *Acacia mearnsii* and *Eucalyptus globulus*. *Can. J. For. Res.* 34, 686-694.
- 10
- Beadle, C. L., 1997. Dynamics of leaf and canopy development. In: Nambiar, E. K. S., Brown, A. G. (Eds.), *Management of Soil, Nutrients and Water in Tropical Plantation Forests*. Australian Centre for International Agricultural Research, Canberra, pp. 169-212.
- Bell, D. T., Williams, J. E., 1997. Eucalypt ecophysiology. In: Williams, J. E., Woinarski, J. C. Z. (Eds.), *Eucalypt ecology - Individuals to ecosystems*. Cambridge Univ. Press, Cambridge, pp. 168-196.
- 15
- Bellei, M. M., Garbaye, J., Gil, M., 1992. Mycorrhizal succession in young *Eucalyptus viminalis* plantations in Santa Catarina (southern Brazil). *For. Ecol. Manage.* 54, 205-213.
- Bellgard, S. E., 1991. Mycorrhizal associations of plant species in Hawksbury sandstone vegetation. *Aust. J. Bot.* 39, 357-364.
- 20
- Benson, D. R., Silvester, W. B., 1993. Biology of *Frankia* strains, actinomycete symbionts of actinorhizal plants. *Microbiol. Rev.* 57, 293-319.
- Berg, B. 2000. Litter decomposition and organic matter turnover in northern forest soils. *For. Ecol. Manag.* 133, 13-22.
- 25
- Berg, B., Ekbohm, G., 1991. Litter mass-loss rates and decomposition in some needle and leaf litter types. Long-term decomposition in scots pine forest. VII. *Can. J. Bot.* 69, 1449-1456.

- Berg, B., McClaugherty, C., 2003. Plant litter: decomposition, humus formation, carbon sequestration. Springer. New York.
- Bertness, M. D., Callaway, R. M., 1994. Positive interactions in communities. *Trends Ecol. Evol.* 9, 191-193.
- 5 Bi, H., Turvey, N. D., 1994. Interspecific competition between seedlings of *Pinus radiata*, *Eucalyptus regnans* and *Acacia melanoxylon*. *Aust. J. Bot.* 42, 61-70.
- Binkley, D., 1983. Ecosystem production in Douglas-fir plantations: Interaction of Red Alder and site fertility. *For. Ecol. Manage.* 5, 215-227.
- Binkley, D., 1992. Mixtures of nitrogen-fixing and non-nitrogen-fixing tree species. In: Cannell, M. G. R., Malcolm, D. C., Robertson, P. A. (Eds.), *The ecology of mixed species stands of trees*. Blackwell Scientific, London, pp. 99-123.
- 10 Binkley, D., Giardina, C., 1997. Nitrogen fixation in tropical forest plantations. In: Nambiar, E. K. S., Brown, A. G. (Eds.), *Management of Soil, Nutrients and Water in Tropical Plantation Forests*. Australian Centre for International Agricultural Research, Canberra, pp. 297-337.
- 15 Binkley, D., Ryan, M. G., 1998. Net primary production and nutrient cycling in replicated stands of *Eucalyptus saligna* and *Albizia facaltaria*. *For. Ecol. Manage.* 112, 79-85.
- Binkley, D., Menyailo, O., 2005. Gaining insights on the effects of tree species on soils. In: Binkley, D., Menyailo, O. (Eds.), *Tree Species Effects on Soils: Implications for Global Change*. NATO Science Series, Kluwer Academic Publishers, Dordrecht, pp. 1-16.
- 20 Binkley, D., Cromack, K. J., Baker, D. D., 1994. Nitrogen fixation by red alder: biology, rates and controls. In: Hibbs, D., DeBell, D., Tarrant, R. (Eds.), *The biology and management of Red Alder*. Oregon State University Press, Corvallis, pp. 57-72.
- Binkley, D., Giardina, C., Bashkin, M. A., 2000. Soil phosphorous pools and supply under the influence of *Eucalyptus saligna* and nitrogen-fixing *Albizia facaltaria*. *For. Ecol. Manage.* 25 128, 241-247.

- Binkley, D., Senock, R., Cromack, K. J., 2003a. Phosphorus limitation on nitrogen fixation by *Facaltaria* seedlings. *For. Ecol. Manage.* 186, 171-176.
- Binkley, D., Stape, J. L., Ryan, M. G., 2004. Thinking about efficiency of resource use in forests. *For. Ecol. Manage.* 193, 5-16.
- 5 Binkley, D., Dunkin, K. A., DeBell, D., Ryan, M. G., 1992. Production and Nutrient Cycling in Mixed Plantations of *Eucalyptus* and *Albizia* in Hawaii. *For. Sci.* 38, 393-408.
- Binkley, D., Senock, R., Bird, S., Cole, T. G., 2003b. Twenty years of stand development in pure and mixed stands of *Eucalyptus saligna* and N-fixing *Facaltaria moluccana*. *For. Ecol. Manage.* 182, 93-102.
- 10 Bouillet, J. P., Gonçalves, J. L. M., Ranger, J., Galiana, A., Nzila, J. d. D., Deleporte, P., Laclau, J. P., 2004. Potential for legume introduction in short rotation plantation forests as a means to improve productivity and soil fertility? The need for coordinated research. In: Parrotta, J. A., Maître, H. F., Auclair, D., Lafond, M. H. (Eds.), Meeting the challenge: Silvicultural research in a changing world, 14-18 June, Montpellier, France. pp. 17-19.
- 15 Boyden, S., Binkley, D., Senock, R., 2005. Competition and facilitation between *Eucalyptus* and nitrogen-fixing *Falcataria* in relation to soil fertility. *Ecology* 86, 992-1001.
- Briones, M. J. I., Ineson, P., 1996. Decomposition of eucalyptus leaves in litter mixtures. *Soil Biology and Biochemistry* 28, 1381-1388.
- Bristow, M., Vanclay, J., Brooks, L., Hunt, M., 2006. Growth and species interactions of
20 *Eucalyptus pellita* in a mixed and monoculture plantation in the humid tropics of north Queensland. *For. Ecol. Manage.* doi:10.1016/j.foreco.2006.05.010.
- Brockwell, J., Searle, S. D., Jeavons, A. C., Waayers, M., 2005. Nitrogen Fixation in Acacias: An untapped Resource for Sustainable Plantations, Farm Forestry and Land Reclamation. ACIAR Monograph No. 115.

- Bruck, H., Payne, W. A., Sattelmacher, B., 2000. Effects of phosphorus and water supply on yield, transpirational water-use efficiency, and carbon isotope discrimination of pearl millet. *Crop Sci.* 40, 120-125.
- Bruck, H., Jureit, C., Hermann, M., Schulz, A., Sattelmacher, B., 2001. Effects of water and
5 nitrogen supply on water use efficiency and carbon isotope discrimination in edible canna
(*Canna edulis* Ker-Gawler). *Plant Biol.* 3, 326-334.
- Brundrett, M. C., Abbott, L. K., 1991. Roots of Jarrah Forest Plants. I. Mycorrhizal Associations of shrubs and herbaceous plants. *Aust. J. Bot.* 39, 445-457.
- Brussaard, L., 1998. Soil fauna, guilds, functional groups and ecosystem processes. *Appl. Soil Ecol.*
10 9, 123-135.
- Caldwell, M. M., Virginia, R. A., 1989. Root Systems. In: Pearcy, R. W., Ehleringer, J., Mooney, H. A., Rundel, P. W. (Eds.), *Plant Physiological Ecology - Field Methods and Instrumentation*. Chapman and Hall, London, pp. 367-398.
- Callaway, R. M., 1995. Positive interactions among plants. *The Botanical Review* 61, 306-349.
- 15 Cannell, M. G. R., 1985. Dry matter partitioning in tree crops. In: Cannell, M. G. R., Jackson, J. E. (Eds.), *Attributes of trees as crop plants*. Inst. Terrestrial Ecol., Abbots Ripton, Huntingdon, Essex U. K., pp. 160-193.
- Cannell, M. G. R., Malcolm, D. C., Robertson, P. A., 1992. *The ecology of mixed species stands of trees*. Blackwell Scientific. London.
- 20 Clearwater, M. J., Meinzer, F. C., 2001. Relationships between hydraulic architecture and leaf photosynthetic capacity in nitrogen-fertilized *Eucalyptus grandis* trees. *Tree Physiol.* 21, 683-690.
- Close, D. C., Battaglia, M., Davidson, N. J., Beadle, C. L., 2004. Within-canopy gradients of nitrogen and photosynthetic activity of *Eucalyptus nitens* and *Eucalyptus globulus* in
25 response to nitrogen nutrition. *Aust. J. Bot.* 52, 133-140.

- Cook, R.D., Weisberg, S., 1999. *Applied Regression Including Computing and Graphics*, Wiley, New York.
- Crews, T. E., Peoples, M. B., 2005. Can the synchrony of nitrogen supply and crop demand be improved in legume and fertilizer-based agroecosystems? A review. *Nutr. Cycl. Agroecosys.* 72, 101-120.
- 5 Cromer, R. N., Cameron, D. M., Rance, S. J., Ryan, P. A., Brown, M., 1993. Response to nutrients in *Eucalyptus grandis*. 1. Biomass accumulation. *For. Ecol. Manage.* 62, 211-230.
- Danso, S. K. A., Bowen, G. D., Sanginga, N., 1992. Biological nitrogen-fixation in trees in agroecosystems. *Plant Soil* 141, 177-196.
- 10 DeBell, D. S., Whitesell, C. D., Schubert, T. H. 1985. Mixed plantations of *Eucalyptus* and leguminous trees enhance biomass production. USDA For. Serv. Res. Paper PSW-175.
- DeBell, D. S., Whitesell, C. D., Crabb, T. B. 1987. Benefits of *Eucalyptus-Albizia* mixtures vary by site on Hawaii Island. USDA For. Serv. Res. Paper PSW-187.
- DeBell, D. S., Whitesell, C. D., Schubert, T. H., 1989. Using N₂-Fixing *Albizia* to increase growth
15 of *Eucalyptus* plantations in Hawaii. *For. Sci.* 35, 64-75.
- DeBell, D. S., Cole, T. C., Whitesell, C. D., 1997. Growth, development, and yield of pure and mixed stands of *Eucalyptus* and *Albizia*. *For. Sci.* 43, 286-298.
- deWit, C. T., 1960. On competition. *Verslagen van landbouwkundige onderzoekingen*. No. 66.8. Institute for biological and chemical research on field crops and herbage. Wageningen.
- 20 Dixon, R. O. D., Wheeler, C. T., 1983. Biochemical, physiological and environmental aspects of symbiotic nitrogen fixation. In: Gordon, J. C., Wheeler, C. T. (Eds.), *Biological nitrogen fixation in forest ecosystems: foundations and applications*. Martinus Nijhoff, The Hague, pp. 107-171.
- Dommergues, Y. R., 1995. Nitrogen fixation by trees in relation to soil nitrogen economy. *Fertilizer
25 Research* 42, 215-230.

- Ewel, J. J., 1986. Designing agricultural ecosystems for the humid tropics. *Annu. Rev. Ecol. Syst.* 17, 245-271.
- FAO. 1992. Mixed and pure forest plantations in the tropics and subtropics. FAO Forestry paper 103 (based on the work of T. J. Wormald). FAO forestry paper 103, Food and Agriculture Organization of the United Nations, FAO of the UN, Rome, Italy.
- Firbank, L. G., Watkinson, A. R., 1990. On the effects of competition: from monocultures to mixtures. In: Grace, J. B., Tilman, D. (Eds.), *Perspectives on plant competition*. Academic Press, Inc., San Diego, pp. 165-192.
- Fisher, R. F., Binkley, D., 2000. *Ecology and Management of Forest Soils*. John Wiley & Sons. New York; Chichester.
- Forrester, D. I. 2004. Mixed-species plantation of nitrogen-fixing and non-nitrogen-fixing trees. PhD Thesis. The Australian National University, Canberra.
(<http://thesis.anu.edu.au/public/adt-ANU20050202.164252/index.html>)
- Forrester, D. I., Bauhus, J., Khanna, P. K., 2004. Growth dynamics in a mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. *For. Ecol. Manage.* 193, 81-95.
- Forrester, D. I., Bauhus, J., Cowie, A. L., 2005a. On the success and failure of mixed-species tree plantations: lessons learned from a model system of *Eucalyptus globulus* and *Acacia mearnsii*. *For. Ecol. Manage.* 209, 147-155.
- Forrester, D. I., Bauhus, J., Cowie, A. L., 2005b. Nutrient cycling in a mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. *Can. J. For. Res.* 35, 2942-2950.
- Forrester, D. I., Bauhus, J., Cowie, A. L., 2006a. Carbon allocation in a mixed-species plantation of *Eucalyptus globulus* and *Acacia mearnsii*. *For. Ecol. Manage.*, doi:10.1016/j.foreco.2006.05.018.
- Forrester, D. I., Cowie, A. L., Bauhus, J., Wood, J., Forrester, R. I., 2006b. Effects of changing the supply of nitrogen and phosphorus on growth and interactions between *Eucalyptus globulus* and *Acacia mearnsii* in a pot trial. *Plant Soil* 280, 267-277.

- Freckleton, R.P., Watkinson A.R., 2000. Designs for greenhouse studies of interactions between plants: an analytical perspective. *Journal of Ecology* 88, 386–391.
- García-Barrios, L., Ong, C. K., 2004. Ecological interactions, management lessons and design tools in tropical agroforestry systems. *Agrofor. Sys.* 61, 221-236.
- 5 Gardina, J. H., Malajczuk, N., 1988. Recolonisation of Rehabilitated Bauxite Mine Sites in Western Australia by Mycorrhizal Fungi. *For. Ecol. Manage.* 24, 27-42.
- Gartner, T. B., Cardon, Z. G., 2004. Decomposition dynamics in mixed-species leaf litter. *Oikos* 104, 230-246.
- Giardina, C. P., Ryan, M. G., 2002. Total belowground carbon allocation in a fast-growing
10 *Eucalyptus* plantation estimated using a carbon balance approach. *Ecosystems* 5, 487-499.
- Giardina, C. P., Ryan, M. G., Binkley, D., Fownes, J. H., 2003. Primary production and carbon allocation in relation to nutrient supply in a tropical experimental forest. *Global Change Biol.* 9, 1438-1450.
- Grassi, G., Meir, P., Cromer, R., Tompkins, D., Jarvis, P. G., 2002. Photosynthetic parameters in
15 seedlings of *Eucalyptus grandis* as affected by rate of nitrogen supply. *Plant, Cell Environ.* 25, 1677-1688.
- Green, T. H., Mitchell, R. J., 1992. Effects of Nitrogen on the Response of Loblolly Pine to Water Stress. I. Photosynthesis and Stomatal Conductance. *New Phytol.* 122, 627-633.
- Grove, T. S., Malajczuk, N., 1985. Nutrient accumulation by trees and understorey shrubs in an
20 age-series of *Eucalyptus diversicolor* F. Muell. *Stands. For. Ecol. Manage.* 11, 75-95.
- Guo, L. B., Sims, R. E. H., 1999. Litter decomposition and nutrient release via litter decomposition in New Zealand eucalypt short rotation forests. *Agric., Ecosyst. Environ.* 75, 133-140.
- Guo, L. B., Sims, R. E. H., 2001. Effects of light, temperature, water and meatworks effluent irrigation on eucalypt leaf litter decomposition under controlled environmental conditions.
25 *Appl. Soil Ecol.* 17, 229-237.

- Haines, S. G., DeBell, D. S., 1980. Use of nitrogen-fixing plants to improve and maintain productivity of forest soils. Proceedings: Impact of Intensive Harvesting on Young Nutrition Cycling, 279-303.
- Hamilton, S. D., Hopmans, P., Chalk, P. M., Smith, C. J., 1993. Field estimation of N₂ fixation by *Acacia* spp. using ¹⁵N isotope dilution and labelling with ³⁵S. For. Ecol. Manage. 56, 297-313.
- Hara, T., 1986. Effects of density and extinction coefficient on size variability in plant populations. Ann. Bot. 57, 885-892.
- Harper, J. L., 1977. Population Biology of plants. Academic Press. New York.
- 10 Harrington, C. A., Deal, R. L., 1981. Sitka alder, a candidate for mixed stands. Can. J. For. Res. 12, 108-111.
- Hatton, T., Reece, P., Taylor, P., McEwan, K., 1998. Does leaf water efficiency vary among eucalypts in water-limited environments? Tree Physiol. 18, 529-536.
- Haynes, B. E., Gower, S. T., 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. Tree Physiol. 15, 317-325.
- 15 He, X., -H., Critchley, C., Bledsoe, C., 2003. Nitrogen transfer within and between plants through common mycorrhizal networks (CMNs). Crit. Rev. Plant Sci. 22, 531-567.
- Hingston, F. J., Turton, A. G., Dimmock, G. M., 1979. Nutrient distribution in karri (*Eucalyptus diversicolor* F. Muell.) ecosystems in southwest Western Australia. For. Ecol. Manage. 2, 20 133-158.
- Hobbie, E. A., Colpaert, J. V., 2004. Nitrogen availability and mycorrhizal colonization influence water use efficiency and carbon isotope patterns in *Pinus sylvestris*. New Phytol. 164, 515-525.
- Holmgren, M., Scheffer, M., Huston, M. A., 1997. The interplay of facilitation and competition in 25 plant communities. Ecology 78, 1966-1975.

- Hubbard, R. M., Ryan, M. G., Giardina, C. P., Barnard, H., 2004. The effect of fertilization on sap flux and canopy conductance in a *Eucalyptus saligna* experimental forest. *Global Change Biol.* 10, 427-436.
- Hunt, M. A. 1998. Competition between plantation *Eucalyptus nitens* (Dead and Maiden) Maiden and naturally regenerating *Acacia dealbata* Link. PhD Thesis. University of Tasmania, Hobart.
- Hunt, M. A., Battaglia, M., Davidson, N. J., Unwin, G., 2006. Competition between plantation *Eucalyptus nitens* and *Acacia dealbata* weeds in north-eastern Tasmania. *For. Ecol. Manage.*, doi:10.1016/j.foreco.2006.05.017.
- 10 Ingestad, T., 1980. Growth, nutrition, and nitrogen fixation in grey alder at varied rates of nitrogen addition. *Physiol. Plant.* 50, 353-364.
- James, R., Del Lungo, A. 2005. The potential for fast-growing commercial forest plantations to supply high value roundwood. *Planted Forests and Trees Working Papers, Working Paper 33.* Forest Resources Development Service, Forest Resources Division. FAO, Rome, Rome, Italy.
- 15 James, S. A., Bell, D. T., 2000. Leaf orientation, light interception and stomatal conductance of *Eucalyptus globulus* ssp. *globulus* leaves. *Tree Physiol.* 20, 815-823.
- Jolliffe, P. A., 2000. The replacement series. *J. Ecol.* 88, 371-385.
- Jose, S., Gillespie, A. R., Pallardy, S. G., 2004. Interspecific interactions in temperate agroforestry. *Agrofor. Sys.* 61-62, 237-255.
- 20 Kaye, J. P., Resh, S. C., Kaye, M. W., Chimmer, R. A., 2000. Nutrient and carbon dynamics in a replacement series of *Eucalyptus* and *Albizia* trees. *Ecology* 81, 3267-3273.
- Keenan, R., Lamb, D., Sexton, G., 1995. Experience with mixed species rainforest plantations in North Queensland. *Commonwealth Forestry Review* 74, 315-321.
- 25 Keith, H., Raison, R. J., Jacobsen, K. L., 1997. Allocation of carbon in a mature eucalypt forest and some effects of soil phosphorus availability. *Plant Soil* 196, 81-99.

- Kelty, M. J., 1992. Comparative productivity of monocultures and mixed-species stands. In: Kelty, M. J., Larson, B. C., Oliver, C. D. (Eds.), *The Ecology and Silviculture of Mixed-Species Forests*. Kluwer Academic Publishers, Dordrecht, pp. 125-141.
- Kelty, M. J., 2006. The role of species mixtures in plantation forestry. *Forest Ecology and Management*, doi:10.1016/j.foreco.2006.05.011.
- Kelty, M. J., Cameron, I. R., 1995. Plot designs for the analysis of species interactions in mixed stands. *Commonwealth Forestry Review* 74, 322-332.
- Khanna, P. K., 1997. Comparison of growth and nutrition of young monocultures and mixed stands of *Eucalyptus globulus* and *Acacia mearnsii*. *For. Ecol. Manage.* 94, 105-113.
- Khanna, P. K., 1998. Nutrient cycling under mixed-species tree systems in southeast Asia. *Agrofor. Sys.* 38, 99-120.
- Kikuzawa, K., Umeki, K., 1996. Effect of canopy structure on degree of asymmetry of competition in two forest stands in northern Japan. *Ann. Bot.* 77, 565-571.
- Küppers, B. I. L., 1996. Nitrogen and Rubisco contents in eucalypt canopies as affected by *Acacia* neighbourhood. *Plant Physiol. Biochem.* 34, 753-760.
- Lambers, H., Chapin III, F. S., Pons, T. L., 1998. *Plant physiology and ecology*. Springer. New York.
- Landsberg, J. J., 1997. The biophysical environment. In: Nambiar, E. K. S., Brown, A. G. (Eds.), *Management of Soil, Nutrients and Water in Tropical Plantation Forests*. Australian Centre for International Agricultural Research, Canberra, pp. 65-96.
- Little, K. M., Schumann, A. W., Noble, A. D., 2002. Performance of a *Eucalyptus grandis* x *E. camaldulensis* hybrid clone as influenced by a cowpea cover-crop. *For. Ecol. Manage.* 168, 43-52.
- May, B. M., Attiwill, P., M., 2003. Nitrogen-fixation by *Acacia dealbata* and changes in soil properties 5 years after mechanical disturbance or slash-burning following timber harvest. *For. Ecol. Manage.* 181, 339-355.

- McColl, J. G., 1966. Accession and decomposition of litter in spotted gum forest. *Aust. For.* 30, 191-198.
- McConnaughay, K. D. M., Coleman, J. S., 1999. Biomass allocation in plants: ontogeny or optimality? A test along three resource gradients. *Ecology* 80, 2581-2593.
- 5 McGee, P. A., 1986. Mycorrhizal associations of plant species in a semiarid community. *Aust. J. Bot.* 34, 585-593.
- Medhurst, J. L., Pinkard, E. A., Beadle, C. L., Worledge, D., 2003. Growth and stem form responses of plantation-grown *Acacia melanoxylon* (R. Br.) to form pruning and nurse-crop thinning. *For. Ecol. Manage.* 179, 183-193.
- 10 Medhurst, J. A., Pinkard, E. A., Beadle, C. L., Worledge, D., 2006. Photosynthetic capacity increases in *Acacia melanoxylon* following form pruning in a two-species plantation. *For. Ecol. Manage.* doi:10.1016/j.foreco.2006.05.016.
- Meentemeyer, V., 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* 59, 465-472.
- 15 Meentemeyer, V., Box, E. O., Thompson, R., 1982. World patterns and amounts of terrestrial plant litter production. *BioScience* 32, 125-128.
- Montagnini, F., 2000. Accumulation in above-ground biomass and soil storage of mineral nutrients in pure and mixed plantations in a humid tropical lowland. *For. Ecol. Manage.* 134, 257-270.
- 20 Montagnini, F., Gonzáles, E., Porras, C., 1995. Mixed and pure forest plantations in the humid neotropics: a comparison of early growth, pest damage and establishment costs. *Commonwealth Forestry Review* 74, 306-314.
- Montagu, K. D., Kearney, D. E., Smith, R. G. B., 2003. The biology and silviculture of pruning planted eucalypts for clear wood production - a review. *For. Ecol. Manage.* 179, 1-13.
- 25 Mooney, H. A., Ferrar, P. J., Slatyer, R. O., 1978. Photosynthetic capacity and carbon allocation patterns in diverse growth forms of *Eucalyptus*. *Oecologia* 36, 103-111.

- Moraes De Jesus, R., Brouard, J. S., 1989. Eucalyptus-Leucaena mixture experiment I. growth and yield. *The International Tree Crops Journal* 5, 257-269.
- Nagy, L. A., Macauley, B. J., 1982. Eucalyptus leaf-litter decomposition: effects of relative humidity and substrate moisture content. *Soil Biol. Biochem.* 14, 233-236.
- 5 Neave, I. A., Florence, R. G., 1994. The effect of root configuration on the relative competitive ability of *Eucalyptus maculata* Hook. regrowth following clearfelling. *Aust. For.* 57, 49-58.
- O'Connell, A. M., 1986. Effect of legume understorey on decomposition and nutrient content of eucalypt forest litter. *Plant Soil* 92, 235-248.
- O'Connell, A. M., Grove, T. S., 1996. Biomass production, nutrient uptake and nutrient cycling in
10 the Jarrah (*Eucalyptus marginata*) and Karri (*Eucalyptus diversicolor*) forests of southwestern Australia. In: Attiwill, P. M., Adams, M. A. (Eds.), *Nutrition of Eucalypts*. CSIRO Australia, Collingwood, pp. 155-189.
- Pares, A. 2002. Soil Organic Carbon Sequestration in Mixed and Monospecific Plantations of
15 *Eucalyptus globulus* ssp. *pseudoglobulus* and *Acacia mearnsii*. Honours Thesis. The Australian National University, Canberra.
- Parrotta, J. A., 1999. Productivity, nutrient cycling, and succession in single- and mixed-species plantations of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in Puerto Rico. *For. Ecol. Manage.* 124, 45-77.
- Parrotta, J. A., Baker, D. D., Fried, M., 1994. Application of ¹⁵N-enrichment methodologies to
20 estimate nitrogen fixation in *Casuarina equisetifolia*. *Can. J. For. Res.* 24, 201-207.
- Parrotta, J. A., Baker, D. D., Fried, M., 1996. Changes in dinitrogen fixation in maturing stands of *Casuarina equisetifolia* and *Leucaena leucocephala*. *Can. J. For. Res.* 26, 1684-1691.
- Paul, K., Polglase, P., Bauhus, J., Raison, J., Khanna, P. 2004. Modelling change in litter and soil
25 carbon following afforestation or reforestation: Calibration of the FULLCAM 'BETA' model. National Carbon Accounting System Technical Report No. 40. Australian Greenhouse Office, Canberra.

- Peoples, M. B., Herridge, D. F., Ladha, J. K., 1995. Biological nitrogen fixation: An efficient source of nitrogen for sustainable agricultural production? *Plant Soil* 174, 3 - 28.
- Polglase, P. J., Attiwill, P., M., 1992. Nitrogen and phosphorus cycling in relation to stand age of *Eucalyptus regnans* F. Muell. I Return from plant to soil in litterfall. *Plant Soil* 142, 157-166.
- 5
- Pongracic, S. 2001. Influence of irrigation and fertilization on the belowground carbon allocation in a pine plantation. PhD Thesis. The University of New South Wales, Sydney.
- Prescott, C., 2005. Do rates of litter decomposition tell us anything we really need to know? For. *Ecol. Manage.* 220, 66-74.
- 10
- Raich, J. W., 1998. Aboveground productivity and soil respiration in three Hawaiian rain forests. For. *Ecol. Manage.* 107, 309-318.
- Rao, M. R., Nair, P. K. R., Ong, C. K., 1998. Biophysical interactions in tropical agroforestry systems. *Agrofor. Sys.* 38, 3-50.
- Reddell, P., Milnes, A. R., 1992. Mycorrhizas and other specialised nutrient-acquisition strategies: their occurrence in woodland plants from Kakadu and their role in rehabilitation of waste rock dumps at a local uranium mine. *Aust. J. Bot.* 40, 223-242.
- 15
- Resh, S. C., Binkley, D., Parrotta, J. A., 2002. Greater soil carbon sequestration under nitrogen-fixing trees compared with *Eucalyptus* species. *Ecosystems* 5, 217-231.
- Rothe, A., Binkley, D., 2001. Nutritional interactions in mixed species forests: a synthesis. *Can. J. For. Res.* 31, 1855-1870.
- 20
- Ryan, M. G., Hubbard, R. M., Pongracic, S., Raison, R. J., McMurtrie, R. E., 1996. Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. *Tree Physiol.* 16, 333-343.
- Sackville Hamilton, N. R., 1994. Replacement and additive designs for plant competition studies. *J. Appl. Ecol.* 31, 599-603.
- 25

- Samraj, P., Chinnamani, S., Haldorai, B., 1977. Natural versus man-made forest in Nilgris with special reference to run-off, soil loss and productivity. *Indian Forester* 103, 460-465.
- Sanginga, N., Mulongoy, K., Ayanaba, A., 1989a. Nitrogen fixation of field-inoculated *Leucaena leucocephala* (Lam.) de Wit estimated by the ^{15}N and the difference methods. *Plant Soil* 117, 269-274.
- Sanginga, N., Danso, S. K. A., Bowen, G. D., 1989b. Nodulation and growth-response of *Allocauarina* and *Casuarina* species to phosphorus fertilization. *Plant Soil* 118, 125-132.
- Sanginga, N., Bowen, G. D., Danso, S. K. A., 1991. Intra-specific variation in growth and P accumulation of *Leucaena leucocephala* and *Gliricidia sepium* as influenced by soil phosphate status. *Plant Soil* 133, 201-208.
- Sanginga, N., Vanlauwe, B., Danso, S. K. A., 1995. Management of biological N_2 fixation in alley cropping systems: Estimation and contribution to N balance. *Plant Soil* 174, 119-141.
- Schulze, E. D., Chapin, I. F. S., Gebauer, G., 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. *Oecologia* 100, 406-412.
- Shearer, G., Kohl, D. H., 1986. N_2 -fixation in field settings: estimations based on natural ^{15}N abundance. *Aust. J. Plant Physiol.* 13, 699-756.
- Sheriff, D. W., Nambiar, E. K. S., Fife, D. N., 1986. Relationships between nutrient status, carbon assimilation and water use efficiency in *Pinus radiata* (D. Don) needles. *Tree Physiol.* 2, 73-88.
- Silvester, W. B., 1983. Analysis of nitrogen fixation. In: Gordon, J. C., Wheeler, C. T. (Eds.), *Biological nitrogen fixation in forest ecosystems: Foundations and applications*. Martinus Nijhoff, The Hague. pp. 173-212.
- Smethurst, P., Baillie, C., Cherry, M., Holz, G., 2003. Fertilizer effects on LAI and growth of four *Eucalyptus nitens* plantations. *For. Ecol. Manage.* 176, 531-542.
- Snowdon, P., Wichienopparat, W., Khanna, P. K., 2003. Growth, above-ground biomass and nutrient content of eucalypts and acacias grown in mixture in a tropical environment -

- Evaluation for one full rotation. International Conference on Eucalypt Productivity, Hobart, Australia.
- Sprent, J. I., 1987. The ecology of the nitrogen cycle. Cambridge University Press. Cambridge, UK.
- Sprent, J. I., 1994. Harnessing symbiotic associations: the potentials of nitrogen-fixing trees. In:
 5 Leahey, R. R. B., Newton, A. C. (Eds.), Tropical trees: the potential for domestication and
 the rebuilding of forest resources. HMSO, London, pp. 176-182.
- Stock, W. D., Weinand, K. T., Baker, A. C., 1995. Impacts of invading N₂-fixing *Acacia* species on
 patterns of nutrient cycling in two Cape ecosystems: Evidence from soil incubation studies
 and ¹⁵N natural abundance values. *Oecologia* 101, 375-382.
- 10 Sun, J. S., Simpson, R. J., Sands, R., 1992. Nitrogenase activity of two genotypes of *Acacia*
 mangium as affected by phosphorus nutrition. *Plant Soil* 144, 51-58.
- Swift, M. J., Heal, O. W., Anderson, J. M., 1979. Decomposition in terrestrial ecosystems.
 Blackwell Scientific Publications. Oxford.
- Taylor, B. R., Prescott, C. E., Parsons, J. F., Parkinson, D., 1991. Substrate control of litter
 15 decomposition in four Rocky Mountain coniferous forests. *Can. J. Bot.* 69, 2242-2250.
- Thevathasan, N. V., Gordon, A. M., 2004. Ecology of tree intercropping systems in the North
 temperate region: Experiences from southern Ontario, Canada. *Agrofor. Sys.* 61, 257-268.
- Toky, O. P., Singh, V., 1993. Litter dynamics in short-rotation high-density tree plantations in an
 arid region of India. *Agric., Ecosyst. Environ.* 45, 129-145.
- 20 Trenbath, B. R., 1974. Biomass productivity of mixtures. *Adv. Agron.* 26, 177-210.
- Turvey, N. D., Attiwill, P. M., Cameron, J. N., Smethurst, P. J., 1984. Growth of planted pine trees
 in response to variation in the densities of naturally regenerated acacias. *For. Ecol. Manage.*
 7, 103-117.
- Van Kessel, C., Farrell, R. E., Roskoski, J. P., Keane, K. M., 1994. Recycling of the naturally-
 25 occurring ¹⁵N in an established stand of *Leucaena leucocephala*. *Soil Biol. Biochem.* 26,
 757-762.

- Vanclay, J. K., 2006. Experiment designs to evaluate inter- and intra-specific interactions in mixed plantings of forest trees. *Forest Ecology and Management*, doi:10.1016/j.foreco.2006.05.034.
- Vandermeer, J., 1989. *The Ecology of Intercropping*. Cambridge University Press. New York.
- 5 Vezzani, F. M., Tedesco, M. J., Barros, N. F., 2001. Alteracoes dos nutrientes no solo e nas plantas em consorcio de eucalipto e acacia negra. *Revista brasileira de Ciencia do solo* 25, 225-231.
- Walker, J. C. G., Klein, C., Schidlowski, M., Schopf, J. W., Stevenson, J. D., Walker, R. M., 1983. Environmental evolution of the Archean-Early Proterozoic Earth. In: Schopf, J. W. (Eds.),
10 Earth's earliest biosphere. Princeton University Press, Princeton, pp.
- Warren, C. R., Adams, M. A., 2004. What determines rates of photosynthesis per unit nitrogen in *Eucalyptus* seedlings? *Funct. Plant Biol.* 31, 1169-1178.
- Weiner, J., 1985. Size hierarchies in experimental populations of annual plants. *Ecology* 66, 743-752.
- 15 Weiner, J., 1986. How competition for light and nutrients affects size variability in *Ipomea tricolor* populations. *Ecology* 67, 1425-1427.
- Weiner, J., 1990. Asymmetric competition in plant populations. *Tree* 5, 360-364.
- Wichiennopparat, W., Khanna, P. K., Snowdon, P., 1998. Contribution of acacia to the growth and nutrient status of eucalypts in mixed-species stands at Ratchaburi, Thailand. Recent
20 Developments in Acacia Planting. Proc. Intern. Workshop Hanoi, Vietnam 27-30 Oct. 1997, Australian Centre for International Agricultural Research, Canberra.
- Williams, A. C., McCarthy, B. C., 2001. A new index of interspecific competition for replacement and additive designs. *Ecol. Res.* 16, 29-40.
- Xiao, W., Wang, S., Chen, X., Lu, J., Wu, G., Xiao, L., Chen, Y., Kang, S., Chen, J., Lin, J., Zhou,
25 Q., Zhang, X., 1999. Biomass of eucalypts and *Acacia crassicarpa* mixed forest and its influence to soil. *Forest Science and Technology* 15, 8-15.

- Xiao, W., Wang, S., Chen, X., Xiao, L., Wu, G., Lou, Z., Chen, Y., Kang, S., Lin, J., Su, G.,
Chaohui, Y., Lin, L., Yu, Y., 1999. Economic benefits analysis of eucalypts and *Acacia*
crassicaarpa mixed forest. *Forest Science and Technology* 15, 1-7.
- Yoshida, T., Kamitani, T., 2000. Interspecific competition among three canopy-tree species in a
5 mixed-species even-aged forest of central Japan. *For. Ecol. Manage.* 137, 221-230.
- Zak, D. R., Pregitzer, K. S., 1998. Integration of ecophysiological and biogeochemical approaches
to ecosystem dynamics. In: Pace, M. L., Groffman, P. M. (Eds.), *Successes, limitations and*
frontiers in ecosystem science. Springer, New York, pp. 372-403.
- Zhang, N. 2003. Experiment on Eucalypt U6 Clone Intercropping with *Acacia crassicaarpa*. Masters
10 (in Mandarin) Thesis. Research Institute of Tropical Forestry and Leizhou Forest Bureau.

Table 1. Productivity of mixtures in field and pot trials. For more examples of mixed species stands see (Cannell et al., 1992; FAO, 1992; Forrester, 2004). The table is continued on the following pages.

Study number	System, age, location	Species	Species Proportions (based on stems ha ⁻¹). Numbers are %.	Total above ground biomass (Mg ha ⁻¹)			RY		RYT ^g	Interactions	Stocking (stems ha ⁻¹). All mixed within rows unless otherwise stated.	Source
				E	A	Total	E	A				
1	Plantation, 11 years, East Gippsland, Australia	<i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> *	100E (fertilised)	70		70				Improved nutrition due to accelerated rates of N and P cycling through litterfall (100%Euc: 2.4 Mg litter, 13.7 kg N, 0.5 kg P; 50%Euc:50%Aca: 3.7 Mg litter, 39.2 kg N, 0.8 kg P; 100%Aca: 3.3 Mg litter, 48.8 kg N, 0.8 kg P; all ha ⁻¹ yr ⁻¹ ; (Forrester et al., 2005b) and reduced light competition due to canopy stratification (Bauhus et al., 2004; Forrester et al., 2004).	Fertilised monoculture was 1212 stems ha ⁻¹ and all other treatments were 1010 stems ha ⁻¹ . By 14 months fertilised 100%Euc had received 250 kg ha ⁻¹ N, 160 kg ha ⁻¹ P and 170 kg ha ⁻¹ K. All other treatments received 25 kg ha ⁻¹ P at 3 months.	Khanna, 1997; Bauhus et al., 2000; Bauhus et al., 2004; Forrester et al., 2004
			100E	47		47						
			75E : 25A	46.1	38	84.1	0.98	0.50	1.48			
			50E : 50A	38.9	54.2	93.1	0.83	0.71	1.53			
			25E : 75A	19.8	63.2	83	0.42	0.82	1.25			
100A		76.7	76.7									
2	Plantation, 10 years, India	<i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> *	100E	E**	A**	Total**	E	A		Possible interactions not discussed.	Alternate rows 2500 stems ha ⁻¹ 818 stems ha ⁻¹ 750 stems ha ⁻¹ 692 stems ha ⁻¹ 600 stems ha ⁻¹ 1600 stems ha ⁻¹	Samraj et al., 1977
			50E : 50A	322	180	454	0.85	1.44	2.29			
			50E : 50A	274	228	494	0.83	1.82	2.65			
			50E : 50A	460	90	550	1.43	0.72	2.15			
			50E : 50A	318	108	426	0.99	0.86	1.85			
100A		125	125									
3	Plantation, 5 years, Eden, Australia	<i>Eucalyptus nitens</i> and <i>Acacia mearnsii</i> * A _i = inoculated with superior strains of rhizobia, A = uninoculated.	100E	E	A	Total	E	A		Mixtures were intermediate in productivity between the monocultures. Growth may have been limited more by soil moisture availability than by soil N availability.	Alternate rows. 2500 stems ha ⁻¹ .	Forrester, 2004
			50Euc :50A	38.4		38.4						
			50Euc :50A _i	17.9	40.6	58.5	0.47	0.57	1.04			
			100A	20.6	44.6	65.2	0.54	0.61	1.14			
			100A _i		71.2	71.2						
100A _i		73.7	73.7									
4	Plantation, 2 years, Nowra, Australia	<i>Eucalyptus saligna</i> and <i>Acacia mearnsii</i> *	100E	E	A	Total	E	A		Foliar N concentrations of <i>E. saligna</i> leaves were higher in mixture than monoculture but any increase in nutrient availability was outweighed by competition for other resources (soil moisture or P).	Alternate rows, 2500 stems ha ⁻¹	Forrester, 2004
			50E : 50A	5.9		5.9						
			100A	2.3	14.1	16.4	0.39	0.53	0.92			
100A		26.4	26.4									
5	Plantation, 98 months, Ratchaburi, Thailand	<i>Eucalyptus camaldulensis</i> and <i>Acacia auriculiformis</i> *	100E	E	A	Total	E	A		<i>E. camaldulensis</i> were larger in 50:50 mixture at 28 and 48 months probably due to improved N nutrition from N fixation by <i>A. auriculiformis</i> . Later <i>A. auriculiformis</i> were taller than <i>E. camaldulensis</i> and probably competed for water, P and light, thus reducing the growth of <i>E. camaldulensis</i> in mixture compared to monoculture.	1250 stems ha ⁻¹	Wichiennopparat et al., 1998; Snowdon et al., 2003
			75E : 25A	38.42		38.42						
			50E : 50A	27.85	16.02	43.87	0.72	0.24	0.97			
			25E : 75A	21.76	37.44	59.2	0.57	0.57	1.13			
			100A	5.46	57.43	62.89	0.14	0.87	1.01			
100A		65.96	65.96									

Table continued on next page.

Table 1. Continued.

Study number	System, age, location	Species	Species Proportions (based on stems ha ⁻¹). Numbers are %.	Total above ground biomass (Mg ha ⁻¹)			RY		RYT ^o	Interactions	Stocking (stems ha ⁻¹). All mixed within rows unless otherwise stated.	Source
				E**	A**	Total	E	A				
6	Plantation, 45 months, Rio Grande do Sul, Brazil	<i>Eucalyptus saligna</i> and <i>Acacia mearnsii</i> *	100E 50E : 50A 100A	109 71	39 78	109 110 78	0.65	0.50	1.15	Improved N nutrition of <i>E. saligna</i> .	Alternate rows, 1667 stems ha ⁻¹	Vezzanni et al., 2001
7	Plantation, 20 years, Hawaii, USA	<i>Eucalyptus saligna</i> and <i>Falcataria moluccana</i> * (= <i>Albizia falcataria</i>)	100E (fertilised) 89E : 11F 75E : 25F 66E : 33F 50E : 50F 25E : 75F 100F	235 238 268 275 287 223	F*** 62 47 80 70 192 200	Total*** 235 300 315 355 357 415 200	1.01 1.14 1.17 1.22 0.95	0.31 0.24 0.40 0.35 0.96	1.32 1.38 1.57 1.57 1.91	Improved nutrient use efficiency of <i>E. saligna</i> , greater nutrient cycling under <i>F. moluccana</i> and greater light capture and high light use efficiency in mixed stands. Higher N availability under <i>F. moluccana</i> and reduced light competition due to canopy stratification.	2500 stems ha ⁻¹ . During the first 55 months all treatments received 120 kg ha ⁻¹ N, 108 kg ha ⁻¹ P and 219 kg ha ⁻¹ K. 100%Euc also received an additional 250 kg ha ⁻¹ N in this time.	DeBell et al., 1989; Binkley et al., 1992; DeBell et al., 1997; Binkley et al., 2003b
8	Plantation, 65 months, Hawaii, USA	<i>E. saligna</i> or <i>E. grandis</i> and <i>Falcataria moluccana</i> *	100E (fertilised) 50E : 50F	37.6 58.2	F 37.1	Total 37.6 95.3	E 1.55			Higher foliar N in Eucalyptus in mixture than monoculture especially when with <i>F. moluccana</i> . However, soil N concentration declined in mixtures compared to <i>Eucalyptus</i> monocultures. <i>Eucalyptus</i> grew taller in mixtures and overtopped <i>A. melanoxylon</i> but was overtopped between 2 and 4 years by <i>F. moluccana</i> .	Alternate rows. 2500 stems ha ⁻¹ .	DeBell et al., 1985
		<i>E. saligna</i> or <i>E. grandis</i> and <i>A. melanoxylon</i> *	100E (fertilised) 50E : 50A	37.6 35.3	A 16.2	Total 37.6 51.5	E 0.94					
9	Coppiced plantation, 4 year rotation, Hawaii, USA	<i>Eucalyptus grandis</i> and <i>Leucaena leucocephala</i> x <i>L. diversifolia</i> *, <i>Eucalyptus grandis</i> and <i>Falcataria moluccana</i> *, <i>Eucalyptus grandis</i> and <i>Enterolobium cyclocarpum</i> *	100E 50E : 50%L 50E : 50%F 50E : 50%Ent 100L 100F 100Ent	E 60.3	L/F/Ent 63.4 57.6 59.6	Total 60.3 53.6 60.2 78.5 63.4 57.6 59.6				Yield in mixtures were not significantly different to monocultures. There was intense competition for light for <i>E. saligna</i> with <i>Leucaena leucocephala</i> and <i>Falcataria moluccana</i> .	6667 stems ha ⁻¹	Austin et al., 1997
10	Plantation, 7 years, Espirito Santo, Brazil	<i>Eucalyptus urophylla</i> and two <i>Leucaena leucocephala</i> * varieties (K8 and K72)	100E 50Euc : 50LK8 50Euc : 50LK72 100LK8 100%LK72	E 174	LK8/LK72 146 133	Total 174 163 169 146 133				Both species contributed approximately equally in both mixture treatments in terms of productivity. <i>E. urophylla</i> overtopped <i>L. leucocephala</i> from year one. Survival of <i>E. urophylla</i> declined in mixture due to attack from the <i>Eucalyptus</i> canker <i>Cryphonectria</i> , possibly due to higher humidity in mixtures. Diameters of both species were larger in mixtures. Lack of stand biomass increase in mixture may result from relatively higher site fertility and application of inorganic fertilisers.	Alternate rows. 1342 stems ha ⁻¹ .	Moraes De Jesus and Brouard, 1989

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Table 1. Continued.

Study number	System, age, location	Species	Species Proportions (based on stems ha ⁻¹). Numbers are %.	Total above ground biomass (Mg ha ⁻¹)			RY		RYT _g	Interactions	Stocking (stems ha ⁻¹). All mixed within rows unless otherwise stated.	Source	
				E	C/L		E	C/L					
11	Plantation, 4 years, Puerto Rico	<i>Eucalyptus x robusta</i> , <i>Casuarina equisetifolia</i> *, and <i>Leucaena leucocephala</i> *	100E	E						<i>E x robusta</i> growth was not enhanced in mixture despite high rates of N fixation. Accelerated rates of nutrient cycling through litterfall and higher soil N (although not always significant) in mixtures with N fixers compared to <i>E x robusta</i> monocultures. Both N fixers grew larger in mixture with <i>E x robusta</i> than in monoculture but <i>E x robusta</i> was smaller in mixture.	10 000 stems ha ⁻¹	Parrotta et al., 1996; Parrotta, 1999	
			100C		C/L								
			100L										
			50E : 50C	27.1	105.3	63	0.43	0.66	1.09				
			50E : 50L	31.4	69.5	72	0.50	0.96	1.46				
12	Plantation 7 years, Mtunzini, South Africa	<i>Eucalyptus grandis x E. camaldulensis</i> and <i>Vigna unguiculata</i> * (Vig I = one row of Vig and Vig II = two rows of Vig)	Weeds retained	E [#]						<i>Eucalyptus grandis x E. camaldulensis</i> responded to the reduction in competition from weeds and to the facilitative influence from <i>Vigna unguiculata</i> . However, while the net effect of the <i>Vigna unguiculata</i> increased growth compared to the unweeded treatment, <i>Eucalyptus</i> growth was even better in the absence of both weeds and <i>Vigna</i> .	<i>Eucalyptus grandis x E. camaldulensis</i> planted at 1333 stems ha ⁻¹ in all treatments and <i>Vigna unguiculata</i> planted in one or two rows between <i>Eucalyptus grandis x E. camaldulensis</i> rows.	Little et al., 2002	
			Weeds removed	167									1.28
			Weeds retained + VigI	213									1.03
			Weeds removed + VigI	172									1.22
			Weeds retained + VigII	204									1.09
Weeds removed + VigII	182						1.18						
			197										
13	Plantation 6 years, Leizhou, Guangdong, China	<i>Eucalyptus urophylla</i> and <i>Acacia crassiparpa</i> *	100E	E**	A**	Total**	E	A		<i>E. urophylla</i> generally had larger diameters and heights in mixtures than in monocultures but <i>A. crassiparpa</i> were generally smaller in mixture. Reduced competition for light for <i>E. urophylla</i> due to canopy stratification.	2400 stems ha ⁻¹ . Trees mixed within or in alternate rows: 1 row of <i>Aca</i> and 1 row of <i>Euc</i> . 1 row of <i>Aca</i> and 2 rows of <i>Euc</i> . 1 row of <i>Aca</i> and 3 rows of <i>Euc</i> . 2 rows of <i>Aca</i> and 3 rows of <i>Euc</i> . 1 <i>Aca</i> tree and 1 <i>Euc</i> tree in the same row. 1 <i>Aca</i> tree and 2 <i>Euc</i> trees in the same row. 1 <i>Aca</i> tree and 3 <i>Euc</i> trees in the same row. 2 <i>Aca</i> trees and 3 <i>Euc</i> trees in the same row.	Zhang, 2003	
			50E : 50A	82.8			83						
			66E : 34A	55.9	41.9	98	0.68	0.46	1.14				
			75E : 25A	61.1	21.2	82	0.74	0.23	0.97				
			60E : 40A	71.4	11.7	83	0.86	0.13	0.99				
			50E : 50A	60.1	23.9	84	0.73	0.26	0.99				
			66E : 34A	63.9	31.4	95	0.77	0.35	1.12				
			75E : 25A	72.8	17.6	90	0.88	0.19	1.07				
			60E : 40A	79.0	14.9	94	0.95	0.16	1.12				
			100A	61.1	37.6	99	0.74	0.41	1.15				
			91										
14	Plantation 6 years, Leizhou, Guangdong, China	<i>Eucalyptus urophylla</i> and <i>Acacia crassiparpa</i> *	100E	E	A	Total	E	A		Reduced light competition for <i>E. urophylla</i> , which over topped <i>A. crassiparpa</i> . Forest floor litter layers in mixtures contained more mass and N, P, K, Ca and Mg than <i>E. urophylla</i> monocultures. Soil N, P and K were also higher in mixtures than in monocultures.	<i>E. urophylla</i> monocultures contained 2555 stems ha ⁻¹ . Mixture with 68% <i>Euc</i> contained 2631 <i>Euc</i> stems ha ⁻¹ and 1243 <i>Aca</i> stems ha ⁻¹ (mixed in alternate rows such that every second row contained both <i>Aca</i> and <i>Euc</i> ; other rows contained only <i>Euc</i>), mixture with 57% <i>Euc</i> contained 1293 <i>Euc</i> stems ha ⁻¹ and 980 <i>Aca</i> stems ha ⁻¹ (mixed in alternate rows).	Xiao et al., 1999	
			68E: 32A	61		61							
			57E: 43A	65	18	83	1.06						
			37	26	62	0.60							

Table continued on next page.

Table 1. Continued.

Study number	System, age, location	Species	Species Proportions (based on stems ha ⁻¹). Numbers are %.	Total above ground biomass (Mg ha ⁻¹)			RY		RYT ^o	Interactions	Stocking (stems ha ⁻¹). All mixed within rows unless otherwise stated.	Source
				E**	A**	Total**	E	A				
15	Plantation 10.1 years, Atherton Tablelands, Australia	<i>Eucalyptus pellita</i> and <i>Acacia peregriana</i> *	100E 84E : 16A 41E : 59A 37E : 63A 100A	170 160 88 72	8 17 27 50	168 169 102 88 48	0.94 0.52 0.42	0.15 0.34 0.55	1.10 0.86 0.97	Reduced light competition due to canopy stratification.	Alternate rows. 375 to 480 stems ha ⁻¹ (after cyclone damage reduced stocking from 1000 stems ha ⁻¹ at age 2 and 3 years).	Bristow et al., 2006
16	Pot trial, 18 months	<i>Eucalyptus globulus</i> and <i>Casuarina cunninghamiana</i> *	100E 50E : 50C 100C	E## 128 104 224	C## 150	Total 128 254 224	E 0.81	C 0.67	1.48	Higher N availability for <i>E. globulus</i> .	4 plants per pot	Baker et al., 1994
17	Pot trial, 211 days	<i>Eucalyptus regnans</i> and <i>Acacia melanoxylon</i> *	100E 83E : 17A 67E : 33A 50E : 50A 33E : 67A 17E : 83A 100A	E## 5.2 1.9 0.4 0.8 0.4 0	A## 3 3.7 5.6 4.4 4 5.7	Total 5.2 4.9 4.1 6.4 4.8 4 5.7	E 0.37 0.08 0.15 0.08 0.00	A 0.53 0.65 0.98 0.77 0.70	0.89 0.73 1.14 0.85 0.70	<i>A. melanoxylon</i> was a more aggressive competitor than <i>E. regnans</i> . <i>A. melanoxylon</i> had a lower root: shoot ratio than <i>E. regnans</i> and may be more efficient at taking up water and nutrients.	6 plants per pot	Bi and Turvey, 1994
18	Pot trial, 50 weeks	<i>Eucalyptus globulus</i> and <i>Acacia mearnsii</i> *	Low nitrogen 100E 50E : 50A 100A High nitrogen 100E 50E : 50A 100A Low phosphorus 100E 50E : 50A 100A High phosphorus 100E 50E : 50A 100A	E### 726 498	A### 461 696 277 750 495 972 243 472	Total 726 959 696 1792 1606 750 1182 1182 972 1336 1383 472	E 0.69 0.74 0.58 0.85	A 0.66 0.37 0.51 0.51	1.35 1.11 1.09 1.37	At high N and both high and low levels of P fertiliser <i>E. globulus</i> appeared to dominate and suppress <i>A. mearnsii</i> . The greater competitiveness of <i>E. globulus</i> in these situations may have resulted from its higher N and P use efficiency and greater growth response to N and P fertilisers compared to <i>A. mearnsii</i> .	2 plants per pot	Forrester et al., 2006b

*N-fixing species, **Volume (m³ ha⁻¹), ***stem biomass (Mg ha⁻¹) estimated from graph, # volume (m³ ha⁻¹) estimated from graph, ## plant biomass estimated from graph (g pot⁻¹), ### aboveground biomass (g pot⁻¹). ^oRYT = RY (species A) + RY (species B) in a mixture of two species (A and B).

Table 2. Analysis of Variance indicates that mixtures contribute higher yields.

Source	df	SS	MS	F	P
Regression	78	260.646	3.3416	161.98	<0.0001
Intercepts	26	252.676	9.7183	471.07	<0.0001
Slopes	27	5.646	0.2091	10.14	<0.0001
Single quadratic	1	1.098	1.0984	53.24	<0.0001
Separate quadratics	24	1.225	0.0510	2.47	0.0092
Residual	31	0.640	0.0206		
Lack of fit	20	0.523	0.0261	2.46	0.0633
Pure error	11	0.117	0.0106		

Table 3. Parameter estimates for β_2 (in ascending order) in the equation $\text{Log}_{10}Y = \beta_0 + \beta_1 P_e + \beta_2 P_e^2$.

Study	Estimate	s.e.	Student's t	P
14	-0.0008067	0.0005192	-1.554	0.1304
2	-0.0003479	0.0000498	-6.993	0.0000
18.HiP	-0.0002219	0.0000704	-3.154	0.0036
7	-0.0002205	0.0000565	-3.901	0.0005
1	-0.0001758	0.0000614	-2.862	0.0075
16	-0.0001622	0.0000704	-2.305	0.0280
11.L	-0.0001619	0.0000704	-2.300	0.0283
18.HiN	-0.0001304	0.0000704	-1.853	0.0735
18.LoN	-0.0001198	0.0000704	-1.702	0.0987
4	-0.0001092	0.0000704	-1.553	0.1307
9.Ent	-0.0001078	0.0000704	-1.533	0.1355
6	-0.0000706	0.0000704	-1.003	0.3236
11.C	-0.0000698	0.0000704	-0.992	0.3287
3	-0.0000631	0.0000537	-1.175	0.2490
5	-0.0000468	0.0000614	-0.761	0.4522
10.K72	-0.0000421	0.0000704	-0.598	0.5542
18.LoP	-0.0000391	0.0000704	-0.556	0.5822
13	-0.0000280	0.0000494	-0.565	0.5758
15	-0.0000271	0.0000429	-0.633	0.5316
12.rem	-0.0000178	0.0002152	-0.083	0.9347
10.K8	-0.0000090	0.0000704	-0.127	0.8994
9.F	-0.0000085	0.0000704	-0.121	0.9047
17	0.0000255	0.0000566	0.450	0.6559
12.ret	0.0000408	0.0002152	0.190	0.8508
9.L	0.0000571	0.0000704	0.812	0.4230
8.F	aliased			
8.A	aliased			

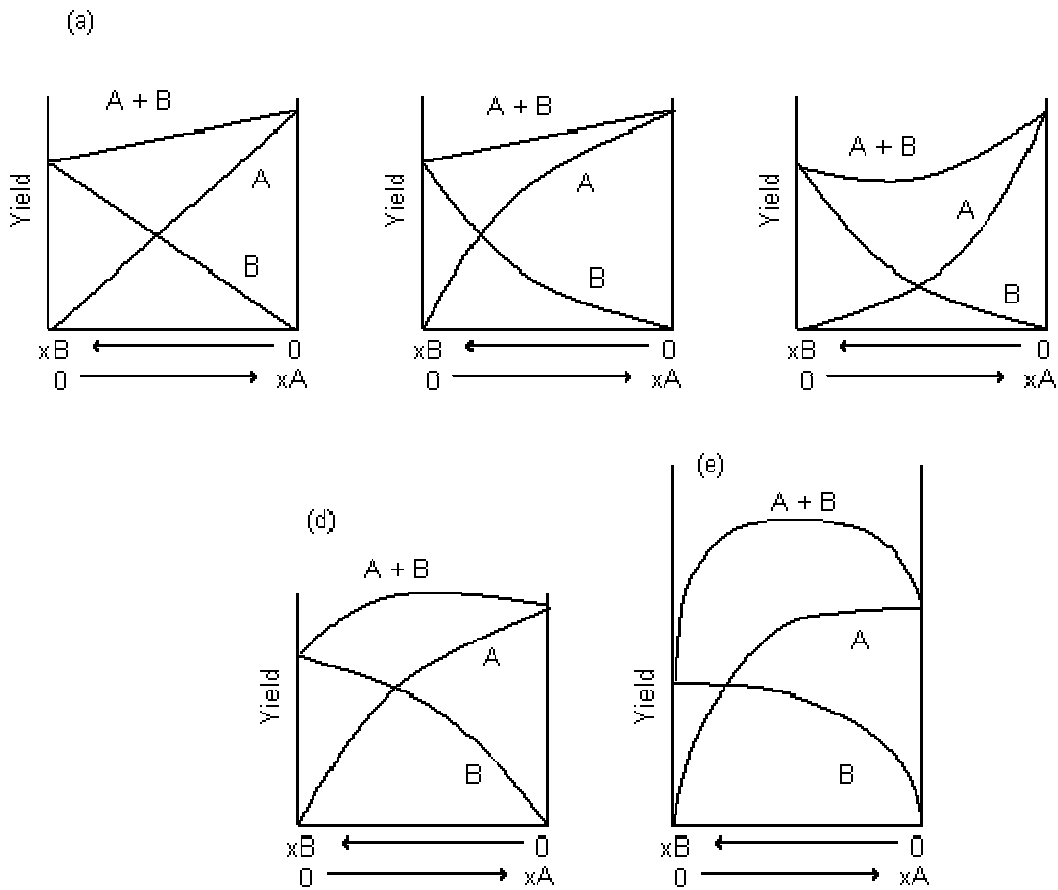


Figure 1. The yield of mixtures containing species A and B, where the proportion of each species in mixture changes from no individuals (0) up to x individuals and the total number of individuals remains constant (adapted from Harper, 1977). Depending on the nature of the interaction between species, there may be substitution (a-b), a reduction in yield (c), or an increase in yields (d-e).

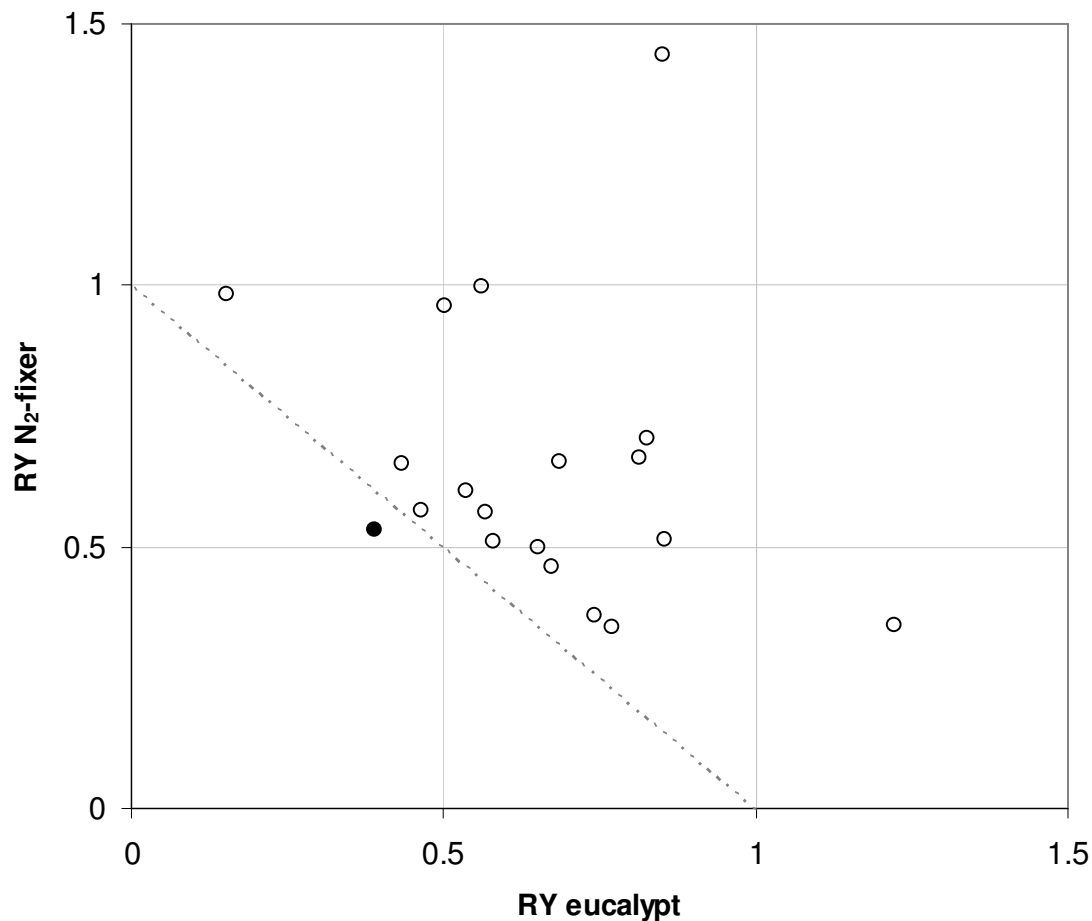


Figure 2. The relative yield of aboveground biomass or volume (RY) of 1:1 mixtures of *Eucalyptus* and N₂-fixing species in 13 different mixed-species stands and 6 pot trial mixed species treatments (all studies in Table 1, except 8-10, 12 & 14). RY above 0.5 indicates a higher productivity in mixture when compared to monocultures. Only one study (4, ●) has a lower yield in the mixed stand (below the dashed line), but the stimulus provided by a mixture is rarely shared equally between the species involved.

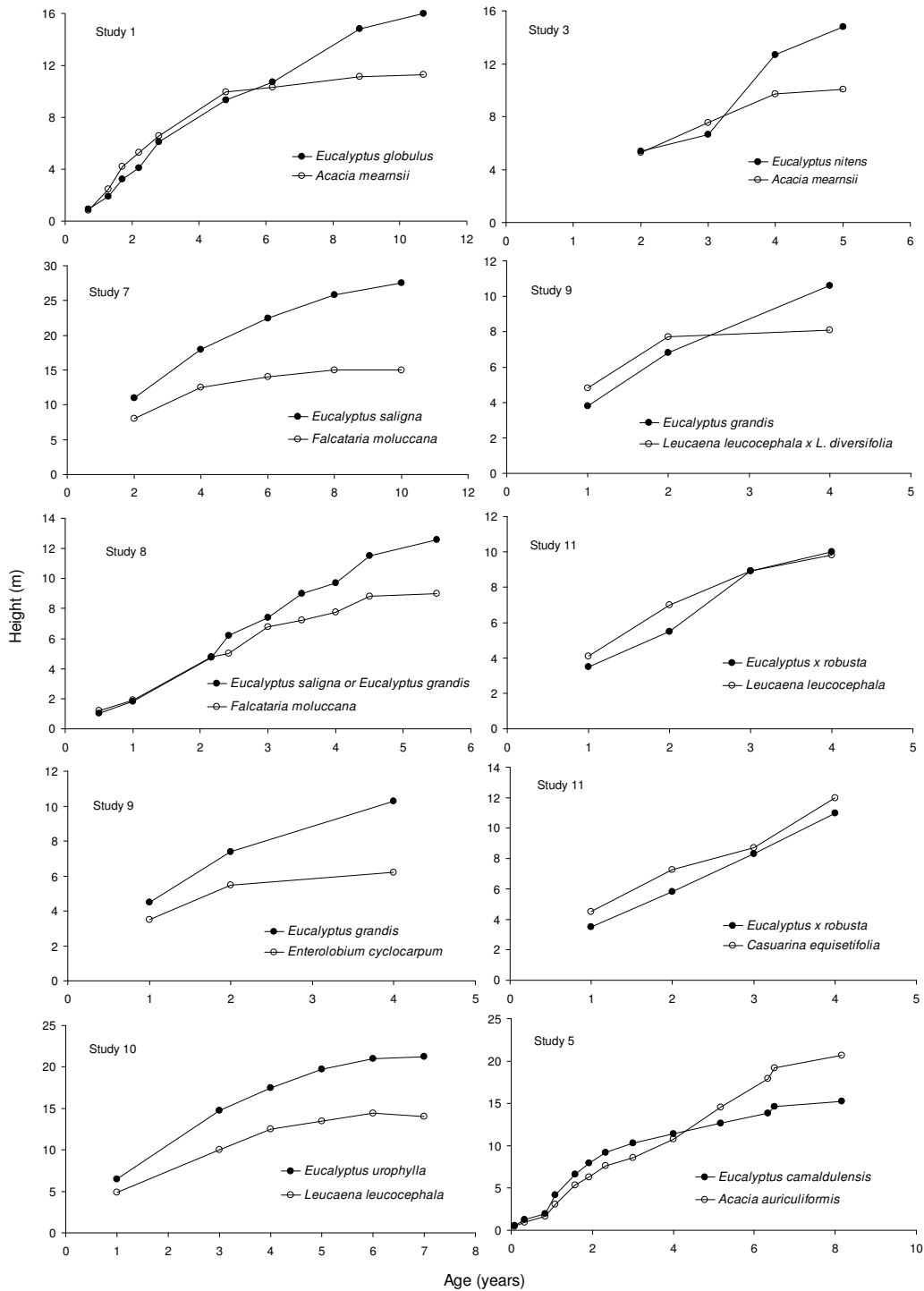


Figure 3. Height-age curves of *Eucalyptus* sp. growing with N_2 -fixing species in 1:1 mixtures. Study numbers refer to the studies in Table 1 where the data were obtained. Improved growth of *Eucalyptus* was observed in trials in the left hand column, while no significant effect (Studies 3, 9 & 11), or a reduction in growth (Studies 5 & 11) was observed in trials in the right hand column.

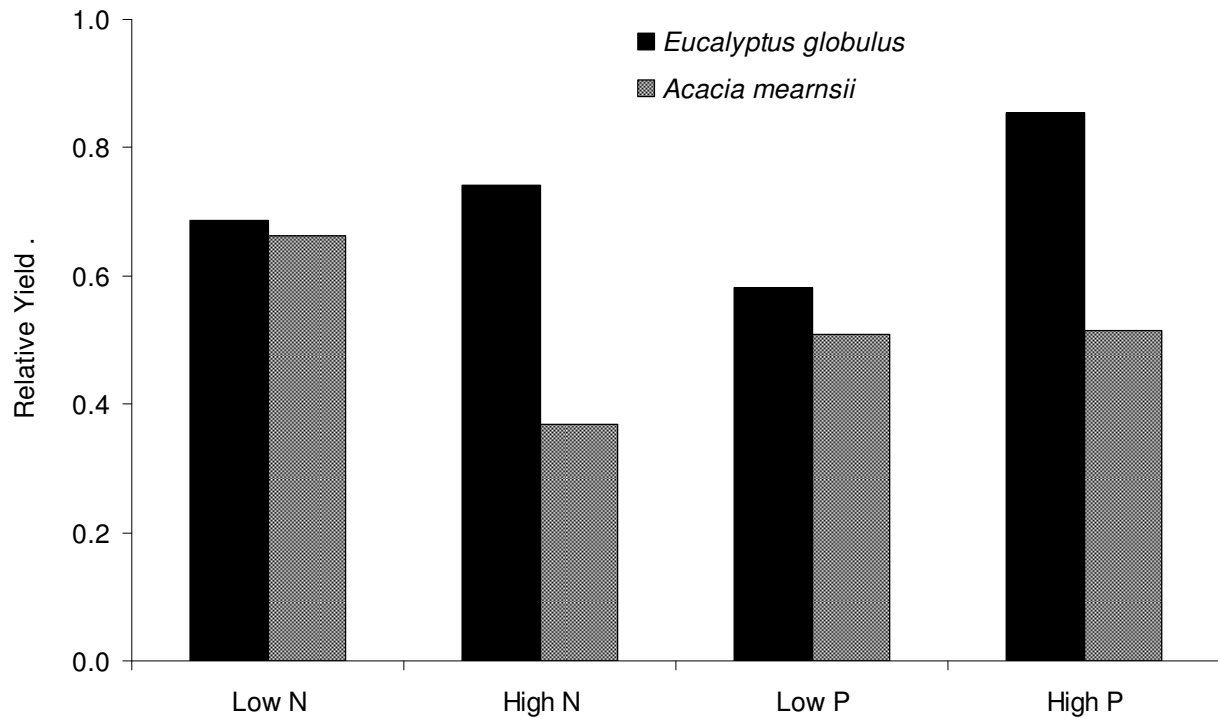


Figure 4. Relative yields of *Eucalyptus globulus* and *Acacia mearnsii* growing in 1:1 mixtures at age 50 weeks in a pot trial (Study 18 in Table 1). RY > 0.5 indicates that plants were larger in mixture than in monoculture. Modified from Forrester et al. (2006).

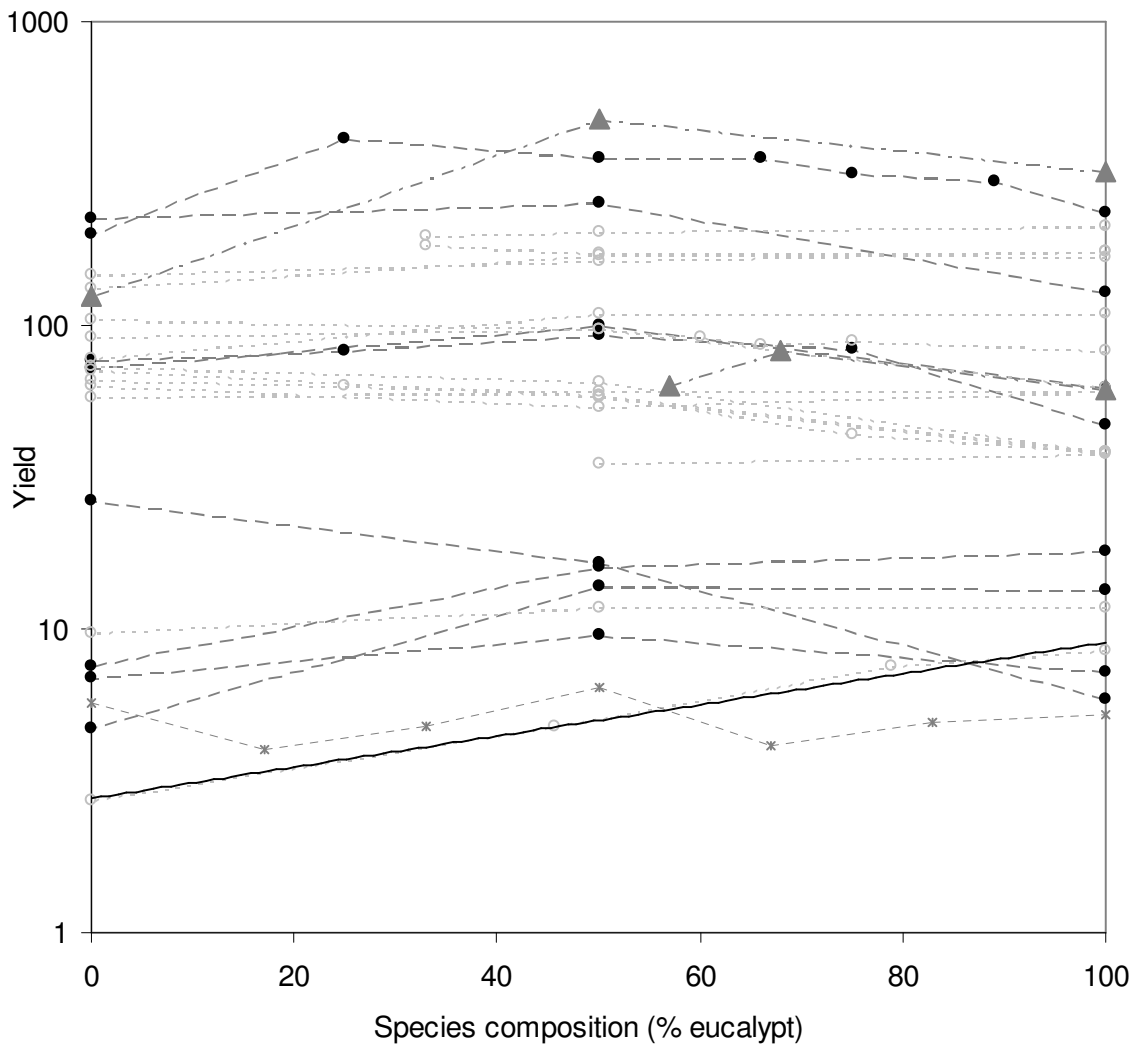


Figure 5. Yield data from studies reported in Table 1. Replications within a study have been averaged for clarity in this figure. Symbols correspond to those in Figure 6 (Group 1 shown as ▲, Group 2 as ●, and Group 3 as ○; Study 17 as *). The solid line is a linear regression, for clarity shown only for Study 15. Yields from study 18 have been scaled (*0.01) for clarity.

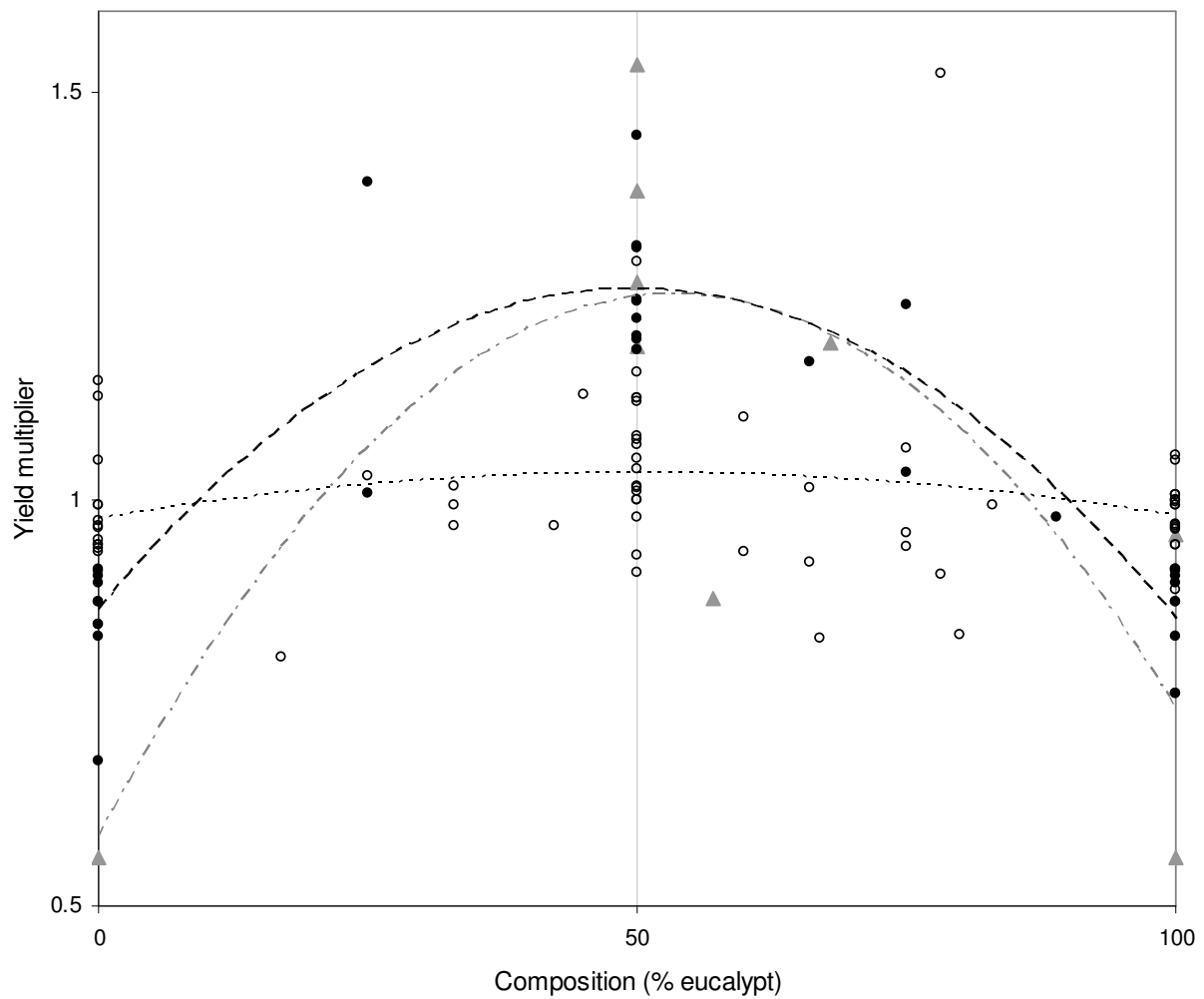


Figure 6. Residuals from the linear regression, expressed as a multiplier (i.e., back-transformed) showing the quadratic trend (Group 1 shown as ▲ and dashed grey line, Group 2 as ● and dashed black line; Group 3 as ○ and dotted line. Each point represents an entry from Table 1; unlike Figure 6, no averages have been used.